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## Structural Parasitism of an Epiphytic Bromeliad upon *Cercidium praecox* in an Intertropical Semiarid Ecosystem<sup>1</sup>

*Key words:* biotic interactions; *Cercidium praecox*; commensalism; epiphytism; semiarid lands; structural parasitism; Tehuacán Valley; *Tillandsia recurvata*.

BIOTIC INTERACTIONS can be classified according to the type of consequences upon the interacting organisms as negative, positive or neutral (Begon *et al.* 1986, Silvertown & Lovett-Doust 1993). In the case of interspecific interactions at the same trophic level, specifically plant-plant interactions, most of the emphasis has been placed on interactions such as competition, among the negative ones (Tilman 1982, Keddy 1989) and the nurse plant syndrome (Niering *et al.* 1963, Steenberg & Lowe 1969), among the positive ones. However, another common type of plant-plant interaction in nature is that of epiphytism. (Here epiphytism is referred to as non-parasitic epiphytism, to distinguish it from that of haustorial hemi- or holo-parasitic plants such as the Loranthaceae.) Epiphytism has typically been regarded as a commensalism (Barbour *et al.* 1987, p. 133), given that the plant that supports the epiphyte (*i.e.* phorophyte *sensu* Benzing, 1990) is assumed not to be negatively affected by the latter, which in turn benefits from the physical support provided by the phorophyte (see Begon *et al.* 1986). Although there is suggestive evidence of some possible negative effects on phorophytes (reviewed by Benzing 1980, 1990), the phorophyte-epiphyte interaction has not been sufficiently researched to reach a conclusive view regarding the sign of such interaction. On the other hand, occupation of plants by lianas has been investigated in relation to their possible effect upon the supporting plant. In his pioneer experimental work, Stevens (1987) found that lianas growing on *Bursera simaruba* female trees reduced fruit production. This, coupled with the fact that lianas require physical contact with trees as a consequence of their growth form, led him to regard them as structural parasites. In this kind of plant-plant interaction the “parasite” has a negative effect on the host without extracting water or nutrients from its vascular system.

In deserts and semideserts epiphytism upon shrubs, treelets, and cacti is relatively common (Mc-

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Ginnies *et al.* 1968, Shreve & Wiggins 1963), but little studied from the ecological point of view (Barbour 1981). In American hot deserts, bromeliads are the most common epiphytes (pers. obs.) and although they are not hemiparasitic, we hypothesized that their presence on shrubs or treelets may adversely affect the growth of colonized branches.

In this paper the effects of a bromeliad on the growth of its phorophyte's supporting branches was assessed using a demographic-modular approach (Harper 1977), specifically by analyzing the dynamics of shoots borne on branches with different epiphyte loads in an intertropical semiarid ecosystem. With this study we attempted to see if the concept of structural parasitism (*sensu* Stevens 1987) can be applicable to this phorophyte-epiphyte interaction.

The study was conducted at Zapotitlán, within the Valley of Tehuacán, in the Mexican state of Puebla, at 1500 m elevation (18°20'N and 97°28'W). Annual rainfall is 400.2 mm (94% falling between May and October) and mean temperature is 21.4°C (García 1973). Soils are rocky, and derived from sedimentary marine rocks of Cretaceous age (Brunet 1967). The vegetation is of a thorn-scrub cactus type as described by Smith (1965) and dominated by deciduous woody species and giant columnar cacti. One of the most important features of the area is its floristic richness and high level of endemism (Rzedowski 1978). Villaseñor *et al.* (1990) report nearly 1400 species of vascular plants (30% endemics) and 630 genera in the region. More recently, Dávila *et al.* (1993) raised those figures to 2703 species and 922 genera but do not mention a value for endemism.

*Cercidium praecox* (Ruiz & Pavon) Harms (Leguminosae) grows at the study site as a winter deciduous small tree up to 4 m high. Typical of the genus, *C. praecox* maintains photosynthetic parenchyma in its branches and trunk (Adams & Strain 1968, 1969; Szarek & Woodhouse 1978). Branches support variable densities of *Tillandsia recurvata* L. (Bromeliaceae), a small plant made up of a rudimentary root system and shoots bearing 5–8 linear leaves (forming a rosette) covered with peltate, absorptive trichomes (Benzing 1980). Older plants develop multiple ramets that may completely surround smaller branches to form a spherical tussock up to 10 cm diameter (hence its common name “ball moss”). Capsular fruits release plumed seeds capable of long-range dispersal. Although Benzing (1980) has reported that this species grows on a variety of phorophytes, at the study site it occurred predominantly on *C. praecox*.

