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ORIGINAL PAPER

Interaction between epiphytic chemical allelopathy and ant-pruning determining the composition of Amazonian ant-garden epiphytes

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Abstract

In Ant-gardens, ants build nests with organic materials and take specific seeds of some species of epiphytes which germinate. In this mutualistic interaction, a variety of other epiphytes could colonize the nests and develop, but it doesn't happen. We assume that there is chemical allelopathy with epiphytes inhibiting the germination and growth of other species of epiphytes, and with ants cutting off non-mutualistic epiphyte species. To investigate this, we performed chemical and prune tests which determine the composition of the epiphyte species of Ant-Gardens of parabiotic ants, *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003. For the chemical allelopathic test, we administered the extract of the stem and leaves of *Peperomia macrostachya* (Vahl) A. Dietr. and *Codonanthe calcarata* (Miq.) Hanst. (the most common species in parabiotic AGs) in different concentrations. For the prune test, we used seedlings of the mutualistic plant *Peperomia macrostachya* and non-mutualistic plant *Cucumis sativus* as a control, then we inspected the nests to evaluate the ants pruning the seedlings. In the chemical allelopathy tests, the species *Codonanthe calcarata* decreased the germination speed indexes in relation to the control (distilled water). On the contrary, the length and weight of the seedlings were positively influenced by epiphyte extract. In the prune test, most of the plants pruned were non-mutualistic. The results of the chemical allelopathy and prune experiments showed that both mutualistic epiphytes and ants play a decisive role in the composition of epiphytes in Ant-Gardens.

Keywords Competition · Formicidae · Mutualism · Nesting · Parabiosis · Pruning · Rainforest

Introduction

Considering all the mutualistic interactions between ants and plants (Heil and Mckey 2003; Michelangeli 2010; Dáttilo et al. 2013; Campos and Camacho 2014; Fagundes et al. 2016), the Ant-gardens (henceforward AGs) are the more complex because they involve several of these mechanisms in a single interaction (Orivel and Leroy 2011; Vicente et al. 2020). In this mutualistic interaction where ants build nests of cardboard made of organic matter and incorporate seeds of some species of epiphytes to the nests. These seeds germinate and grow by structuring the nest through its tangles of roots (Orivel and Leroy 2011) and maintain moisture (Yu 1994). With this, ants protect epiphytes against herbivory (Vantaux et al. 2007; Vicente et al. 2014) and provide nutrients to epiphytes (Davidson 1988; Blüthgen et al. 2001). These interactions are mandatory for both participating ants and plants and occur in tropical Americas and Southeast Asia (Kleinfeldt 1978; Davidson 1988; Kaufmann and Maschwitz 2006).

Some species of ants can live in AGs, but in the Amazon region the most common AGs are those of the parabiotic ants *Camponotus femoratus* (Fabricius) (Formicinae) and *Crematogaster levior* Longino 2003 (Orivel and Leroy 2011; Vicente et al. 2020). In the neotropical region, the floristic

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composition of parabiotic AGs comprises four families and six genera (Orivel and Leroy 2011; Vicente et al. 2014). We know that epiphyte species are not randomly distributed in parabiotic AGs but that there are some preferential associations between ants and some epiphyte species, as of the 15,500 epiphyte species known in the Neotropics only a few are found in the AGs (Orivel and Leroy 2011; Vicente et al. 2014, 2020). In addition, within the species of epiphytes found in AGs, few are present in the vast majority of nests (Davidson 1988; Dejean et al. 2000; Vicente et al. 2014). This epiphyte species that are seen in AGs are brought by the ants that inhabit it and recognize the seeds of the mutualist epiphyte species (Davidson 1988; Youngsteadt et al. 2009, 2010). However, the carton that constitutes the nest walls is rich in nutrients and other species of epiphytes could colonize the nests via dispersion by wind or birds (Davidson 1988; Paolucci et al. 2016; Dejean et al. 2000; Blüthgen et al. 2001) but this does not occur. Therefore, some biological process not yet determined, is involved in the composition of AGs epiphytes.

