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Postponing the production of ant domatia as a strategy promoting an escape from flooding in an Amazonian myrmecophyte

Thiago J. Izzo[1,*], Maria Teresa Fernandez Piedade[2] and Wesley Dáttilo[3,*]

[1]*Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, CEP 78060–900, Brazil,*
[2]*Departamento de Biologia Aquática e Limnologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, CEP 69011970, Brazil and* [3]*Red de Ecoetología, Instituto de Ecología AC, Carretera antigua a Coatepec 351, El Haya, CP 91070, Xalapa, Veracruz, Mexico*
* *For correspondence. E-mail: wdattilo@hotmail.com or izzothiago@gmail.com*

- **Background and Aims** Even when adapted to flooding environments, the spatial distribution, growing strategies and anti-herbivore defences of plants face stressful conditions. Here we describe the effects of flooding on carbon allocation on growth, domatia and leaf production, and the herbivory on the myrmecophyte domatia-bearing *Tococa coronata* Benth. (Melastomataceae) growing along river banks in the Amazon region.
- **Methods** In an area of 80 000 m² of riparian forest along the Juruena River we actively searched for individuals of *T. coronata*. In each plant we evaluated the size of the plant when producing the first domatium and determined its best predictor: (1) plant total height; (2) size of plants above flood level; or (3) length of time each plant spent underwater. We also compared the herbivory, internode elongation, foliar asymmetry and specific leaf weight between *T. coronata* individuals growing above and below the maximum flooding level. The distance to the river and the height of the first domatium produced were compared between *T. coronata* and its sympatric congener, *T. bulifera*.
- **Key Results** We found that *T. coronata* invests in rapid growth in the early ontogenetic stages through an elongation of internodes rather than in constitutive anti-herbivore defences to leaves or domatia to exceed the maximum flooding level. Consequently, its leaf herbivory was higher when compared with those produced above the flooding level. Individuals with leaves above flood levels produce coriaceous leaves and ant-domatias. Thus, flooding seems to trigger changes in growth strategies of the species. Furthermore, *T. coronata* occurs within the flood level, whereas its congener *T. bullifera* invariably occurs at sites unreachable by floods.
- **Conclusion** Even in conditions of high stress, *T. coronata* presents both physiological and adaptive strategies that allow for colonization and establishment within flooded regions. These mechanisms involve an extreme trade-off of postponing adult plant characteristics to rapid growth to escape flooding while minimizing carbon allocation to defence.

Key words: Ant–plant mutualisms, trade-off, fluctuating asymmetry, flood stress, plant strategies, submergence tolerance.

INTRODUCTION

The Amazon Basin is formed by large rivers subjected to an annual flood pulse with an amplitude of up to 10 m and flood duration up to 270 d (Junk *et al.*, 1989; Junk, 1997). This dynamic of inundation directly influences the vegetative and reproductive growth of riparian vegetation along these river banks (Junk *et al.*, 1989; Waldhoff *et al.*, 1998; Piedade *et al.*, 2000). For the plants growing on the margin of rivers, the flooding imposes a seasonal stress, such as the reduction of soil oxygen to extremely low levels (Pezeshki, 2001; Jackson and Colmer, 2005; Mommer and Visser, 2005).

Over evolutionary time, some plant species have developed different morphological and physiological strategies to escape and tolerate survival in flooded conditions (Kramer, 1963; Navas and Garnier, 2002; Parolin, 2009; Ferreira *et al.*, 2010). In fact, there are species that have adapted and occur exclusively or primarily in floodplains (Foster, 1992; Wittmann *et al.*, 2013). If vegetative parts of the plant become completely submerged during periods of inundation, one of the principal strategies employed by the plant is growth restriction and quiescence (i.e. unavailability of favourable conditions) (Fukao and Bailey-Serres, 2008; Bailey-Serres *et al.*, 2012). However, some plant species allocate resources to the rapid elongation of stems (Fu, 2001; Nagai *et al.*, 2010; Bailey-Serres *et al.*, 2012) to escape inundation and maintain vegetative parts above water levels (Parolin, 2002). Through this escape strategy, the plants remain in contact with the air and can maintain the structures responsible for gas exchange, even when other parts of the plant are submerged during flooding (Bailey-Serres *et al.*, 2012; Nishiuchi, *et al.*, 2012).