Sampling was done towards the end of the summer (early September) of 1992, when all new shoots (*i.e.*, born during the current growth season) had already been produced and remained clearly recognizable (by color and softness). Eight individuals of *C. praecox* were randomly selected for study. For each tree, two terminal branches arising from the same node (thus, of comparable size and the same age) and having contrasting loads of *T. recurvata* (*i.e.*, high and low levels of epiphytism) were selected. The rationale behind this selection criterion was to sample branches of contrasting epiphyte load but, simultaneously, of similar colonizable surface and the same time of exposure to colonization by *T. recurvata*. This insured that sampled branches were comparable on all relevant accounts except their epiphyte loads (see Benzing 1990). This procedure was replicated twice for each chosen tree. For each branch, the number of shoots produced in the current year (new shoots), the number of older but still alive shoots (old shoots), and the number of leafless and dried-out (dead shoots) were counted. The number of *T. recurvata* tussocks was also recorded for each branch, and an Epiphyte Load Index (ELI), *i.e.*, the quotient of the number of *T. recurvata* tussocks and the branch's total number (*i.e.*, dead plus alive) of shoots was calculated. Thus, this index will equal 1.0 when the number of *T. recurvata* tussocks is the same as the number of shoots.

Data were analyzed with a multinomial logit model (Aitkin *et al.* 1989). For this model the values of ELI, a continuous variable, were treated as a categorical explanatory variable (6 categories) and the proportion of shoots as a categorical response variable with three categories (new, old, and dead shoots). The fitted model thus predicts, for each ELI value, the proportions of new, old, and dead shoots that can be expected in a branch having that ELI value. Data were fitted to the model using the GLIM statistical procedure (Aitkin *et al.* 1989).

The analysis of the multinomial model indicated that there was a highly significant relationship between the ELI and the proportions of new, old, and dead shoots in each branch ( $X^2 = 174.6$ ;  $P < 0.001$ ) and the model explained 85 percent of the total variance. There were very few dead shoots (*ca* 2%) in branches free of epiphytes, while shoots produced during the current growth season amounted to *ca* 20 percent and about 80 percent corresponded to shoots produced in previous years. An increase of the ELI resulted in an increase of dead shoots and a decrease of alive (both new and old) shoots (Fig. 1). In the case of old (but live) shoots, it is notable that, according to the pattern predicted by the model,

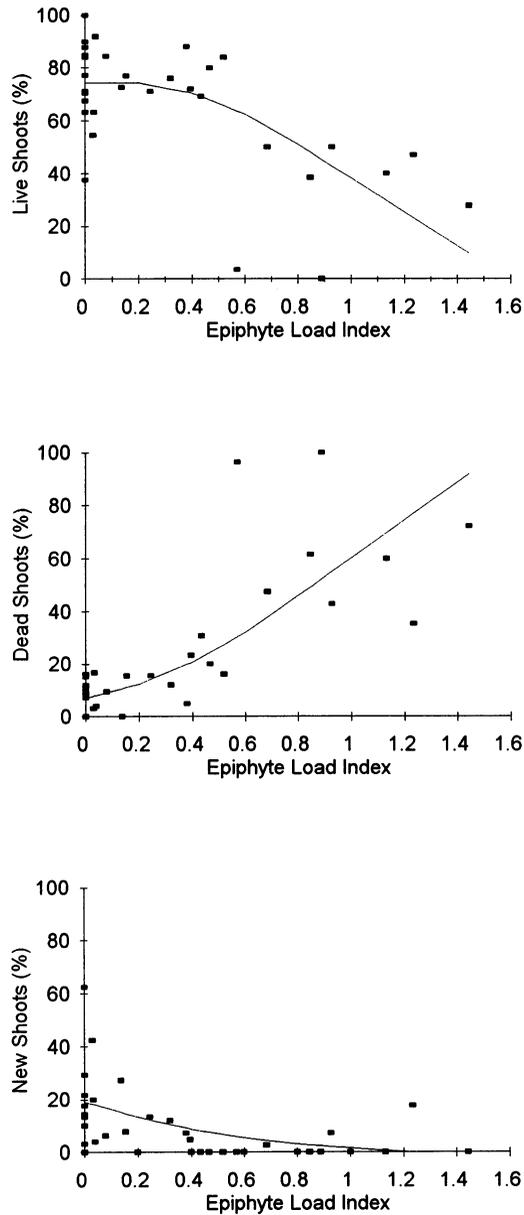


FIGURE 1. Proportions of old but alive (top), dead (middle), and new (bottom) shoots in branches of *Cercidium praecox*, as a function of their Epiphyte Load Index (quotient between the number of *Tillandsia recurvata* tussocks and the branch's total number of shoots) in an intertropical semiarid scrubland of central México. Lines indicate the expected proportions of the three types of shoots after fitting the data to a multinomial model.