It is known that outside these systems, plants can exhibit chemical allelopathy, in which plants release chemical compounds into the environment that interact with neighboring organisms, inhibiting or stimulating their growth or development (Rice 1984; Duke 2010). The chemical allelopathic compounds, which can be phenols, terpenoids, ethylene and other substances, can be released from leaves or other parts of the plant, or can be washed away by the dew or rain. In addition, these compounds can be incorporated into the substrate by the living roots exudation or the decomposition of residues by soil microorganisms. Both these compounds can accumulate on the substrate where they can remain for longer periods (Reigosa et al. 1999; Kato-Noguchi et al. 2017). Thus, the vegetation of a given area may have a succession model conditioned to pre-existing plants and the chemical substances they have released into the environment (Ferreira and Aqüila 2000; Fernandez et al. 2013).

Similar to the negative allelochemicals produced by plants, ants that inhabit myrmecophytes can act pruning and injecting formic acid in the competing plants to inhibit their development, which contributes to the survival and reproduction of host plants, and consequently, modifying the composition of plants (Janzen 1969; Federle et al. 2002; Weir et al. 2012; Amador-Vargas 2019). For example, ants of the genus *Azteca* that live associated with trees of the genus *Cecropia* cut the ends of the branches of lianas that touched their mutualistic species (Janzen 1969). In the devil's garden that occur in the rainforests of the western Amazon, the ants *Myrmelachista schumanni* Emery that lives in the *Duroia hirsute* (Poeppig and Endl.) K. Schum (Rubiaceae) myrmecophyte tree, kill plants around your host plant, and over time other *D. hirsuta* trees establish in the vegetation-free zone created by the ants (Frederickson and Gordon 2007).

Knowing that plants can show chemical allelopathy and that mutualistic ants can prune non-mutualistic plants, we conducted experiments in the laboratory and in the field to determine whether the composition of epiphytes in parabiotic AGs is determined by the chemical allelopathy of the most frequent epiphytes and by inhabitant ants pruning. To find out whether the limiting factor for the establishment of other epiphytes was determined by chemical allelopathy, we surveyed the local epiphyte composition and analyzed the allelopathic potential of the aqueous extracts of the stem and leaf of the two more frequent epiphytes *Peperomia macrostachya* (Vahl) A. Dietr. and *Codonanthe calcarata* (Miq.) Hanst. in different concentrations. To check for the existence of ants interference pruning the seedlings, we conducted field experiments administering seedlings of the mutualistic plant *Peperomia macrostachya* and of the non-mutualistic plant *Cucumis sativus* L. Our hypotheses were that (1) the plants of parabiotic AGs had chemical allelopathy inhibiting germination and development of non-AG plant species; and that (2) the ants demonstrate interference in epiphyte composition by pruning the seedlings of non-mutualistic plants from the parabiotic AGs.

Material and methods

Study area

We performed the study at Fazenda São Nicolau (9°48′S and 58°15′W, elev. 254 m), located in the municipality of Cotriguaçu, Mato Grosso state, Brazil. We conducted the collections and experiments on an abandoned road in advanced regeneration stage bordering a native forest with a reforestation site of *Ficus* spp. (Moraceae) (Vicente et al. 2014). According to the Köppen classification, for the region the climate is humid tropical (Am) with a temperature of 24–26 °C and precipitation of 3000 mm per year (Alvares et al. 2013). In Cotriguaçu the local vegetation is classified as Open Ombrophilous and Ombrophilous Dense Forest (IBGE 2004).

Methodology for the study of chemical allelopathic potential

After a floristic inventory in the area, we chose two of the most frequent epiphyte species in parabiotic AGs and we collect plants from at least five AGs to carry out the chemical allelopathic tests. The chemical allelopathic test was carried out at the Laboratório de Sementes of the Centro de Pesquisa e Técnologia da Amazônia—CEPTAM, of the Universidade do Estado de Mato Gross—UNEMAT, Campus of Alta Floresta. Before preparing the extracts, we placed two sheets of filter paper, previously autoclaved

in plastic boxes of the Gerbox type, made of transparent crystal polystyrene. In these boxes, we place 30 cucumber seeds symmetrically spaced. We used cucumber seed (*Cucumis sativus*) as a test organism because it comprises a species that is easy to manipulate and also because it presents fast and uniform germination and because it is sensitive to allelochemicals even in low concentrations (Ferreira and Aqüila 2000).

