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Mediation of herbivore attack and induced resistance by plant vigor and ontogeny

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ABSTRACT

A large number of insect galls induced by *Contarinia* sp. (Cecidomyiidae) on cashew plants, *Anacardium occidentale* L. (Anacardiaceae), and induced resistance (hypersensitivity) against galling were observed in five restored different-aged stands in the Amazonian tropical rain forest. We tested three hypotheses: (1) the effect of age-dependent changes on the attack by *Contarinia* sp. and on induced resistance of *A. occidentale* to herbivory (plant ontogeny – herbivory hypothesis); (2) the effect of leaf size on the oviposition preference by the gall-midge (plant vigor hypothesis), and (3) whether past attack could influence future attack and induced resistance (attack prediction hypothesis). Tree age positively influenced attack levels and gall density. The leaves of older trees experienced four-fold greater attack and supported two-fold more galls. Hypersensitive response was also positively affected by tree age. This induced resistance was six-fold higher on older trees. Therefore, we suggest that induced resistance in *A. occidentale* was age-dependent, hence supporting the plant ontogeny – herbivory hypothesis. Higher preference of *Contarinia* sp. on larger sized leaves of *A. occidentale* was only observed in old stands, hence providing support for the plant vigor hypothesis. The same trend was observed in hypersensitive response. Only two older plots (5–7-year-old) were better predictors of current attack and resistance of *A. occidentale*, hence supporting the attack prediction hypothesis. Our results suggest that plant development is an important factor that contributes to the structuring of interactions between host plant and insect herbivores. However, more information about ontogenetic changes and regeneration processes is needed to understand plant–herbivore interactions in the Amazonian forest.

1. Introduction

Interactions among plants and herbivorous insects constitute an important component of most terrestrial and aquatic ecosystems (e.g. Dorn et al., 2001; Cebrian and Lartigue, 2004). These interactions occur at low trophic levels and consequently result in a cascade of effects that often influence entire food webs (Polis et al., 2000). Species interactions have a crucial role in the recycling of matter, energy and nutrient flows in an ecosystem (Price, 1997, 2002). Insect herbivory has shown to be influenced by disturbance (e.g., Ayres and Lombardero, 2000), but may have a positive or negative influence on plant succession (e.g., Turner et al., 1998; Schädler et al., 2004), plant distribution and species diversity (e.g., Olff and Ritchie, 1998).

Herbivory in natural communities, as well as in man-made ecosystems such as in agriculture and forestry, can be high, reducing growth and reproduction of individual plants (Price, 1997). Nevertheless, to diminish the impact of herbivores, plants present a wide spectrum of defensive mechanisms (Fernandes, 1994; Karban and Baldwin, 1997). Among them, induced responses by the host may reduce the performance and/or preference of herbivores. Previous studies have demonstrated that initial herbivore attack decreases the nutritional quality of the attacked plant tissue and/or increases levels of chemical and physical defenses in a wide variety of plants (reviewed by Karban and Baldwin, 1997). Among the many hypotheses raised to explain the patterns of attack by herbivorous insects the plant vigor hypothesis (PVH; Price, 1991) has gained strong support (see Cornelissen et al., 2008). This hypothesis predicts that insect herbivores will choose preferentially large, more vigorously growing plants or plant modules and that offspring performance will be greater on these more vigorous plants or plant modules (see also Thompson, 1988; Thompson and Pellmyr, 1991).

Hypersensitivity is an induced defense mechanism whereby plants locate and kill the gall-inducing larva (Fernandes, 1990; Fernandes et al., 2000; Harris et al., 2003). The occurrence of galls

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and plant-induced defense to galling offered a unique opportunity to study the interactions in a system involving the host plant, its cecidomyiid galling herbivore and plants of different ages. Plants can be exposed to different levels of herbivory as they develop from seeds to mature stages. Hence, a plant's defenses can change during development (see Boege and Marquis, 2005; Korndörfer and Del-Claro, 2006). In several systems, induced resistance has been found to be strongly affected by plant ontogeny. According to Karban and Baldwin (1997) plant ontogeny should produce age-dependent patterns in induced resistance to herbivores. Moreover, the ontogenic stage, can also positively or negatively, affect the damage, abundance and preference of herbivores, as well as plant defenses (see Boege and Marquis, 2005), and contribute to the structuring of insect communities (e.g., Waltz and Whitham, 1997).

In this study, we tested the plant vigor hypothesis (Price, 1991) which predicts that galling insects prefer and achieve higher performance on larger plant modules compared to smaller plant modules. If leaves or plants are preferentially attacked, they should present more resources that would enhance offspring survivorship. Also, we expected that plants should be more responsive to attack on the preferentially attacked host organs or plants as a direct attempt to diminish herbivore performance. Consequently, a higher frequency of hypersensitive reactions against the galling herbivore should also be found on the most vigorous or attacked hosts and host organs. We also tested the plant ontogeny – herbivory hypothesis (Boege and Marquis, 2005) which predicts that plant ontogeny in the restored forest causes age-dependent changes in herbivore attack and induced resistance to herbivory. In addition, we test the attack prediction hypothesis that predicts that past attack and resistance to the galling herbivore influence future attack and induced resistance. Little is known of the effects of herbivore attack and plant defense on future attacks on plants (see Karban and Adler, 1996; Prado and Vieira, 1999; Cornelissen et al., 2002).