The use of different strategies to decrease the effects of flooding can generate stress which may be reflected in changes to its phenotype (Vierling and Kimpel, 1992; Dat *et al.*, 2000). This is mainly due to a reduction in nutrient uptake and assimilation levels as a result of limitations imposed on the plants during

flood periods (Louda, 1986; Renaud *et al.*, 1990). Nutrient availability is a determinant in the allocation of metabolites for defence against herbivores (Coley *et al.*, 1985). Plants growing in environments with low nutrient concentrations tend to invest in quantitative carbon-based chemical defences with consequent slower growth (McKey, 1988; Coley and Barone, 1996). In view of this situation, plants growing in floodplains may be confronted by the following challenge in terms of energy balance: while there is pressure to hold the nutrients within tissues against herbivory, there is also a pressure for rapid growth as an escape mechanism from floods (Parolin, 2002, 2009). In fact, some plants found in floodplain environments which are either completely or partially submerged during floods invest less in chemical defences and are more susceptible and less tolerant to herbivore damage (Stout *et al.*, 2002; Chen, 2008). Therefore, could frequent flooding events influence energy allocation in plants that use biotic defence?

Biotic defences in plants are extremely common in Amazonian environments, most of them provided by ants in the deterrence of potential herbivores (Benson, 1985; Vasconcelos, 1991). One example of biotic defence is myrmecophytes (or ant-plant). Mymecophyte plant species invest in the production of physical structures called domatia to house colonies of highly specialized ants. In exchange for the protective shelter provided by the domatia, ants defend and protect the host plant against herbivores (Benson, 1985; Agrawal and Dubin-Thaler, 1999).

One myrmecophyte species often found near rivers and small streams of the Amazon is *Tococa coronata* Benth. (Melastomataceae) (Guarim-Neto and Asakawa, 1978; Benson, 1985). This plant species has foliar domatia consisting of a pair of small pockets in the leaf limb with individual entrances, with all domatia occupied by a single colony of ants (Benson, 1985). In myrmecophytes, the colonies' effectiveness in protecting the plant depends on a minimum number of worker ants patrolling the leaves of the plant (Izzo and Vasconcelos, 2005). In areas subject to periodic flooding such as those in which *T. coronata* is found, the rise of the water column can lead to total submersion of the plant, promoting stress to the plant and causing the death of the ant colony. Since the production of domatia implies energy expenditure (Fonseca, 1999), and given the infeasibility of plant defence by small ant colonies (e.g. Izzo and Vasconcelos, 2005), this energy could be redirected to vertical growth and flood escape.

A tool commonly used to measure the influence of external factors on the phenotype of an individual is called fluctuating asymmetry (FA) (Palmer and Strobeck, 1986). The FA measures the deviation from morphological symmetry in an individual's ontogeny of organisms growing under constant stress (Møller and Eriksson, 1994; Wilsey *et al.*, 1998; Graham *et al.*, 2010). Here, we evaluated the effect of flooding on growth–defence trade-offs (Herms and Mattson, 1992) for the myrmecophyte *T. coronata* along river banks of the Juruena River located in the southern Brazilian Amazon. We approached the escape of flooding in the elongation of the internodes, the carbon allocation in defence against herbivores, herbivory and production of domatia. The FA was used to infer environmental stress on plants growing on total flooding conditions. In this case, we also compared some of these aspects with the myrmecophytic congeneric species *Tococa*

cff. *bullifera* Mart. and Schrank ex DC (Melastomataceae) which inhabits the same riparian forests, but is commonly associated with non-floodable environments (Michelangeli, 2005). Specifically, we tested the following hypotheses: (1) the production of leaves with domatia by *T. coronata* occurs only after the plant surpasses the height of the river's maximum flood level; (2) when growing in flood areas, *T. coronata* invests resources in the rapid growth and elongation of internodes, but less in the leaf, until reaching a height that has surpassed the maximum flood level; (3) the herbivory of *T. coronata* individuals is higher on leaves produced below the maximum flood level; and (4) plants growing below the river's maximum flood level produce more asymmetric leaves (indicative of a stressing environment).