The aqueous plant extracts of the epiphyte's species were obtained from the stem and fresh leaves separately. Therefore, firstly we separate the leaves and stems of the collected epiphytes into different pots, the stems being cut into sticks of about 10 cm. To prepare the extracts, we take randomly and crushed 5, 10, 20 and 30 g of each vegetable organ in 100 mL of distilled water in a blender and then filtered, obtaining extracts in concentrations of 5, 10, 20 and 30 g/100 mL. We add in each Gerbox 5 mL of the extract from each of the four concentrations. We also used a control treatment, equivalent to zero extract concentration, where the filter paper was moistened with distilled water. We used five replications of 30 seeds for each extract concentration, totaling 20 Gerboxes per bioassay. We carried out the bioassays in a germination chamber with a controlled temperature with a minimum of 23 °C and maximum of 27 °C with a 12-h photoperiod.

For the germination speed index (GSI) we performed daily counts, according to the rules for seed analysis (Brasil, Ministério da Agricultura, Pecuária e Abastecimento 2009). For the GSI calculations, we used the Maguire formula (Maguire 1962):

$$IVG = N1/D1 + N2/D2 + \cdots$$

where N1 is the number of seedlings germinated on day 1, D1 is first day of germination, N2 is number of seedlings germinated on day 2, D2 is the second day of germination.

And so successively by the number of days that the experiment took place.

We calculated the germination percentage (G) according to Labouriau and Viladares (1976), using the following formula:

$$G(\%) = NA \times 100$$

Being N the number of germinated seeds, and, A the total number of seeds.

After 7 days, at the end of the test, we carried out seedling length measurements. Subsequently, these were packed in a kraft paper bag and dried in an oven for 72 h at 65 °C to obtain the dry mass value (total weight). For the germination analysis of each species, we used a completely randomized design, consisting of a $2 \times 4 + 1$ factorial scheme, two parts of the plant (stem and leaf extract) and with four concentrations (5, 10, 20 and 30 g/100 mL) and a control treatment (distilled water), with five repetitions of 30 seeds per treatment.

Methodology for the study of plant prune

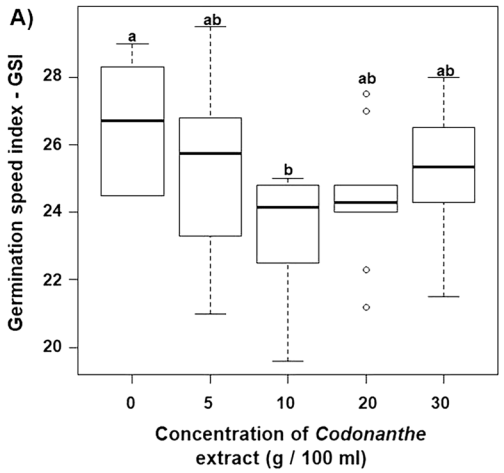
To test for the ant pruning, we marked 21 nests of a large colony located in a wide forest gap formed by an abandoned road that divides an area of a planted forest and an area of a native forest located at Fazenda São Nicolau, in the same place where the epiphytes were surveyed and sampled for the chemical allelopathy experiment. In each

