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Position, position, position: Mites occupying leaf domatia are not uniformly distributed in the tree canopy

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ABSTRACT

Leaf domatia are plant-produced cavities usually found in the axils of major veins on the abaxial side of leaves. These structures are found in many woody dicotyledonous plants and mediate a mutualistic relationships between predacious and fungivorous mites and the host plants they protect. Mites inhabit leaf domatia for shelter and to reproduce and develop. In turn, the plants are hypothesized to benefit from increased defense against pathogens and small arthropod herbivores. Here, we assess the distribution of mites throughout the tree canopy to determine if certain regions of the canopy are preferred. Our results suggests that mites prefer leaves found in the lower regions of the tree canopy and avoid leaves at the top, where they may be exposed to harsher climatic conditions. This study is one of the first to document aspects of the plant–mite mutualism from African species.

1. Introduction

Forest canopies support a diverse range of arthropod assemblages and these are usually distinct from those of the forest floor (Nadkarni, 1994; Arroyo et al., 2010; Erwin, 2013). These organisms are an important component of forests, as they carry out a range of vital ecosystem services including decomposition and nutrient cycling in above ground deposits of litter and soils (Walter and Behan-Pelletier, 1999; Dial et al., 2006). Inventories of arthropods have shown that forest canopies contain a high abundance and diversity of arthropods and that these animals may respond to environmental gradients within the forest from the top of canopy to forest floor (Dial et al., 2006).

Forests canopies alter environmental and climatic variables such as solar radiation, air and soil temperature, rainfall, air humidity and wind, and thus create a micro-climate inside forests (Parker, 1995). The greatest changes to the micro-climate (patterns of temperature, moisture, wind and light) are brought about by adult stands with closed canopies and high leaf area indices (Aussenac, 2000). Forest trees may also modify their canopy micro-climate along a vertical gradient, and air temperature generally declines with canopy depth due to within-crown shading (e.g. Harley et al., 1996; Zweifel et al., 2002). Canopy structure therefore has a direct effect on the climate surrounding individual leaves and on the large-scale environment of forest regions. These changes in micro-climate play an important role in determining the diversity of micro-organisms, insects, birds and vascular epiphytes found in forest canopies (Nadkarni, 1994).

Within the tree crown, arthropods are associated with or graze on leaves. The phylloplane of leaves may provide a wide range of animals with suitable micro-habitat, and the surfaces of leaves are an important environment due to their diversity of anatomical, morphological and physiological properties (Pereira et al., 2002). These structures may support a rich arthropod fauna which is usually dominated by mites. Within forest canopies, mites exceed all other arthropods in species abundance (Walter and Behan-Pelletier, 1999; Beaulieu et al., 2010), and mite assemblages comprise multiple families of predators, scavengers, grazers and plant parasites. Most of the mites encountered on leaves graze on phylloplane fungi or are predatory on other mites (Pemberton and Turner, 1989; O'Dowd and Willson, 1991; Walter and O'Dowd, 1992; O'Dowd and Pemberton, 1998; Matos et al., 2006). However, harmful phytophagous mites may also be found (Pemberton and Turner, 1989; Walter and O'Dowd, 1995; Agrawal, 1997; Norton et al., 2000).

Some plant species possess leaves which bear structures known as leaf domatia (Fig. 1). These often house large numbers of predatory mites, perhaps because this micro-habitat provides higher relative humidity than surrounding air (Pemberton and Turner, 1989; O'Dowd and Willson, 1991; Walter and O'Dowd, 1992; O'Dowd and