MATERIALS AND METHODS

Study area

This study was conducted in three field campaigns in the beginning of the rainy season (2009, 2010 and 2012) in riparian forests along the margins and islands of the Juruena River at São Nicolau Farm (9°48'S, 58°15'W, elevation 254 m), located in the municipality of Cotriguaçu, north of the State of Mato Grosso, Brazil. The reserve area covers 7000 ha of dense rain forest in the Brazilian Meridional Amazon, surrounded by >50 000 ha of continuous forest. The climate is wet tropical (Am – according to Köppen classification) with an annual average temperature of 24 °C, 85 % humidity and 2300 mm precipitation (Camargo *et al.*, 2010). The Juruena River is approx. 400 km in length and joins the Teles-Pires river to form the Tapajos river, one of the tributaries of the Amazon river. Dynamics of the water level in the Juruena River are driven by two distinct seasons, a high-water level season between November and April and a low-water level season between May and October. According to the Brazilian Water Agency's System of Hydrological Information, the river's range of flood elevation in our study area was 4.6–10 m between the years 1984 and 2014. An ANA station (Brazilian National Agency for Water Availability) is located approx. 500 m from the study site, which takes daily readings of the Juruena River's water level. All data on the Juruena River's water level are available at http://www.snirh.gov.br/hidroweb or at http://hidroweb.ana.gov.br/default.asp.

Distribution of T. coronata

To describe the life history and abundance distribution of the myrmecophyte species *T. coronata*, we surveyed a 2000 × 40 m (80 000 m^2) stretch of riparian forest along the Juruena River. For each individual of *T. coronata* found, we measured: the base height of the individual from the ground that was not submerged on the day of observation; the height of the first domatium, when present, from the base of the individual; and the distance of the individual from the river bank. In addition, we also measured the river's maximum water level from the previous year's flood. This was done by locating the flood mark left on the trunks of trees near the sampled plants, then using a laser level to measure this flood mark in relation to the river level at

the time of data collection. This measurement was compared with data provided by São Nicolau Farm, where the study was conducted. The heights of plants and first domatia in relation to flood level were obtained in two campaigns (2010 and 2011).

Leaf fluctuating asymmetry (LFA) and internode elongation

We used leaf fluctuating asymmetry (LFA) as a proxy for *T. coronata* stress against water saturation and compared LFA of plant parts above and below the maximum flood level observed in the year prior to this study. For this, we selected 30 individuals that had vegetative parts growing above the river's maximum water level in the previous year, and 30 individuals whose vegetative parts would remain totally submerged during the high-water period. For the calculation of internodal symmetry we chose the first three leaves arranged in the first three internodes below the apical bud. In each leaf, the asymmetry index was calculated: $AI = LA – LB/LA \times LB) \times 100$, where LA = greatest distance from the central vein to the margin of one side of the leaf and LB = greatest distance from the central vein to the margin of the side opposite the one previously measured. In addition, we measured the length of the first six internodes from the base of individuals ($n = 30$ for each of the two categories), with the objective of finding possible differences in internode elongation between individuals with emergent parts and individuals of *T. coronata* that would remain totally submerged at peak flood.

Specific leaf weight index

To evaluate carbon investment in leaves of *T. coronata* individuals growing above and below the maximum flooding level, we used specific leaf weight (SLW). SLW is obtained by the division of an oven-dry mass of a given leaf by its area ($SWF = M/A$; where M = dry weight in g and A = leaf area in cm^2). Higher SLW values represent a greater allocation of resources in carbon-based structural compounds and macromolecules and lower amounts of nitrogen (Dyer *et al.*, 2001; Westoby *et al.*, 2002). From each of 15 individuals growing under or above the flooding level, we obtained 27 cm^2 of the leaf limb of three leaves (excluding the central and peripheral veins). These pieces of leaves were then dried at 60 °C for 48 h (until constant weight) and weighed using a 0.005g (Marte®, AM-220) precision scale.

