



# Foraging behavior of *Atta sexdens* (Hymenoptera, Formicidae) on leaves of *Thiloo glaucocarpa* (Mart.) Eichler (Combretaceae) in a Brazilian seasonally dry tropical forest

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## Abstract

*Thiloo glaucocarpa* is a toxic plant as a food item for bovine cattle. However, dry leaves are frequently collected to cultivate the symbiotic fungi of several colonies of *Atta sexdens* throughout the Caatinga Seasonally Dry Tropical Forest biome in Brazil and such behavior is not clear. In this study, we analyzed the removal of *T. glaucocarpa* leaves for *A. sexdens* and tested the hypothesis that the preference for removal of dry leaf material over fresh leaves may be related to the decay of chemical defenses. Dried leaf discs of *T. glaucocarpa* were offered to laboratory-raised colonies of *A. sexdens*. Overall, there was a lower consumption of *T. glaucocarpa* than the previous report, but it is possible to observe a preference for mature and fresh leaves removal, contradicting initial predictions. Probably, the removal of dried leaves is a specific solution learned by natural colonies to reduce the number of secondary compounds and guarantee diet availability in a highly seasonal and food-poor environment. The preference for mature leaves is not usual and is probably the result of a higher production of secondary compounds in young leaves, which could guarantee protection for leaves against herbivory in early rains and improve the productivity of *T. glaucocarpa* at the beginning of the rainy season.

**Keywords** Herbivory · Leaf-cutting ants · Secondary compounds · Seasonally dry tropical forest · SDTF · Caatinga

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## Introduction

The Caatinga biome, the greatest Seasonally Dry Tropical Forest (SDTF) in South America (Pennington et al. 2000), with c.a. 912,000 km<sup>2</sup>, is the dominant environment in northeastern Brazil (Pennington et al. 2000; Silva et al. 2017a, b; Fernandes and Queiroz 2018). Due to its high environmental heterogeneity, especially high temperatures and high shortage and seasonality in precipitation, most plant species in Caatinga (around 70–100%, depending on the locality) are deciduous (Prado 2003), and may remain without their leaves from 7 to 10 months throughout the year (Barbosa et al. 2003).

Since many evergreen plant species in SDTF are exposed to herbivores during long periods, secondary metabolites, allelochemicals with low function in the primary metabolism of plants and which affect population biology of other species, are the mainly investment to leaves defense, while deciduous species invest more in chemical structural compounds to intensive leaf production in the wet season, and, as a tradeoff, invest less in

chemical and physical defenses against herbivory (Aerts 1995; Dirzo and Boege 2008). The strategy adopted by deciduous species results in herbivory rates up to 2.8 higher in this phenological group, when compared to rates in evergreen species (Dirzo and Boege 2008), a pattern that is also observed in the Caatinga biome (Dourado et al. 2016).

Search-and-choice strategy, regarding the plant material taken into nests, is a common foraging behavior of leaf-cutting ants (genera *Atta* and *Acromyrmex*), including *A. sexdens* (Wirth et al. 2003; Herz et al. 2008). Leaf-cutting ants are generalist herbivores in the America continent, being able to cut up to 80% of species available in the vicinity of their nests to raise symbiont fungi, which are the main food item for larvae (Wirth et al. 2003; Leal et al. 2014). Although they are social insects capable of collective decision-making, assessing the quality of a plant resource in this group of ants may arise in individuals from local information (Arenas and Roces 2016a, b). In this sense, the selection of plants by leaf-cutting ants are influenced by leaf characteristics, such as nutritional content, leaf hardness, ontogeny, quality and quantity of secondary compounds (Vasconcelos and Cherrett 1996; Wetterer et al. 2000; Meyer et al. 2006; Herz et al. 2008; Corrêa et al. 2010; Leal et al. 2014; Silva et al. 2015), as well as by innate preferences or preferences derived from previous experiences in foraging individuals (Arenas and Roces 2016a), which learn to avoid plant that are not suitable or that are toxic for fungi (Herz et al. 2008; Abril 2011; Arenas and Roces 2016a, b; Green and Kooij 2018).

