



Original article

Resource allocation in an annual herb: Effects of light, mycorrhizal fungi, and defoliation



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ARTICLE INFO

Article history:

Received 13 February 2015

Received in revised form

25 December 2015

Accepted 26 December 2015

Available online 7 January 2016

Keywords:

Experimental defoliation

Herbivory

Solanaceae

Tolerance to herbivory

Trophic interactions

ABSTRACT

Concurrent interactions and the availability of resources (e.g., light) affect the cost/benefit balance during mutualistic and antagonistic interactions, as well as plant resource allocation patterns. Mycorrhizal interactions and herbivory concur in most plants, where mycorrhizae can enhance the uptake of soil nutrients by plants as well as consuming a large fraction of the plant's carbon, and defoliation usually reduces light interception and photosynthesis, thereby causing direct losses to the hosts of mycorrhizal fungi. Both types of interactions affect the carbon budget of their host plants and thus we predict that the relative costs of herbivory and mycorrhizal colonization will increase when photosynthesis is reduced, for instance in light limited environments. We conducted a greenhouse experiment using *Datura stramonium* to investigate the effects of defoliation and mycorrhizal inoculation on the resource allocation patterns in two different light environments. Defoliated plants overcompensated in terms of leaf mass in both light environments, but total seed mass per fruit was negatively affected by defoliation in both light environments. Mycorrhizal inoculation had a positive effect on vegetative growth and the leaf nitrogen content, but defoliation negates the benefit of mycorrhizal interactions in terms of the leaf nitrogen content. In general, *D. stramonium* compensated for the relative costs of concurrent mycorrhizal interactions and defoliation; plants that lacked both interactions exhibited the same performance as plants with both types of interactions.

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1. Introduction

The conceptual formalization of plant multitrophic interactions (Bennett et al., 2006) highlights the fact that plants grow and reproduce while interacting with mutualistic (e.g., pollinators and symbionts) and antagonistic (e.g., pathogens and herbivores) agents. Mutualistic and antagonistic interactions have direct effects on plants, and these interactions may have positive or negative feedback effects on each other, thereby affecting their hosts indirectly. These interactions affect the carbon balance of the plant by consuming tissues or photosynthates (cf. Herrera et al., 2002), which may increase the cost/benefit ratios for concurrent interactions in the host plants. Furthermore, the cost/benefit ratio for trophic interactions in plants is often affected by the availability of resources, such as light and soil nutrients (Silvertown et al., 1997; Bazzaz et al., 2000; Lambers et al., 2008), thereby influencing plant fitness, defense against antagonists, and the capacity to

support mutualists (Bennett et al., 2006).

Much evidence supports the role of herbivory as a selective pressure that has shaped antiherbivore defenses throughout the evolutionary history of plants (Agrawal, 2008). Although defensive mechanisms are costly for plants (due to the production and storage of defensive compounds for resisting herbivory, as well as the regrowth of lost tissues to tolerate herbivory), it is generally agreed that these mechanisms minimize fitness losses due to antagonists (Strauss et al., 2002). The carbon-nutrient balance hypothesis predicts that when plant growth is limited by carbon (shaded conditions) there would be a surplus of nutrients such as nitrogen which would be allocated mostly to nitrogen-base defenses. On the contrary, when growth is limited by soil nutrients (e.g., nitrogen) the surplus of carbon is allocated to carbon-base defenses (Bryant et al., 1983).

Overall mycorrhizal interactions are well known to improve the soil nutrients uptake of their host, and because of that often improve photosynthesis. Mycorrhizal interactions often have positive effects on plant growth and fitness (Philip et al., 2001; Koide and Dickie, 2002; Poulton et al., 2002; Nuortila et al., 2004) by

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improving plant tolerance to biotic and abiotic stresses (Smith, 1988; Harrison, 1999; Augé, 2001). Therefore, mycorrhizal interactions have the potential to shift resource allocations to defenses in low fertility environments, from carbon-base to nitrogen-base defenses providing light (photosynthesis) does not become a limiting factor. Also, because plant growth is improved mycorrhizal interaction can change antiherbivore defense strategies from resistance to tolerance. On the other hand, defoliation reduces photosynthesis and in consequence carbon availability to support mutualists such as mycorrhizal interactions. Like antiherbivore defenses, mycorrhizal interactions demand a significant share of energy. Mycorrhizal fungi can consume up to 3–30% of the carbon assimilated by plants (Fogel and Hunt, 1983; Finlay and Söderström, 1992; Smith and Read, 2008; Olsson et al., 2010), therefore understanding resource availability is critical in order to understand the dynamics of concurrent defoliation and mycorrhizal colonization.

Previous studies of the feedback dynamics between mycorrhizal fungi and aboveground herbivory are inconclusive. Based on a meta-analysis (99 experiments derived from 33 studies), Barto and Rillig (2010) reported an overall reduction in mycorrhizal colonization of 3% following defoliation (natural or simulated), although the response varied widely from 12% reduction (annual crops) to 4% increase (manual removal of shoots from grasses). In addition, the effects of mycorrhizal colonization on plant antiherbivore defenses ranged from no effects to gains in defenses.