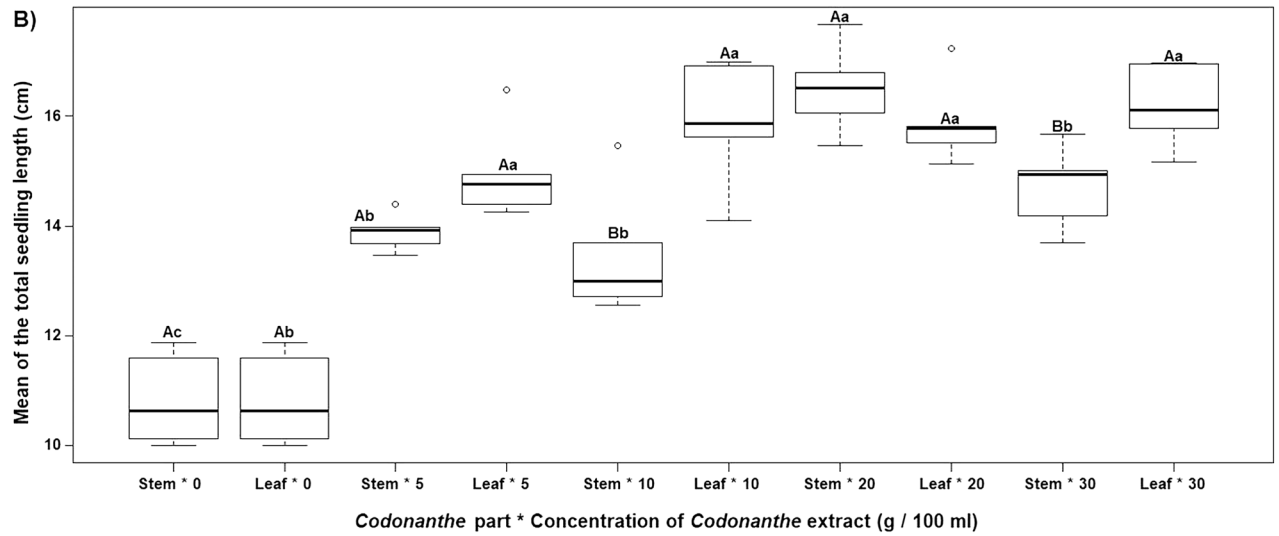
Table 1 Result of analysis of variance—ANOVA of the effects of extracts of *Codonanthe calcarata* and *Peperomia macrostachya* on the germination of *Cucumis sativus* seeds

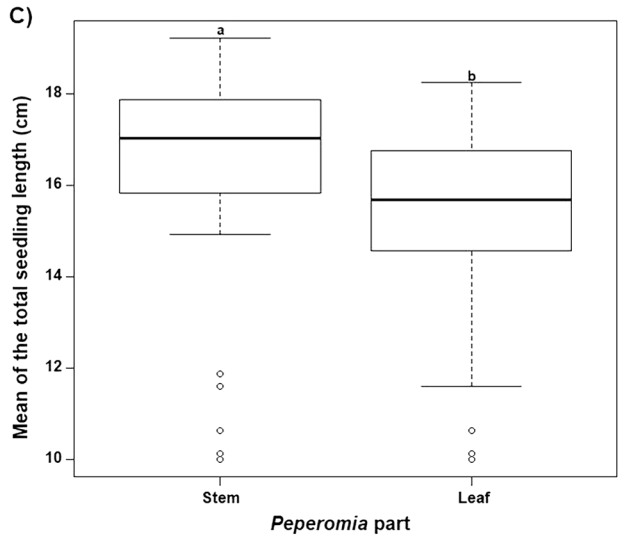
Dependent variable	Independent variable	*Codonanthe calcarata* MS	*Peperomia macrostachya*
GSI	Part	2.880	0.165
	Concentration	12.357*	8.099
	Interaction	2.305	0.954
% of Germination	Part	0.160	0.00
	Concentration	− 0.919	156.33
	Interaction	− 0.317	11.67
Total length	Part	9.56**	13.09**
	Concentration	42.49***	70.81***
	Interaction	3.58**	2.10
Total weight	Part	0.003562**	0.001282*
	Concentration	0.001147*	0.002195***
	Interaction	0.001312*	0.000176