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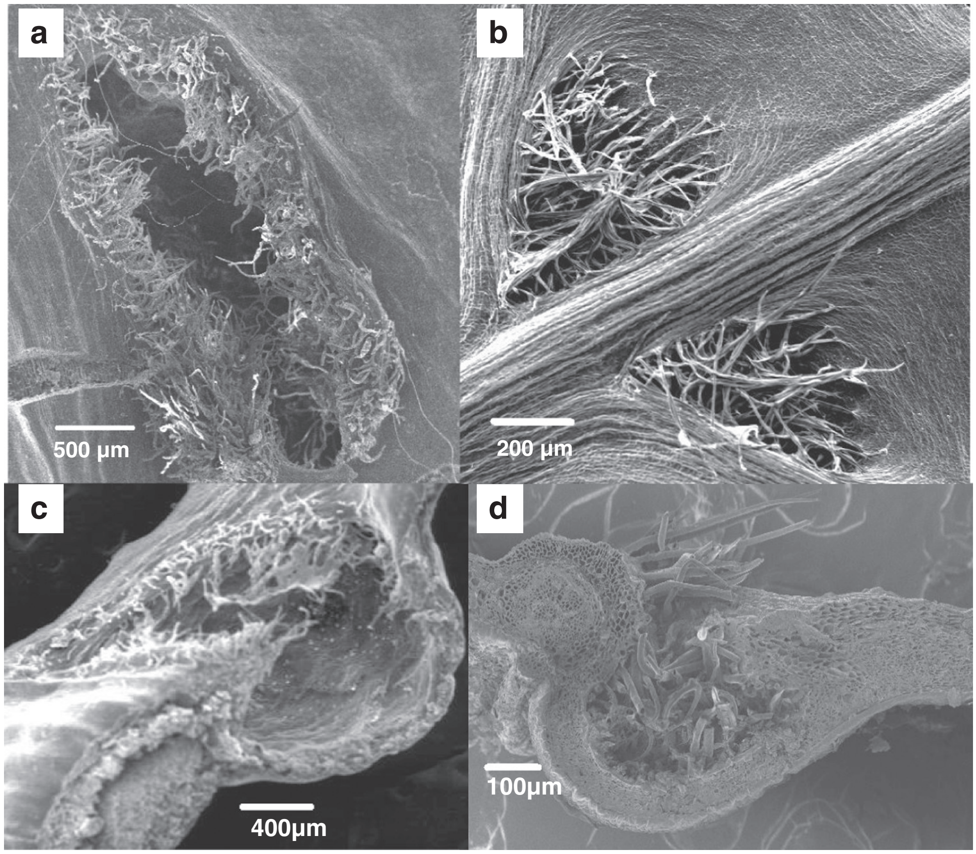

Fig. 1. Scanning electron micrographs of leaf domatia of the study species: (a) external view of domatium of *Ocotea bullata*; (b) external view of domatium of *Gardenia thunbergia*; (c) SEM of transverse section through the domatium of *O. bullata*; (d) SEM of transverse section through the domatium of *G. thunbergia*.

Pemberton, 1998; Walter and Behan-Pelletier, 1999; Matos et al., 2006). These structures influence the distribution and diversity of mites found on leaves.

Studies assessing the abundance of mites within forests have focused mainly on comparing the mite biota of the tree canopy and the forest floor (Lindo and Winchester, 2006; Arroyo et al., 2010; Beaulieu et al., 2010). A few studies (Wilson et al., 1983; Pickett et al., 1988; Onzo et al., 2003; Magalhães et al., 2012) that look at mite distribution within the tree canopy only focus on vertical movement of mites in response to predator–prey relationship. This study thus has the following aims:

1) To assess whether mite diversity and abundance is uniformly distributed throughout the canopy, irrespective of tree species.
2) To measure changes in temperature and humidity at different positions in the canopy and to determine if these might influence mite diversity and abundance.

2. Methods

Two species found in forests in southern Africa were selected. *Ocotea bullata* (Lauraceae) and *Gardenia thunbergia* (Rubiaceae) both have pit-type domatia, surrounded by trichomes (Fig. 1). *O. bullata* (commonly known as stinkwood) is restricted almost entirely to South Africa, where it occurs from Table Mountain (Cape Town) to the northern regions of the country (Boon, 2010). Field sampling of *O. bullata* was conducted in the Tsitsikama forests (33°57′24.7″S, 23°54′33.0″E) near Storms River in the Eastern Cape, South Africa, on the 9th of September 2013 where a stand of these trees were felled as part of another research program on this species. Because of this species rarity, it was sampled only once.

G. thunbergia is an evergreen shrub or small tree that grows up to 6 m in height, being found in both Afromontane and coastal forests of the Eastern Cape and KwaZulu-Natal regions of South Africa (Boon, 2010). The trees sampled here are located in the Grahamstown Botanical Gardens (33°19′09.4″S, 26°31′18.1″E), in the Eastern Cape. This population was sampled on two different occasions.

Five individual trees for each species were selected for sampling. Before sampling, the north-facing side of each tree was marked and then 10 leaves each were sampled from the north, south, east and west outside points, as well as the bottom, inside and top of the canopy. *O. bullata* trees were between 15 and 19.10 m in height and the *G. thunbergia* trees were over 3.5 and 5 m. In the case of *O. bullata*, the leaves were sampled immediately after the tree was felled, and a ladder was used to access the leaves of *G. thunbergia*. Only mature but not senescent leaves were sampled. All 10 leaves from each sampling position were placed in a labeled ziplock bag and kept cool. As soon after collection as possible, all the domatia present in each leaf were viewed under a dissecting microscope and the mites found on and inside the leaf domatia were counted. The number of mites found in each leaf was recorded from each sampling position and the mean number of mites per leaf at each canopy location was calculated. A non-parametric Kruskal–Wallis ANOVA was performed on STATISTICA version 2010 to compare mite abundance between all the canopy locations for each species.

Sampling of leaves of *G. thunbergia* occurred on two different occasions. On the first occasion, five individual trees were sampled in the