The lack of consistency in the outcomes of plant-defoliation-mycorrhizal tritrophic interaction may be linked to the fact that the availability of resources has been rarely considered in the studies. There is solid evidence showing that the relative costs of antiherbivore defense, herbivory and mycorrhizal interactions for the plants vary with the availability of resources such as light and soil nutrients (see Bennett et al., 2006). For instance, in light-limited environments, the relative costs of defoliation and mycorrhizal interactions are higher compared with those in light-rich environments (Smith and Read, 2008; Olsson et al., 2010) simply because plants are carbon limited. Because both interactions have direct effects on the carbon content of a plant, the concurrency of mycorrhizal interactions and herbivory have the potential to generate positive and negative feedbacks between mycorrhizal fungi and herbivores mediated by the carbon balance in their host plants which in turn is modified by the availability of resources (Gehring and Whitham, 2002; Bennett et al., 2006).

In this study, we evaluated the effects of the availability of light, defoliation, and mycorrhizal inoculation on plant performance using the annual herb *Datura stramonium* as a model. Light availability has not been fully explored as a factor in herbivore-plant-mycorrhizal fungi tritrophic interactions. Thus, in the present study, we addressed the following questions. 1) Does concurrent mycorrhizal infection and manual defoliation limit the allocation of resources to growth and reproduction in plants compared with defoliated-only and mycorrhizal infected-only plants? 2) Are the effects of defoliation and mycorrhizal infection affected by the availability of light? 3) Does defoliation affect the intensity of mycorrhizal colonization?

2. Materials and methods

2.1. Study species

Our study system was *D. stramonium* L. (Solanaceae), an annual herb with a life-span of 3–5 months that grows in anthropized systems. *D. stramonium* is facultatively self-compatible but cross-pollination, which is promoted by the abundant nectar and aromatic compounds in the flowers (Baker, 1961; Motten and

Antonovics, 1992; Adler and Bronstein, 2004), increases fecundity and the resistance to herbivores among the progeny (Núñez-Farfán et al., 1996; Bello-Bedoy and Núñez-Farfán, 2010). *D. stramonium* produces up to 20 flowers but only one or two are open at any time (cf. Valverde et al., 2003; van Kleunen et al., 2007). The flowers open at dusk and the anthers dehisce shortly after, which is followed by the maturation of the stigma some hours later (Núñez-Farfán et al., 1996) and the flowers wilt by midday.

D. stramonium is a fast-growing species that produces large flowers, and sphingid moths (the main pollinators) are known to respond to various floral display traits (cf. Bell, 1985; Adler and Bronstein, 2004); thus, changes in resource allocation may have direct reproductive consequences in this species. Furthermore, *D. stramonium* has been used as a model plant to assess plant responses to defoliation (Núñez-Farfán et al., 2007), and is a mycotrophic herb (Tao et al., 2004) with significant mycorrhizal dependence (Garrido et al., 2010) including effects on floral display (Aguilar-Chama and Guevara, 2012).

2.2. Experimental procedure

The experiment (but not the data) was part of a larger experiment reported by Aguilar-Chama and Guevara (2012). Here we concentrate on plants grown in low fertility soil since mycorrhizal colonization are known to be more abundant when plant growth is limited by the availability of soil nutrients (see Treseder, 2004). Further, data collection of the dry mass of vegetative structures was only done for plants grown in the low fertility soil, a decision taken during harvest. A detailed account of the experimental procedure can be found in Aguilar-Chama and Guevara (2012). Briefly, seeds were collected from wild populations of *D. stramonium* around the cities of Xalapa and Coatepec in central Veracruz, Mexico. All seeds used in the experiment were randomly selected for the experiment. Seeds were individually numbered (laid in rows on benches) and picked based on random numbers extracted from a uniform distribution.

The seed latency was interrupted by thermal shock (Fornoni and Núñez-Farfán, 2000) and the seeds were scarified mechanically with sandpaper, soaked in tap water for three days, and transferred to damp cotton wool until the radicles emerged. Next, the seeds were maintained separately on wet vermiculite until the second or third true leaf expanded. The plantlets were then transplanted into individual 3 l pots filled with a steam-sterilized (Pezzani et al., 2006) blend of soil, sand, and vermiculite (2:1:1, respectively). The sterile soil was slightly acid (pH = 6.1 at 1:1 in distilled water) and it had a low mineral nutrient content (0.36% nitrogen, 3.17% carbon, 5.46% organic matter, and trace phosphorus), which are conditions that are likely to promote mycorrhizal infection (Treseder, 2004). The wild microbial community but not the spores of arbuscular mycorrhizal fungi was recreated in each pot by adding 8 ml of soil washings (8 kg of soil from the rhizosphere of wild *D. stramonium* plants was washed with distilled water and made up to 2 l), which had been filtered through a 38 μm sieve (Kula et al., 2005).

2.3. Experimental design

We used two greenhouses (blocks) each partitioned to include two contrasting light environments and a randomized factorial design (mycorrhizal inoculation and manual defoliation). Half of each greenhouse was covered with 35% shade cloth, which resulted in an average photon flux of 765 $\mu\text{mol}^{-2} \text{m}^{-1}$ whereas that in the clear section of the greenhouse received on average 1123 $\mu\text{mol}^{-2} \text{m}^{-1}$.

Inoculation with mycorrhizal fungi was promoted by adding

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