.Leaf area removed

To quantify the percentage of foliar herbivory in plants of *T. coronata* growing above and below the maximum flood level, we used 30 individuals for each of the two categories. In each individual, we measured the leaf area removed through the categorization proposed by Dirzo and Dominguez (1995): (1) 0 % (no loss of leaf area); (2) 1–6 %; 6–12 %; (3) 12–25 %; (4) 25–50 %; and (v) 50–100 % (large loss of leaf area). This method renders herbivory values as accurate as other quantitative methods such as image processing (Vásquez *et al.*, 2007). In this study we consider herbivory to be any loss of photosynthetic area due to the action of chewing, scraping or sucking (necrotic areas) insects, miners and/or gallers.

Comparison with another sympatric myrmecophyte

To compare the height and spatial position of the first leaf with domatia produced in relation to the water between *T. coronata* and the sympatric and phylogenetically similar myrmecophyte *Tococa bullifera*, both species of plants and the ant species found in these myrmecophytes were collected for identification at the Community Ecology Lab (Universidade Federal de Mato Grosso, Brazil). Ant identification was carried out by comparison with the reference collection, while plant identification was obtained using a taxonomical key to the genus (Michelangeli, 2005) and confirmed with specimens from the herbarium at the Instituto Nacional de Pesquisas da Amazônia (Brazil).

Data analysis

All independent variables were first tested to determine any correlation. Evaluation of the three independent factors revealed that the length of time that each plant remained submerged, total plant height and the size of branches that were outside the maximum flood level in the previous year were clearly correlated (Pearson $r > 0.4$), and therefore could not be used in multiple models (Zar, 1996). We used three generalized linear models (GLMs) with binomial error distribution, where the occurrence of a developed domatium (i.e. capable of hosting an ant queen) was related to each factor: (1) total plant height (cm); (2) size of the plant found above the flood level (cm); and (3) length of time that each plant spent underwater (months). We selected the best of the three models to predict the occurrence of the first domatium using the best-fit model (explained deviance) and the ΔAIC (Akaike information criterion) of each GLM. All the statistical analyses were performed using the R software/environment (R Development Core Team, 2015).

Comparison between the production height of domatia, as well as the straight-line distance from the river to the location of *T. coronata* and *T. bulifera* plants within the study area was evaluated using a *t*-test once the normal distribution was confirmed. The comparison between fluctuating asymmetry, elongation of internodes, specific leaf mass and percentage leaf area removed was conducted between plants growing above and below the maximum flood level also using Student *t*-tests.

RESULTS

The production of domatia by *T. coronata* appears to be closely associated with the flood level. Although production of the first domatium in *T. coronata* can vary greatly in relation to the height of the individual, we did not find a single domatium below the previous year's flood level. In fact, the length of time plants spent submerged in the previous year did not show any correlation with the probability of the occurrence of domatia ($z = –0.05$, $P > 0.05$, AIC = 25.35). In contrast, both the total height of the individual in relation to the soil

(d^2 = 0.77; z = 2.57; P = 0.01; AIC = 19.25) and the size of the branches found emerged during the previous period of rising water (d^2 = 0.82; z = 2.82; P = 0.004; AIC = 16.15) appears to be related to the production of the plant's first domatium (Supplementary Data Fig. S1). However, the model containing the size of the emerged part shows a better fit to the data (ΔAIC = 3.1) (Fig. 1). Throughout the 80 000 m² study area, we found only 11 individuals of *T. bullifera*, all of them with at least one mature domatium, while within the same section we found 33 *T. coronata* individuals with domatia. The number of individuals without domatia, however, was not counted, as juvenile *T. coronata* occur in areas that can contain tens to hundreds of individuals. All individuals found with domatia were colonized by some species of ant. In *T. bullifera*, 62.5 % of the plants were colonized by the *Allomerus octoarticulatus* ant, 25 % by *Azteca* sp1 and 12.5 % by *Crematogaster* sp1. For *T. coronata*, 30 % of the plants contained colonies of *Allomerus octoarticulatus*, 30 % with colonies of *Crematogaster* sp1, 20 % with colonies of *Azteca* sp1, 10 % with colonies of *Crematogaster* sp2 and 10 % with *Hylomyrma* sp1.