As an exception, *Thiloa glaucocarpa* (Mart.) Eichler (Combretaceae), a widely distributed deciduous species of Caatinga, locally known as “vaqueta”, contains high concentration of tannins that are considered toxic for the cattle consuming large amounts of its leaves in the beginning of the rainy season, during when leaf regrowth happens in this species (Itakura et al. 1987; Oliveira 2012; Almeida et al. 2017; Helayel et al. 2017) and is a delayed greening species (Coley and Kursar 1996). Tannins are compounds resulting from the plant secondary metabolism which are ubiquitous in ligneous plants (Haslam 1988) and might have negative effects on herbivores (Nichols-Orians 1991) depending on their concentration (Hartmann 2008; Furlan et al. 2011). Despite its toxicity, leaves of *T. glaucocarpa* were among the most frequent leaf material collected by workers of *Atta sexdens* L. (Hymenoptera, Formicidae) in a Caatinga area in the state of Bahia, Brazil (Oliveira 2012; Cruz et al. 2020). However, these leaf-cutting ants carried into their nests only dry leaves and/or leaves that had been cut off in previous days, indicating that drying would be important to determine leaf selection by worker ants (MMC *pers. commun.*), probably because this process may decline the level of chemical defenses and make leaves more palatable to workers during

foraging activity (Vasconcelos and Cherrett 1996; Wetterer et al. 2000).

Therefore, in this study we tested the hypothesis that the foraging behavior in *A. sexdens* on leaves of *T. glaucocarpa* is related to the decay of chemical defenses throughout the drying period. Our premises are that if the drying of leaves is an innate strategy for this species, then laboratory-raised ants, with no prior contact to *T. glaucocarpa*, will overall adopt the same strategy and mostly collect leaves that were dried out, and this will probably happen both in mature and young leaves. Therefore, we have as an objective selecting models of foraging preferences of *A. sexdens* on *T. glaucocarpa* and determining whether this is a threshold time span for leaves to dry out before they are carried out into the nests.

## Methods

### Collection and preparation of leaves

Leaves of *Thiloa glaucocarpa* were collected on November 27th, 2017 near Contendas do Sincorá National Forest (CSNF), at the beginning of the local rainy season. The locality was chosen due to its high density of *T. glaucocarpa* near nests of leaf-cutting ants (Cruz et al. 2020). As ontogenetic changes in *T. glaucocarpa* are accompanied by visual variations in leaf color, young leaves are dark red to purple in color and mature are green, both leaves were collected. A maximum of ten leaves in each color were collected per individual, in order to increase variation within the species.

In order to preserve leaves during transportation, they were fixed by the petiole in wet cotton within plastic trays and taken to the Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia (State University of Southwestern Bahia, Brazil)—UESB, in Vitória da Conquista. In the lab, a circle cutter was used to extract 1600 discs with a fixed diameter of 1.0 cm (Garrett et al. 2016; Toledo et al. 2016) from random samples from collected leaves. The discs were placed in petri dishes, sorted out between mature purple leaves and young green leaves, and left to sun dry in a greenhouse near the experiment site, but the beginning of the experiment was carried out with discs of fresh leaves, and these ones were not left to sun dry.

### Selection of *Atta sexdens* colonies

Six colonies of leaf-cutting ants in the species *A. sexdens* were used in this experiment. The nests are part of the ant colony breeding system in the Laboratory of Myrmecology in UESB. All colonies were formed from sampling wild leaf-cutting ants swarms in Vitória da Conquista which never had previous contact with *T. glaucocarpa*. Cultivated fungi in all

nests presented similar dimensions (approximately 40% of a 750 ml plastic cup) and were all fed with leaves of *Acalypha wilkesiana* (Euphorbiaceae). All nests were composed of three plastic cups, each being by the colony separately as a foraging chamber, a fungus chamber and a discard chamber.

For the experiment, the colonies were not kept in fasting, being alternatively fed with six leaves of *Acalypha wilkesiana* per day, which is considered little when compared to the usual amount offered daily. This procedure was adopted since the rejection of *T. glaucocarpa* leaves by the colony for a period of over a week had the potential to kill the colony and compromise the study.