During an investigation of insect galls on a restored Amazonian rain forest we observed the occurrence of a large number of insect galls induced by a still unidentified species of *Contarinia* sp. (=*Stenodiplosis* sp.) (Diptera: Cecidomyiidae) on the cashew plant, *Anacardium occidentale* L. (Anacardiaceae), in several restored forest stands of different ages. Casual field observations also indicated that *A. occidentale* plants responded to attack by eliciting a hypersensitive reaction to the galling larva. Then, we specifically addressed the following questions: 1) What is the effect of leaf size of *A. occidentale* in the oviposition preference and *Contarinia* larval survival?; 2) Does the frequency of attacked plants of *A. occidentale*, abundance of successfully induced galls, and the plant hypersensitive response to *Contarinia* increase with stand age?; and, 3) Does past attack and *A. occidentale* resistance to *Contarinia* influence future attack and induced resistance?

2. Materials and methods

2.1. Organisms studied

The cashew, *A. occidentale* L. (Anacardiaceae) is an evergreen tree that reaches 5–20 m height, with glabrous leaves, reddish when young, 8–14 cm long and 6–8 cm wide (see Lorenzi, 2000). The commercial cashew nut, native to fields and dunes of the north coast of Brazil, is grown as a plantation crop and has become naturalized in many tropical countries throughout the world. Bleicher and Melo (1996) related the occurrence of 99 insect species and 7 mite species associated with the culture of the cashew in different cultivated areas in Brazil (see also Bleicher et al., 1993a,b, 2002, Bleicher and Melo, 1996; Mesquita et al., 2003 unpublished report). Rickson and Rickson (1998) reported on ant species attracted to a large number of extrafloral nectaries present on the plant. One of the most important herbivore on *A. occidentale* is the galling cecidomyiid (Diptera) *Contarinia* sp. (=*Stenodiplosis* sp.) that has an average degree of infestation of 25% (Mesquita et al., 2002 unpublished report). Otherwise, we were unable to find any published information on the interaction of this important herbivore and the host plant.

2.2. Study location

The study was done in a bauxite mine operated by Mineração Rio do Norte SA in the Saracá-Taquera National Forest on an upland mesa at an elevation of 180 m, 65 km northwest of the town of Oriximiná and 30 km south of the Trombetas River in western Pará State, Brazil (1°40′S, 56°27′W). The regional vegetation is evergreen equatorial moist forest, within which the forests occupying the upland mesas and surrounding slopes have average canopy heights of 20–35 m, with emergent trees up to 45 m tall (Parrotta et al., 1997). Since 1979 the mining company has implemented a pioneer reforestation program, restoring forest cover destroyed at a rate of approximately 100 ha year^{-1} during bauxite ore extraction. At the mine site the reforestation method employed the inclusion of a wide variety of forest species, 80–100 species of native forest species, one of which was *A. occidentale* (for details see Parrotta et al., 1997; Parrotta and Knowles, 1999, 2001).

Gall sampling was carried out in November 2003 in five restored stands, with plantations started in the years 1997, 1998, 1999, 2000 and 2001. Trees on each stand were seven, six, five, four, and three years old respectively at sampling periods. Prior to planting, plant species were grown from seeds collected in the field. Seeds were germinated under ambient temperature, light, and humidity in open-air green houses and then they were transplanted in the field. Plants did not receive any further fertilization or irrigation. On all stand plots, *A. occidentale* individuals grew under similar environmental conditions (light, water, and nutrients).

2.3. Sampling

To address how plants responded to gall induction and how the insect herbivore responded to module vigor and the influence of past generation on new generation of galls, 15 individuals of approximately 4–5 m high were randomly marked in each age stand, except for the 2001 stand, where we sampled only 14 individuals. From each tree, 25 young and 25 old leaves were randomly collected from the canopy up to 2.5 m high. Old leaves represented herbivore attack of the previous generation while young leaves represented the herbivore attack of the current generation. The two leaf age types were readily separated in the field due to their clearly different color pattern and toughness. Sampled leaves were taken to the laboratory in marked plastic bags for measurements of length, number of galls successfully developed and those killed by hypersensitive response (HR). The total attack by *Contarinia* was the result of the sum of the number of galls developed (successful attack) plus HR (unsuccessful attack). Galls killed by the plant's hypersensitive response were inferred by the occurrence of a round necrotic spot around the attempted site of penetration by the galling larva (*sensu* Fernandes, 1990; Fernandes and Negreiros, 2001). Mortality factors caused by parasitism, predation, or pathogens were not addressed in this study.

2.4. Statistical analyses

To determine how leaf traits, *Contarinia* attack, and induced resistance change with age of *A. occidentale* (=stand age) we used Pearson's correlations. At the stand level, we tested PVH using the tree's age through the Kruskal–Wallis test because data were neither