Leaves of *T. coronata* found both above and below the previous year's maximum river level presented a high degree of leaf asymmetry. However, leaves produced on branches below the previous year's maximum flood level were more asymmetrical (mean ± s.d. 8.91 ± 3.22 %) than those on branches produced above that level (1.25 ± 0.86 %; Fig. 2A; t = 13.129; d.f. = 29; P < 0.001). Also, the parts of the plants produced below the maximum flood level presented internodes almost twice as elongated (5.76 ± 1.69 cm) in relation to plants with internodes growing above the maximum flood level (3.36 ± 0.32 cm) (Fig. 2B, t = 7.913; d.f. = 29; P < 0.001).

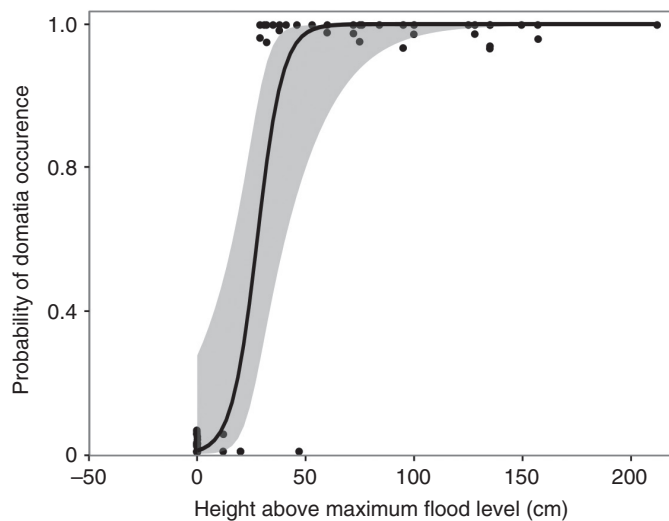FIG. 1. Probability of occurrence of the first domatia in individuals of *Tococa coronata* (Melastomataceae) found in the Juruena River riparian forest modelled as a function of the height of the plant found above the maximum flood level. The smoother line was the predictive result of a generalized linear model [presence of domatia = –4.74 + 0.17 × height above flood level (cm), GLM, family = binomial, link = logit] and the grey area indicates the confidence interval of the model. Each point represents the occurrence of domatia in a single plant. The presence of domatia is categorized as '1', whereas absence is '0'; however, the function 'jitter' was employed to reduce the point overlap and showinged the high number of plants with no domatia when they are without any vegetative part above the maximum flood.
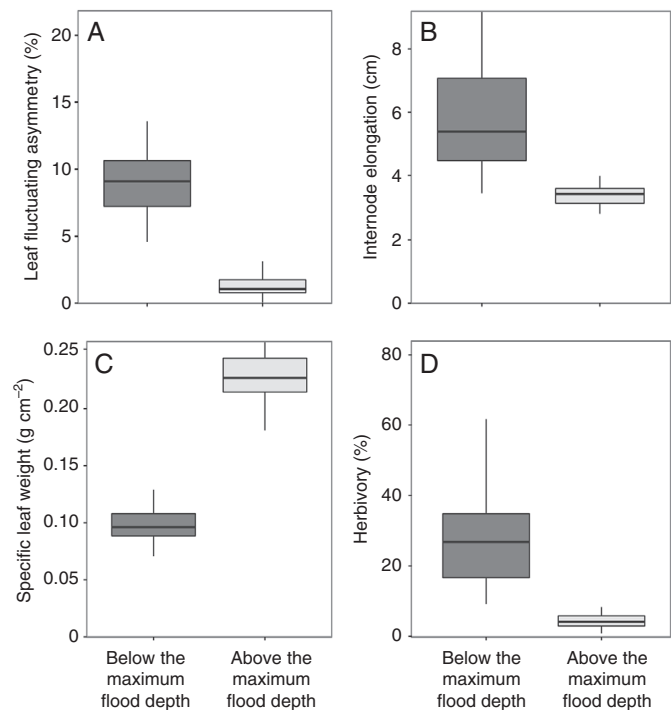

FIG. 2. Box plots of the following variables: (A) leaf fluctuating asymmetry (%), (B) internode elongation (cm), (C) specific leaf weight (g cm⁻²) and (D) leaf area removed (%) in *Tococa coronata* (Melastomataceae) individuals found above and below the maximum flood level in riparian forests of the Juruena River, Southern Amazon, Brazil (n = 30 for each treatment).