## Experiment design

Each leaf-cutting ants' nest was cleaned before the experiment, and the connection between the fungus chamber and the foraging chamber was isolated with cotton. In this experimental design, while the ants were confined in the fungus chamber, five young and five mature discs were placed in the forage chamber. The connection between the chambers was then opened for 30 min, during which it was recorded the number of leaf discs of each type removed by the individuals. After the 30 min period, connection to the forage chamber was closed and a new experimental replica was carried out, until this procedure was repeated five times in each nest. Each researcher observed one to three nests at most during the experiment.

To avoid olfactive trails to become a bias on ants' behavior, the experimental forage chambers were used only once in a day, meaning they were changed after each repetition in each nest. By the end of the experiment for a day, these chambers were cleaned up with detergent soap, alcohol and left to dry for 24 h. All discs discarded in the discard chamber as well as those discarded in the experimental forage chamber during observation procedure were removed and recorded. After the last repetition, the original forage chamber returned to each nest and six leaves of *Acalypha wilkesiana* were offered for each colony.

This experiment was performed for seven days. On the first day, fresh leaf discs were offered, and on the following days, the discs that were dried in the greenhouse were offered. The drying period (i.e., the amount of time that leaves were left drying) was calculated as drying hours based on the recorded moment that leaves were put in the greenhouse, thus the first offer with fresh leaves was considered as drying hour 0.

## Data analysis

The recordings of leaf removal were transformed into three dummy variables, considering the value "1" when a specific event was recorded and "0" when there was no recording of

that event. These variables followed a hierarchical order, considering the number of removed discs, as follows: (1) removal of all leaf discs; (2) removal of half plus one of the offered discs and (3) removal of at least one leaf disc during the 30 min periods of each repetition number for each leaf type.

These three variables were considered dependent variables in the analysis and each was submitted to a model selection procedure using AIC criterion, considering all models with  $AIC \leq 2.0$  as equally valid. A total of 16 models were used in these analyses, eight of these being generalized linear mixed models (GLMM) and the others eight being generalized linear models (GLM). All models adjusted to binomial family error (Table 1). For this experiment, nests were considered as random variables and the drying period (converted to hours), the type of leaf (mature  $\times$  young) and the repetitions (treated as discrete value from 1 to 5) were considered fixed variables. This model selection approach combining GLMM and GLM is unusual, but it is possible if the GLMM is fitted with Maximum Likelihood (Bates et al. 2015). Once this study aims to verify the role of colonies' idiosyncrasies in foraging behavior, comparing models with and without random variables is essential to observe this process. So, in this study we use the fixed variables (drying period, type of leaf and repetitions) and random variables (colonies) as independent variables.

**Table 1** Models compared through AIC criterion

N	Fixed variables	Random variables	Model	Number of parameters <sup>a</sup>
1	DR + LT + R	(1 Colony)	GLMM	3 + 1
2	DR + LT	(1 Colony)	GLMM	2 + 1
3	DR + R	(1 Colony)	GLMM	2 + 1
4	LT + R	(1 Colony)	GLMM	2 + 1
5	DR	(1 Colony)	GLMM	1 + 1
6	LT	(1 Colony)	GLMM	1 + 1
7	R	(1 Colony)	GLMM	1 + 1
8	–	(1 Colony)	GLMM	0 + 1
9	DR + LT + R	–	GLM	3 + 0
10	DR + LT	–	GLM	2 + 0
11	DR + R	–	GLM	2 + 0
12	LT + R	–	GLM	2 + 0
13	DR	–	GLM	1 + 0
14	LT	–	GLM	1 + 0
15	R	–	GLM	1 + 0
16 <sup>b</sup>	–	–	GLM	0 + 0

Models were tested with combinations of all variables and a null model (number 16)

DR drying hours; LT leaf type; R repetition number

<sup>a</sup>Number of fixed variables + Number of random variables

<sup>b</sup>Null model

**Fig. 1** Probability of removal of *Thiloa glaucocarpa* discs by *Atta sexdens* compared to drying time (hours) in experiments with leaf-cutting ants colonies in the Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista. Continuous lines represent the overall trend, whereas dashed lines represent variation across nests. **a** at least one disc; **b** more than half the number of discs; **c** all discs

All analyses were performed in the software R (R Core Team 2020), using a built-in custom to generate the models and order the tables for model selection. For model analysis, we used the package lme4 (Bates et al. 2015) for GLMM and the package stat for GLM.

