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PATTERNS IN THE ORGANIZATION OF THE ARTHROPOD COMMUNITY ASSOCIATED WITH AN AUSTRALIAN RAINFOREST TREE: HOW DISTINCT FROM ELSEWHERE?

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ABSTRACT. Several features of the arthropod community associated with an Australian rainforest tree, *Argyrodendron actinophyllum* Edlin, are summarized. These include: taxonomic composition and its major determinants; species richness and guild structure; arthropod seasonality and, in particular, the influence of leaf production on associated herbivores; spatial distribution of arthropods and of leaf damage; species diversity and body size relationships; synecology and aggregation patterns; and host specificity of associated herbivores. Comparative data from similar arboreal communities are scarce but suggest that some of these features may be similar in other communities, and others dissimilar. Tree species and overall rain forest features may be responsible for these dissimilarities. Due to the extensive structural, phenological and biochemical diversities of rainforest trees, arboreal communities are unlikely to follow a single, well-codified, type of organization. However, it may be possible to recognize several types of arboreal communities by considering the resource base on which the community is founded.

INTRODUCTION

The study of arthropod faunas foraging within rainforest canopies is still in its infancy. However, it represents a growing field of interest in tropical entomology. To date, most of the published information has been obtained using various methods often ground-based, and only a handful of studies have been performed in situ (e.g., Lowman 1985, Nadkarni & Longino 1990). As a result, few studies go beyond the simple description of taxonomic composition, species richness and guild structure of the communities of arboreal arthropods associated with rainforest trees.

In this study, the arthropod fauna foraging within the crowns of an overstory rainforest tree in Australia, *Argyrodendron actinophyllum* Edlin, was studied in situ over a 4-year span. This paper summarizes the information published on this system and emphasizes the salient features of the organization of the arthropod community. As far as possible, these features are contrasted with the information available from other rainforest arthropod-tree systems. However, since comparative data are rather scarce, some more speculative views are also expressed. Referencing has been kept to a minimum, for sake of brevity, and relevant references may be found in the papers cited in the text.

MATERIAL AND METHODS

Argyrodendron actinophyllum Edlin is a tall Sterculiaceae, up to 50 m tall. It is one of the dominant canopy species of the warm subtropical rain forests of Australia. Most of the field work was performed at Mt. Glorious, near Brisbane (details in Basset 1988, 1990). Canopy access was provided by the single rope technique of Perry (1978). Leaf production of *A. actinophyllum* appears to be synchronous among individuals but differs markedly between years for fast-growing individuals and, therefore, does not appear to be highly predictable (Basset 1991a). Foliar nutrients are low and chemical defenses appear to be of the "quantitative" type (Basset 1991b). The arthropod fauna was collected using different sampling methods, which are detailed and discussed in Basset (1988, 1990).

RESULTS AND DISCUSSION

Thanks to the information provided by more than 50 taxonomists, who studied the arthropod material, the major determinants of the taxonomic composition of the arboreal fauna associated with *A. actinophyllum* could be identified (Basset 1991c). These include: biogeographical and historical constraints; rainforest mesoclimate and host phenology; host architecture and biochemistry; and intrinsic composition of the foliage fauna. It is possible that other arthropod-tree systems in rain forests may be determined in a similar way, but the relative contribution of each of these factors is likely to be different.

The abundance of component taxa, species richness and the guild structure of the arthropod community associated with *A. actinophyllum* are detailed in Basset and Arthington (1992). These data suggest that this arboreal community exhibits several features common to arthropod communities from temperate and tropical trees, and point out the distinctness of the system studied.

The temporal organization of the arthropod community is described in Basset (1991a, 1991d). Most of the arthropod activity could be explained primarily in terms of minimal air temperatures and leaf production events; less so by rainfall, relative humidity, or lunar phase. Seasonal ranges were significantly different among arboreal guilds and were related to food resource availability in time. Seasonal peaks of herbivores were more marked than in the tropics but less sharp than in temperate woodlands. Several phenological features of the system could again be classified under both tropical and temperate characteristics. The phenology of leaf production in *Argyrodendron* had also a pronounced effect on the seasonality of most herbivore species. Most herbivore activity occurred during windows of young foliage availability. Host suitability of particular trees during study years depended upon the intensity of leaf production and was different for specialist and generalist herbivores. Many studies reported similar dependence of rainforest herbivores upon young foliage (e.g., Lowman 1985, Aide & Londoño 1989, Ernest 1989). However, the strength of this relationship may ultimately depend on the relative palatibility of young versus mature foliage.