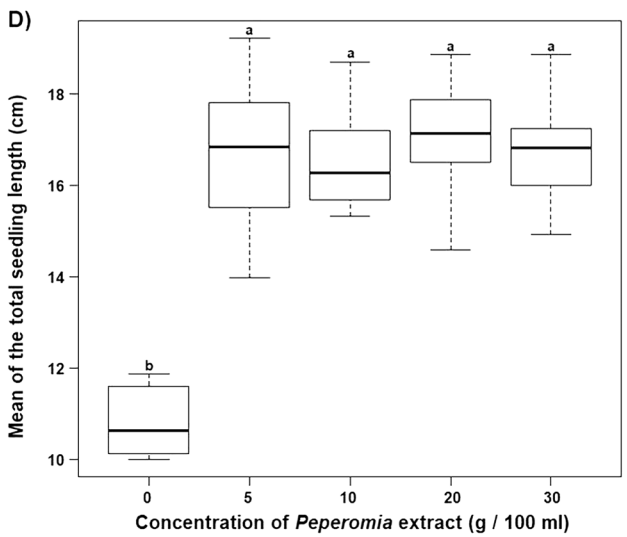
The significant results are represented by asterisk to the according alpha (0.05:'*'; 0.01: '**' and 0.001: '***')

GSI germination speed index, *MS* mean of squares


A)
Germination speed index - GSI
a
ab
b
ab
ab
20
22
24
26
28
0
5
10
20
30
Concentration of Codonanthe extract (g / 100 ml)


B)
Mean of the total seedling length (cm)
Ac
Ab
Ab
Aa
Bb
Aa
Aa
Aa
Bb
Aa
10
12
14
16
Stem * 0
Leaf * 0
Stem * 5
Leaf * 5
Stem * 10
Leaf * 10
Stem * 20
Leaf * 20
Stem * 30
Leaf * 30
Codonanthe part * Concentration of Codonanthe extract (g / 100 ml)


C)
Mean of the total seedling length (cm)
a
b
10
12
14
16
18
Stem
Leaf
Peperomia part


D)
Mean of the total seedling length (cm)
b
a
a
a
a
10
12
14
16
18
0
5
10
20
30
Concentration of Peperomia extract (g / 100 ml)

◂**Fig. 1** Effect of extracts of the species *Codonanthe calcarata* (**a**, **b**) and *Peperomia macrostachya* (**c**, **d**) on *GSI*—Germination speed index (**a**) and mean of the total of seedling length (**b**–**d**) of *Cucumis sativus*. Equal letters do not differ by Tukey's test at 5% significance level. In the presence of interaction between the parameters (**b**), uppercase letters compare the epiphytes parts (stem/leaf) and lowercase letters compare the extract concentrations

nest, we applied two treatments that consisted of fixing seedlings of an epiphytic mutualistic inhabitant of parabiotic AGs and non-mutualistic seedling that do not occur in parabiotic AGs, which were fixed with steel pins (e.g.: Weir et al. 2012). We applied three seedlings of each species per nest, totaling 63 seedlings of mutualistic epiphytes and 63 of non-mutualistic plants.

The seedlings of the mutualist epiphyte species applied were from *P. macrostachya*, which is the most frequent epiphyte in parabiotic AGs in this region (Vicente et al. 2014). We collected the seedlings of *P. macrostachya* in nests distant from where the experiments were being carried out so as not to generate disturbances in the studied nests. We used cucumber seedlings (*Cucumis sativus*) produced from commercial seeds (TopSeed Garden) as non-mutual plants. After fixing the treatments, we inspected the nests observing the prunig of the seedlings at 15 m, 3 and 24 h, respectively.

Statistical analysis

We test the chemical allelopathy effect on seedlings parameters using variance analysis (ANOVA). A posteriori, we used the Barlett homoscedasticity test and the Shapiro–Wilk normality of the residues test to check for the ANOVA assumptions. In the *Codonanthe* germination percentage the ANOVA residues are not normal, therefore, we use General Linear Model (GLM) with quasibinomial distribution. Posteriorly, we compared the averages using the 5% Tukey test. We performed the analysis and graphics with the R program (R Core Team 2020). In the case of interaction between the explanatory variables, the Tukey test was performed using the Genes® program (Cruz 2013).