## Results

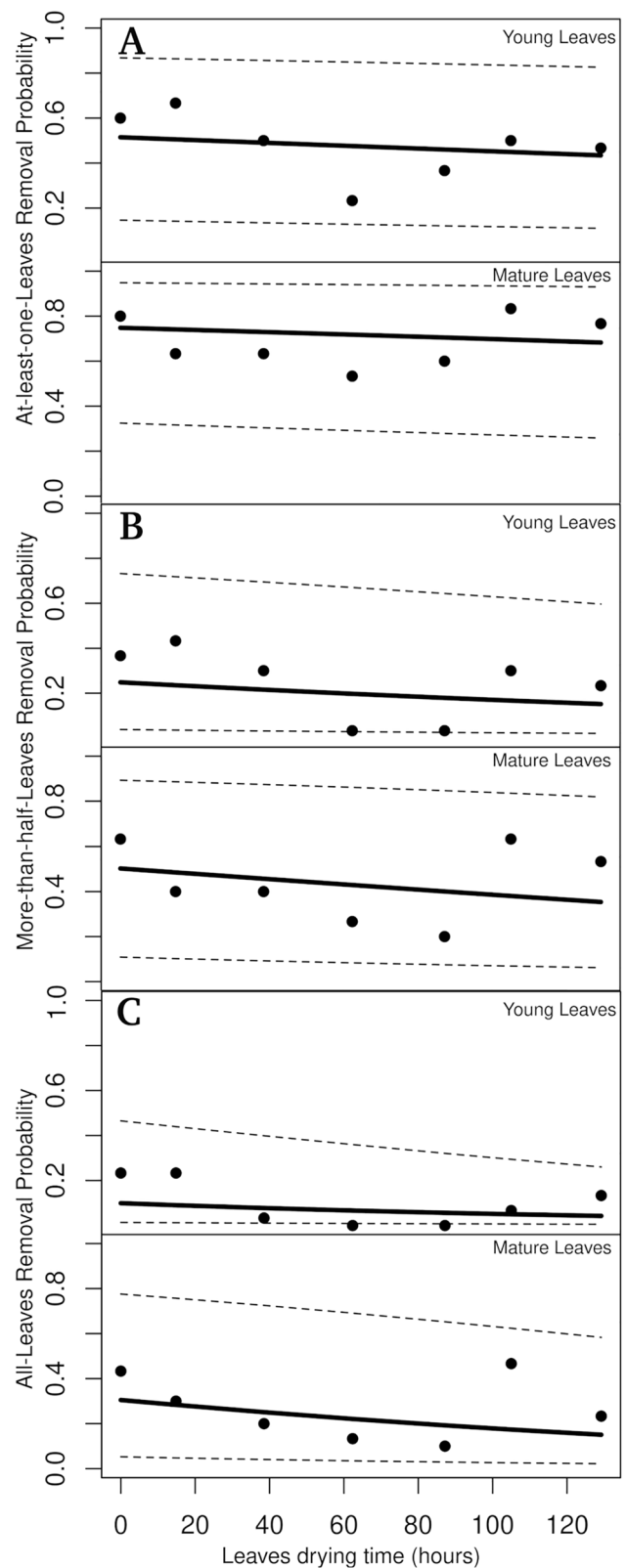
All colonies removed both mature and young leaf discs of *T. glaucocarpa*, with an average removal percentage of  $35.42 \pm 38.90\%$ . There was high variation in the removal percentage between leaf types, across different drying periods and among different nests, which was reflected in the results. Nevertheless, no case allowed us to observe a threshold to define an ideal drying time (Fig. 1).