Individuals of *T. coronata* found above or below the maximum river level presented different strategies for carbon allocation in their leaves (t = –13.617; d.f. = 14; P = 0.001). Leaves produced below the maximum river level presented a lower specific leaf weight (0.09 ± 0.01 g) than leaves produced above the flood level (0.2 ± 0.02 g) (Fig. 2C). In addition, leaf area removed by herbivores also differed (t = 9.507; d.f. = 29; P < 0.001), with individuals found below the previous year's maximum flood level subject to greater leaf damage caused by herbivores (mean ± s.d. 28.42 ± 14.25 %) when compared with individuals found above this level (4.26 ± 1.99 %) (Fig. 2D; additional information can be found in Supplementary Data Table S1). All observed individuals found above the maximum river level produced flowers at the beginning of the rainy season (November 2011 and 2012). On the other hand, even allocating less carbon on the leaves, about 20 individuals among hundreds of small individuals of *T. coronata* found below the maximum river level individuals were observed producing flowers.

Both myrmecophytes found in the area differ in place of occurrence along the river bank (t = –6.571; d.f. = 8; P = 0.001). *Tococa coronata* individuals occurred almost exclusively below the river's maximum flood level (mean ± s.d. 52.1 ± 32.9 cm), whereas *T. bullifera* individuals occurred above the river's flood level (176.9 ± 37.2 cm) (Fig. 3A). The two species also differed in the height of the first domatium developed (t = 5.507; d.f. = 8, P = 0.001). The height of the first domatium in *T. coronata* was 122.2 ± 45 cm, while for *T. bullifera* it was 33.3 ± 19.6 cm (Fig 3B). In addition, both myrmecophytes also differed in distance
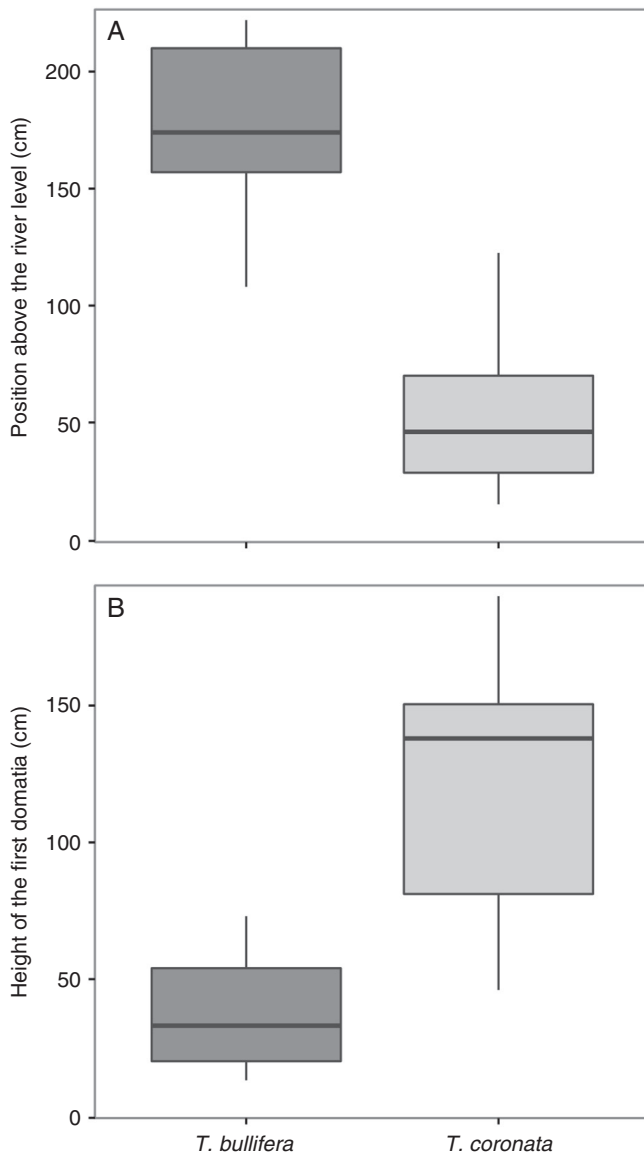
Fig. 3. Box plots showing the median, quartiles and range (whiskers) of the following *Tococa bullifera* (Melastomataceae) and *Tococa coronata* (Melastomataceae) variables: (A) base height of individuals in relation to river level at the time of study (cm) and (B) height of the first domatium (cm) in Juruena River riparian forests, Southern Amazon, Brazil ($n = 11$ for *T. bullifera* and $n = 33$ for *T. coronata*).