To determine whether the number of non-mutualist plant seedlings pruned was superior to the number of mutualist plants, the number of plants pruned was compared between the type of seedling and time, using percentage descriptive statistics. All the graphic figures were carried out with the R program (R Core Team 2020).

Results

Chemical allelopathy

In the germination parameters, only the *Codonanthe calcarata* extract of 10 g/100 mL differed from the control, reducing the GSI (Table 1, Fig. 1a). Regarding the seedling's growth, both *C. calcarata* and *Peperomia macrostachya* extract affect the length and weight seedlings. In total seedling length parameter, the extract of the epiphyte *C. calcarata* showed an interaction between the part of the epiphyte and the concentration of the leaf extract, with the leaf extract increasing the seedling length in the concentrations of 10 and 30 g/100 mL in relation to the stem extract, and with all concentrations of each part being different from the control (Fig. 1b). In the extract of *P. macrostachya*, stem extract increasing the total seedling length in relation to the leaf extract in all concentrations compared to the control (Fig. 1c, d). The total weight was affected by the extract of the two species (Fig. 2a–c). In the *C. calcarata* stem extract, presented positive stimulation to weight gain in the concentrations 20 and 30 g/100 mL in relation to the leaf, and in the concentration 30 g/100 mL in relation to control. In the *P. macrostachya* extract, stem extract stimulated weight gain more than leaf extract. All concentrations of the *P. macrostachya* extract showed an increase in weight compared to the control.

Plant pruning

The ants pruned 53% of the seedling fixed in the AGs ($N=67$). Regarding of these pruned seedlings, 46% were non-mutualistic species ($N=58$), and only 7% were of the mutualistic species ($N=9$, Figs. 3, 4). After 15 min ($N=7$) or 3 h ($N=10$) the pruned plants were exclusively non-mutualistic.

Discussion

In this work, we showed that both the mutualist epiphytes *Peperomia macrostachya* and *Codonanthe calcarata* as well as the parabiotic ants *Camponotus femoratus* and *Crematogaster levior* perform an allelopathic process determining the ant garden epiphytes composition. Also, we emphasize that the chemical allelopathy that epiphytes play has a