The spatial distribution of arthropods within tree crowns is discussed in Basset (1991b, 1992a, 1992b). Most of the variance in arthropod distribution could be attributed to leaf age characteristics, arthropod aggregation patterns, arthropod activity and distance to tree trunk. In contrast, leaf size and foliage compactness were insignificant in this regard. Arthropod stratification was not well-marked within tree-crowns. Illumination patterns significantly influenced insect flight patterns inside tree crowns. The distribution and the abundance of herbivores, and particularly that of phloem-feeders, depended upon the nitrogen content of young leaves. The magnitude of leaf turnover affected both the quantity and the quality of young foliage available. Using path analysis, it was shown that leaf turnover and translocation effects had a more direct influence upon phloem-feeders than did total nitrogen. Since nitrogen is a limiting factor for most insect herbivores, this situation may be similar for other insect-plant systems where the host is evergreen and relatively low in foliar nutrients.

Leaf damage and the presence of mines and galls on the foliage of *A. actinophyllum* was also recorded and quantified (Basset 1991e). Apparently, leaf damage depended on the presence of isolated, abundant and sunny patches of young foliage. This is unlikely to be a general rule, since apparent damage is often influenced by a few particular herbivore species, which may have very different behaviors and feeding strategies. Mines were significantly more abundant in the lower crown than in the upper crown. This type of observation is also likely to depend on the foraging behavior of the dominant miner species, if any.

When the relationships between the number of species, the abundance of species and their body size were considered (Basset & Kitching 1991), it became apparent that a relatively high proportion of rare and small species was represented in the samples. This concurs with several other rainforest studies (e.g., Erwin & Scott 1980, Morse *et al.* 1988, Barlow & Woiwod 1989). The biological meaning of these findings is not clear, and this may result in part from sampling artifacts.

The cohesion of the arthropod community is appraised in Basset (1992c). Apparently, it was not extremely strong. Although most arthropods aggregated on the foliage, species associations were difficult to predict. Prey-predator ratios (expressed as either number of individuals or species) were relatively constant temporally but highly variable spatially. It was concluded that this might be a consequence of both the unpredictability of leaf production and the overall high arthropod species-diversity in the rainforest environment. These observations, at the least, emphasize that arboreal arthropod communities are not always organized into distinct component communities within the rainforest compound community (Basset 1993). However, at the moment, it is difficult to discuss the general validity of the data reported here.

Limited investigations about the diel activity of arthropods within the crowns of the study tree revealed that some herbivores were mostly active during night-time, possibly as a response to day-active, visually oriented, predators (Basset & Springate 1992). This may represent a widespread situation (Janzen 1983) but further testing of this hypothesis is required.

Lastly, little convincing evidence was found that arthropods were closely associated, or host-specific, to *A. actinophyllum.* (Basset 1992d). This was tentatively explained by the low nutrient status of the host, its relative unpredictability of leaf production and the lack of strong predation pressure on its foliage (particularly by arboreal ants). This situation is likely to be different for other rainforest tree species, depending on their biological features.

Conclusion

It was speculated that some of the features of the *Argyrodendron* community could be similar to other rainforest tree species and some others dissimilar. Due to the extensive structural, phenological and biochemical diversities of rainforest trees, it is clear that arboreal communities are unlikely to follow a single, well-codified, type of organization. However, Price (1992) emphasized that the resource base on which a community is founded can influence many aspects of community organization and food web interactions. He further advised to classify resource types in order to detect patterns in nature. The *Argyrodendron* community seems to be founded on a nutrient-poor resource, which is nevertheless of the pulsing type (see classification of resource types in Price 1992). It would be particularly interesting to detail patterns of community organization (as attempted here for *A. actinophyllum*) for an arboreal community associated with a nutrient-rich tree whose leaf production is relatively constant and predictable (steadily renewed type of resource in Price 1992).

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