from the river ($t = -5.590$, d.f. $= 8$, $P = 0.001$), with an average distance of 131.9 ± 83.4 cm for *T. coronata* individuals, and 747.6 ± 278 cm for *T. bullifera*.

DISCUSSION

In this study, we demonstrated that individuals of the myrmecophyte *T. coronata* postpone a typical characteristic of the adult individuals, presenting the first domatia only when vegetative parts are emerged after the maximum water level is reached for the high-water period. In fact, it is easy to find plants with seedling characteristics up to 2 m high, depending upon its position in the riverside. In plants growing below the flood limit,

we observed that several vegetative characteristics are modified, favouring rapid growth. Initially, *T. coronata* invests only in energy for growth through a disproportionately large stretching of their internodes. Rapid development requires a very characteristic trade-off, where smaller individuals that would be entirely submerged in the rainy season grow at the expense of the lower allocation of carbon in their leaves (Nagai *et al.*, 2010; Maurenza *et al.*, 2012). This low investment in constitutive defences is associated with greater rates of observed herbivory (Coley and Barone, 1996). The pressure to escape through rapid growth and the physiological changes by decreasing the anti-herbivore traits probably results in the observed higher herbivory. It also suggests that plants are growing under particularly stressful conditions, which is reinforced by the pronounced asymmetry observed in leaves produced below the maximum flood level. The myrmecophyte *T. coronata* presents two well-defined phases of life, with a set of physiological adaptations allowing escape from floods (Parolin, 2002) when in the 'juvenile' stage, and the development of domatia for ant nesting in the 'mature' stage (Benson, 1985). These stages are not related to the plant's reproduction, but to their persistence in the area, since few 'juveniles' should produce flowers, but the major part die or lose part of their vegetative tissue when submersed. The 'mature' plants certainly produce flowers and in any of the observed mature plants which died over the 4 years in which we studied the population.

The duration of submersion was not a good predictor for first domatia production by the plant, as no submerged plant produced domatia, regardless of time. However, with the size of the plant and the size of the emerged part at the time of flooding, the latter presented a better fit to the data. This explains why, analysing the distribution of *T. coronata* plants along the river planes, only larger plants, taller than 2 m, located near the river produce domatia. In contrast, small plants established in sites which are topographically higher have the ability to produce domatia, as is the case of plants smaller than 50 cm producing domatia in unflooded areas. Such a striking characteristic suggests that the maintenance of a photosynthetic part of the plant above water during the flood period may trigger the development of the first domatium.

During flooding, the entire ant colony residing in a domatium would die. Studies dealing with ant–myrmecophyte interactions have shown that domatia are extremely important structures for myrmecophyte-associated ants, as the growth of ant colonies associated with myrmecophytes is dependent on the number of available domatia (Benson, 1985; Fonseca, 1999). As a consequence of host plant growth, the colony's demand for proteins also grows (Fonseca, 1999). In fact, there are several examples within the literature indicating an increase in protection by ants in plants with more domatia (Duarte-Rocha and Bergallo, 1992; Del-Val and Dirzo, 2003; Izzo and Vasconcelos, 2005). Therefore, if production of domatia is associated with greater defence against herbivory, why does *T. coronata* not produce domatia below the maximum flooding level, even though there would be an annual mortality of the resident ant colony? First, the high-energy cost of producing domatia that would be submerged without ant protection would be a waste in the general energy balance of plants. Domatia located at this level may become unfeasible after flooding due to sediment accumulation. There are ant species that have the ability to ingest water