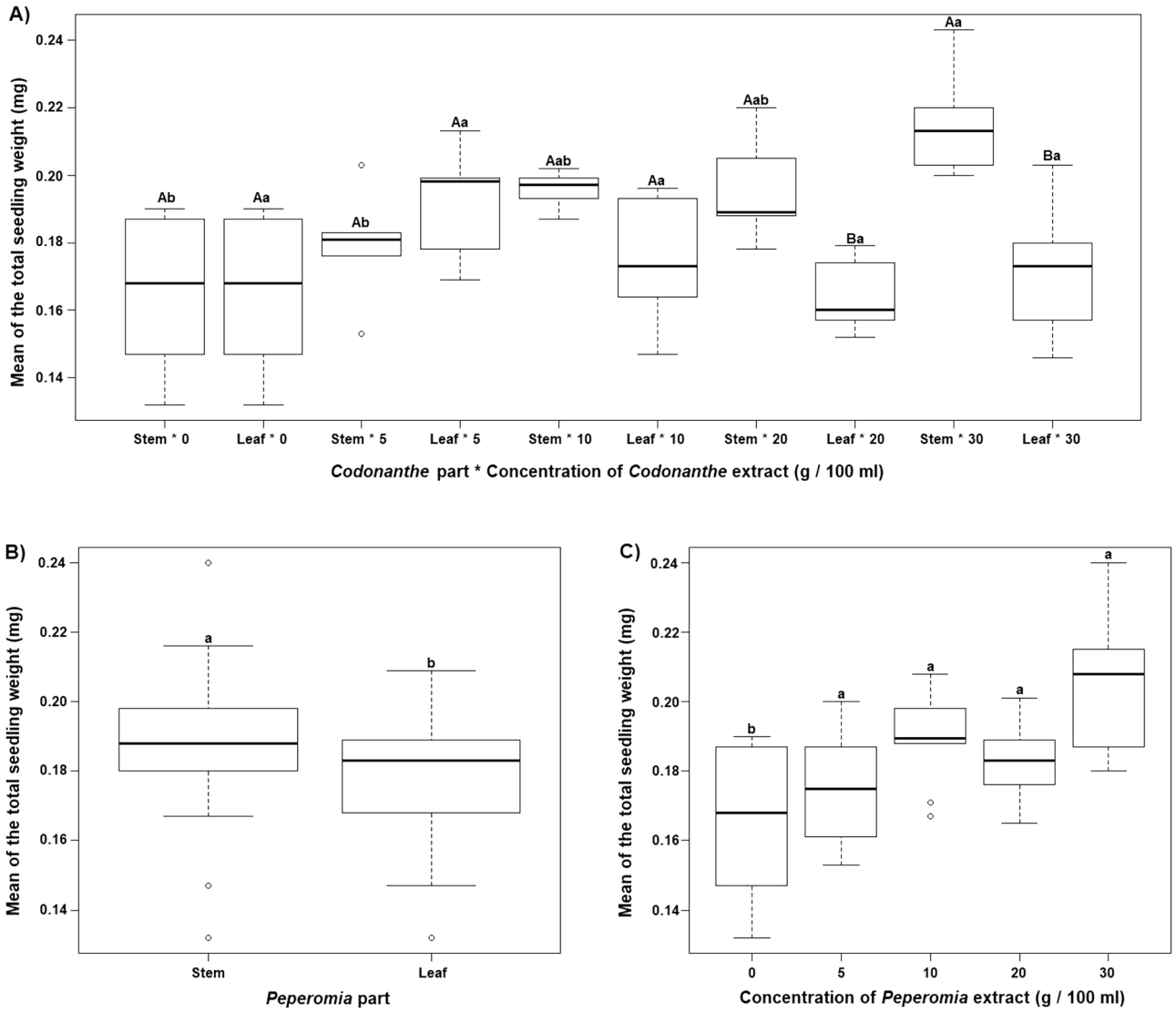


Fig. 2 Effect of extracts of the species *Codonanthe calcarata* (**a**) and *Peperomia macrostachya* (**b**, **c**) on mean of the total weight (**a**–**c**) of *Cucumis sativus* seedlings. Equal letters do not differ by Tukey's test at 5% significance level. In the presence of interaction between the parameters (**a**), uppercase letters compare the epiphytes parts (stem/leaf) and lowercase letters compare the extract concentrations

negative effect on germination speed (GSI) parameter and a positive effect on growth parameters. Meanwhile, ants act selectively, cutting off non-mutualist species.

In the chemical allelopathy tests, the extract of the species of the mutualist epiphytes *Peperomia macrostachya*, decreased the germination speed index (GSI) in relation to the control. The reduction in GSI can be explained by the reactions that can occur between the secondary metabolites of the extract and the cellular content of the seeds, delaying the biochemical reactions necessary to start the seed germination process (Ferreira and Borghetti 2004). However, for the other evaluated parameters, the effects of the mutualist epiphyte extract in AGs were not negative.

The allelopathic effects that occurred for the parameters of length and weight, indicated that there was a positive influence of the extracts stimulating the development of the seedlings. However, compounds with allelopathic activity that inhibit growth is more commonly reported (Einhellig 1999; Ferreira and Aqüila 2000) acting as an essential factor in interspecific competition (Bieberich et al. 2018; Dhungana et al. 2019; Uesugi et al. 2019). However, there are some studies that report stimuli in seedling growth (Rice 1984; Lin et al. 2004; Sausen et al. 2009). Although the beneficial effects of one plant on another should not be separated from the concept of allelopathy (Rice 1979), nevertheless there are few explanations about the stimulus of seedling

Fig. 3 Pruning experiment with seedlings of non-mutualistic plant (*Cucumis sativus*) damaged by parabiotic AG ants (yellow circle) *Camponotus femoratus* and *Crematogaster levior*