their frequencies remain high and constant in values of ELI of up to 0.3. From then on, the frequency of these shoots decreases gradually to a minimum of 15 percent for ELI values in which the tussocks outnumber the shoots by about 50 percent (*i.e.*, ELI = 1.5); an almost opposite pattern was observed in the case of dead shoots and, in fact by an ELI of 1.5 the model predicts a shoot mortality of over 90 percent (Fig. 1). The proportion of shoots produced in the current growth season gradually decreases from about 20 percent in unoccupied branches, to nil when the number of epiphyte tussocks equals the number of shoots per branch (ELI = 1.0). In accordance with the model, no production of new shoots is predicted for all values of ELI > 1.2 (Fig. 1).

Studies directed to assess the possible effects of epiphytic plants, *sensu lato* (*i.e.*, whose growth strategy depends on the support of other plants), upon their hosts, have been few (see reviews in Benzing 1990, Benzing & Seemann 1978) and most biologists have traditionally regarded vascular epiphytes as “commensals except on those occasions when significant shading or mechanical damage occurred to the tree through very heavy infestation” (Benzing 1990, p. 256). Other studies have focused largely on lianas (see Stevens 1987). The interpretation of the latter, in particular, has shown that it is difficult to separate the effect of the lianas from that of the immediate habitat. This is because most of these studies have compared the performance of support plants free of lianas growing on one area, with plants occupied by lianas growing on another. To overcome this limitation, Stevens (1987) experimentally removed the lianas present on *Bursera simaruba* female trees, and compared their reproductive output with that of neighboring unmanipulated female trees. Any attempt to assess the effect of epiphytic plants upon their hosts should take into account the limitations described above. The results of our study system are free of this problem because we compared the dynamics of shoots in branches of contrasting epiphyte load on the same individual trees.

Our results clearly demonstrated a negative effect of *T. recurvata* on the shoot dynamics of *C. praecox* branches. Therefore, the relationships between ELI and shoot dynamics we found can be the effects of *structural parasitism*. This concept is used following Stevens’ (1987) definition of lianas that reduce the reproductive output of phorophytes (as in *B. simaruba* female trees under experimental manipulations) as structural parasites. The proximal cause of this effect in our study system has not been investigated. A mechanical effect cannot be ruled out *a priori*, but probably more important is the inhibition of photosynthesis of this plant’s green branches shaded by the epiphytes. The effects of “nutritional piracy” (*sensu* Benzing & Seemann 1978; *i.e.*, the capture of litter debris and stemflow leachates by the epiphyte) can, under certain circumstances, be responsible for the decline of whole trees (*e.g.*, *Quercus virginiana* infested with *Tillandsia usneoides*; Benzing & Seemann 1978). This mechanism cannot be advocated in comparisons of the dynamics of plant parts, as in our study system.

A commensalism-type biotic interaction can be considered donor-controlled (*sensu* Pimm 1982), in the sense that the species providing the “resource” controls the performance or density of the receiver species. In contrast, the latter does not influence the density of the donor. Although epiphytism in arid and semiarid zones has been considered a form of commensalism (Barbour 1981), our results indicate that the interaction between *T. recurvata* and *C. praecox* may conform better to a parasitism-like relationship (if, due to the detrimental effect of the epiphyte upon the shoot dynamics of the support plant, it can potentially affect the phorophyte’s performance or density).

To the extent that the proximal negative effects on the shoot dynamics documented in this study may scale up to a decrease of the whole phorophyte’s fitness, we could speculate that *C. praecox* may be under selective pressure to reduce/eliminate epiphyte load. In this view, we could consider the epiphytism by *T. recurvata* as a force with potential to generate counter-adaptations (*e.g.*, slippery bark, steep-angled branches) on the part of the phorophyte. Clearly, this is an aspect that warrants further study.

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