and regurgitate outside of the colony after short-term flooding (Moog *et al.*, 1997). However, we believe that such water-bailing behaviour would not be possible with fully submerged domatia during flood periods that may last months. Whole colonies residing in submerged domatia would quickly perish. The migration of ants from lower to upper domatia would not be viable in all cases. In fact, ant colonies in myrmecophytic plants are strongly limited by available nesting space (Fonseca, 1999). A large colony, even if not fully flooded, might not recover, and perish by losing the queen or a large number of workers. If colony death happens, a new colonization may take some time, since initial colony growth is slow because ant–myrmecophyte interactions are highly specialized (Dáttilo *et al.*, 2013). During the period between colonization events, both young and mature plant individuals may remain unoccupied and unprotected against herbivores, until the colony was able to produce a sufficient number of workers for defence. During these periods, herbivory may be of such intensity as to reduce the plant's reproductive success drastically or even lead to its death (Vasconcelos 1993).

One strategy used by individuals without domatia to counterbalance the absence of anti-herbivory protection by ants would be to invest in quantitative defences in the leaves (McKey, 1988). Leaves with a higher specific leaf weight (i.e. higher carbon concentration), due to a higher concentration of cellulose, tannins and lignins, are harder, mechanically resistant and/or unpalatable to herbivores (Dyer *et al.*, 2001; Westoby *et al.*, 2002). However, smaller *T. coronata* individuals showed lower specific leaf weight compared with larger individuals. The possible reabsorption of chlorophyll in submerged leaves (Crawford, 1992; Dyer *et al.*, 2001; Maurenza *et al.*, 2012) cannot explain this difference in specific leaf weight, as all sampling took place during the dry period. Therefore, the observed phenomena resemble the grow–defence trade-off (Herms and Mattson, 1992). The difference in specific leaf weight and high herbivory levels in leaves growing below the maximum flood level may relate to a reduction in carbon allocation to sclerophyll and quantitative defences, leaving the available carbon for investment in growth.

We suggest that, as a strategy to reduce the damage caused by flood seasonality (e.g. absence of domatia and carbon in leaves), *T. coronata* invests in rapid growth to surpass the maximum flood level by elongating the internodes, like several floodplain plant species using the flood escape strategy (Colmer and Voesenek, 1999; Fu, 2001; Parolin, 2002; Pierik *et al.*, 2005; Nagai *et al.*, 2010; Nishiuchi *et al.* 2012). Some plants can significantly increase in length, even daily, through internode elongation (e.g. rice: 25 cm d^{-1}, bamboo: 114 cm d^{-1}) (Vergara *et al.*, 1976; Fu, 2001; Parolin, 2002). In *T. coronata* the difference in internode size, coupled with the drastic modification of tissue quality between leaves above and below flood levels, shows the escape of flood pressure.

In conclusion, even under high stress conditions, *T. coronata* shows physiological mechanisms allowing the species to colonize and establish in flooded environments, a characteristic not observed in its sympatric congener. These mechanisms involve a trade-off, which maximizes plant vertical growth as an escape strategy while drastically minimizing carbon allocation to chemical and biological defence. We do not know what physiological/molecular mechanism triggers hormonal growth modification (Parolin, 2012), or what environmental signal is used by the plant to change its allocation strategy. However, the suppression of domatium production preceding floods is something totally novel in ant-plant studies, demanding eco-physiological and genetic studies focusing on the mechanisms inducing production of domatia on ant-plant species.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Figure S1: two branches of *Tococa coronata* Benth. (Melastomataceae) sampled in riparian forests of the Juruena rRiver, Southern Amazon, Brazil. Table S1: parameters measured in *Tococa coronata* plants growing below or above the maximum flood level of the Juruena River, Cotriguaçú-MT.

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