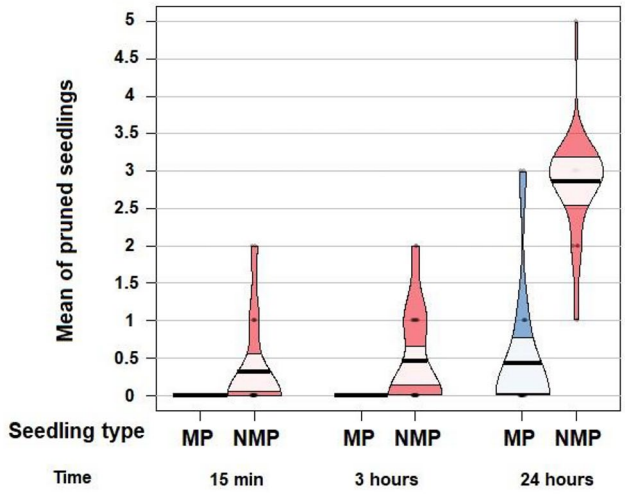


Fig. 4 Mean of mutualist plant *Peperomia macrostachya* seedlings (MP) and non-mutualist plant *Cucumis sativus* seedlings (NMP) pruned over time

growth in allelopathic tests. This positive stimulus for seedling development can suggest that the plant extract may have compounds such as sugars, amino acids and salts in the extract (Sausen et al. 2009) or allelochemicals that can act as phytohormones (Aqüila et al. 1999). Plants can have numerous phytohormones that can increase the resistance of plants to various environmental stresses, making them essential to induce responses to biotic and abiotic stress throughout their life cycle (Sah et al. 2016; Ullah et al. 2017). Some of these phytohormones, such as ethylene, abscisic, jasmonic and salicylic acid, are involved in drought-related processes (Khan et al. 2015; Vishwakarma et al. 2017). These phytohormones are essential for the life of epiphyte plants, since their roots have little contact with substrates with water availability, and the factor is aggravated because these epiphytes inhabit Ant-gardens, which occur in forest gaps, where the stress due to lack of water is greater (Zotz & Hietz 2001; Vicente et al. 2020). In addition to making plants resistant to environmental stresses, phytohormones can act on the growth of some plants and some of them are the same responsible for drought tolerance mentioned above as ethylene, jasmonic and salicylic acid (Arraes et al. 2015; Wasternack 2007; Vicente & Plasencia 2011).

Ants showed pruning behavior, with a negative selective effect for non-mutualistic plants. This is because the ants pruned the seedlings of non-mutualist species almost exclusively, comprising a total of 92% of the non-mutualist plant seedlings fixed. Every time the ants cut the leaves and/or stem of the seedlings, and sometimes we saw the ants pulling the fixed seedlings and removing them from the AG after cutting some tissues. Ants practice pruning in non-mutualistic species, protecting host plants against the overgrowth of competing plants, thus reducing competition for water, light and nutrients (Janzen 1969; Morawetz et al. 1992; Tanaka and Itioka 2011). These factors are so important for plants, that they influence the survival and distribution (Heil and Mckey 2003; Chamberlain and Holland 2009). The pruning of competing plants can increase the fitness of the plant, which invests more resources in the growth of the host plant, benefiting ants with more shelters and food supply (Renner and Ricklefs 1998; Amador-Vargas 2011).

As seen, this is the first study to evaluate both chemical allelopathy and pruning in ant-gardens. Most of these studies focusing in these themes, are carried out alone in biological systems other than AGs, for example, production systems in the case of chemical allelopathy and myrmecophytes in the ants pruning. Furthermore, the data from this study demonstrate that mutualistic epiphytes and ants interact, while the epiphyte *Codonanthe calcarata* inhibits the germination

speed (GSI) and favors the growth of the germinated plants, ants cut the non-mutualist plants. This results in an expected epiphyte species composition constant in parabiotic AGs throughout its occurrence.

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Data availability The data that support the findings of this study are available from the corresponding author, REV, upon reasonable request.

Declaration

Conflict of interest The authors declare that they have no conflict of interest.

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