Almost all leaves removed by leaf-cutting ants were assimilated by the fungus. Only one young leaf disc was recorded to be discarded in the trash chamber. There were records of disc removal by ants before going into the fungus chamber, but in these cases, since discs were placed back again in the foraging chamber, they were considered as not-removed leaves.

Model selection considering the removal probability of at least one disc (Table 2) supported two suitable candidate models ( $\Delta AIC < 2.0$ ): the mixed model with leaf type and repetition number, as well as the complete mixed model included drying time. For this analysis, there was large variation among colonies, but we observed a tendency of decline in leaf removal probability with an increase of drying time (Fig. 1a). Additionally, there was a higher removal probability for mature leaves than young leaves (Figs. 1a and 2a), as well as a higher removal probability in earlier than later repetitions (Fig. 2a).

Model selection considering the removal probability of more than half the number of discs (Table 3) supported the complete mixed model and other containing leaf type, repetition number and colonies as suitable candidate models ( $\Delta AIC < 2.0$ ). The tendency in consumption continued to show a higher removal probability for mature leaves, a leaf removal probability decay by drying time (Figs. 1b and 2b), as well as a higher removal probability in earlier than later repetitions (Fig. 2b).

The complete mixed model, containing the variables drying time, leaf type, repetition number and colonies, was the only suitable candidate model for the removal of all leaf



**Table 2** Model selection for the acceptance of at least one leaf disc of *Thiloa glaucocarpa* by *Atta sexdens* in experiments in leaf-cutting ants colonies from Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista

N	Models	Deviation	df	AIC	$\Delta$ AIC	wAIC
1	LT + R + (1Colony)	471.31	416	500.12	0.00	0.6077
2	DR + LT + R + (1Colony)	470.26	415	501.08	0.96	0.3760
3	LT + (1Colony)	481.66	417	508.31	8.19	0.0101
4	DR + LT + (1Colony)	480.64	416	509.30	9.18	0.0000
5	R + (1Colony)	494.52	417	520.97	20.85	0.0000
6	DR + R + (1Colony)	493.53	416	521.99	21.87	0.0000
7	(1Colony)	504.28	418	528.57	28.45	0.0000
8	DR + (1Colony)	503.31	417	529.62	29.50	0.0000
9	LT + R	543.43	417	549.43	49.31	0.0000
10	DR + LT + R	542.55	416	550.55	50.43	0.0000
11	LT	552.09	418	556.09	55.97	0.0000
12	DR + LT	551.23	417	557.23	57.11	0.0000
13	R	562.92	418	566.92	66.80	0.0000
14	DR + R	562.08	417	568.08	67.96	0.0000
15	NULL Model	571.19	419	573.19	73.07	0.0000
16	DR	570.36	418	574.36	74.24	0.0000

DR drying time (hours); LT leaf type; R repetition number; (1Colony) colony as random variable

discs (Table 4). Mature leaves also tend to be more consumed, as well as leaf removal probability decay by drying time (Figs. 1c and 2c). The higher removal probability in earlier repetitions was also observed (Fig. 2c).

## Discussion

The results confirm that *Atta sexdens* collect and feed the fungus with *Thiloa glaucocarpa* leaves. However, this leaf-cutting ants removed less leaf discs than expected, since Oliveira (2012) reported a high frequency of *T. glaucocarpa* in foraging items of *A. sexdens* throughout the year in the same area where the leaves of this study were collected, i.e., a caatinga shrubland next to Contendas do Sincorá National Forest. Several factors could have influenced this behavior, especially the fact that laboratory ants live in different conditions from those seen in natural colonies, such as regular and ad libitum feeding and lack of intraspecific competition. Another aspect is the lack of previous experience of laboratory colonies with the studied plant species. In this sense, the high consumption of *T. glaucocarpa* by *A. sexdens* reported by Oliveira (2012) in nature probably reflects a history of natural interaction between those species, in a highly seasonal environment with low resources availability and harboring several plant species with defenses against herbivory. Indeed, both species occur in high density in CSNF (Cruz et al. 2020).

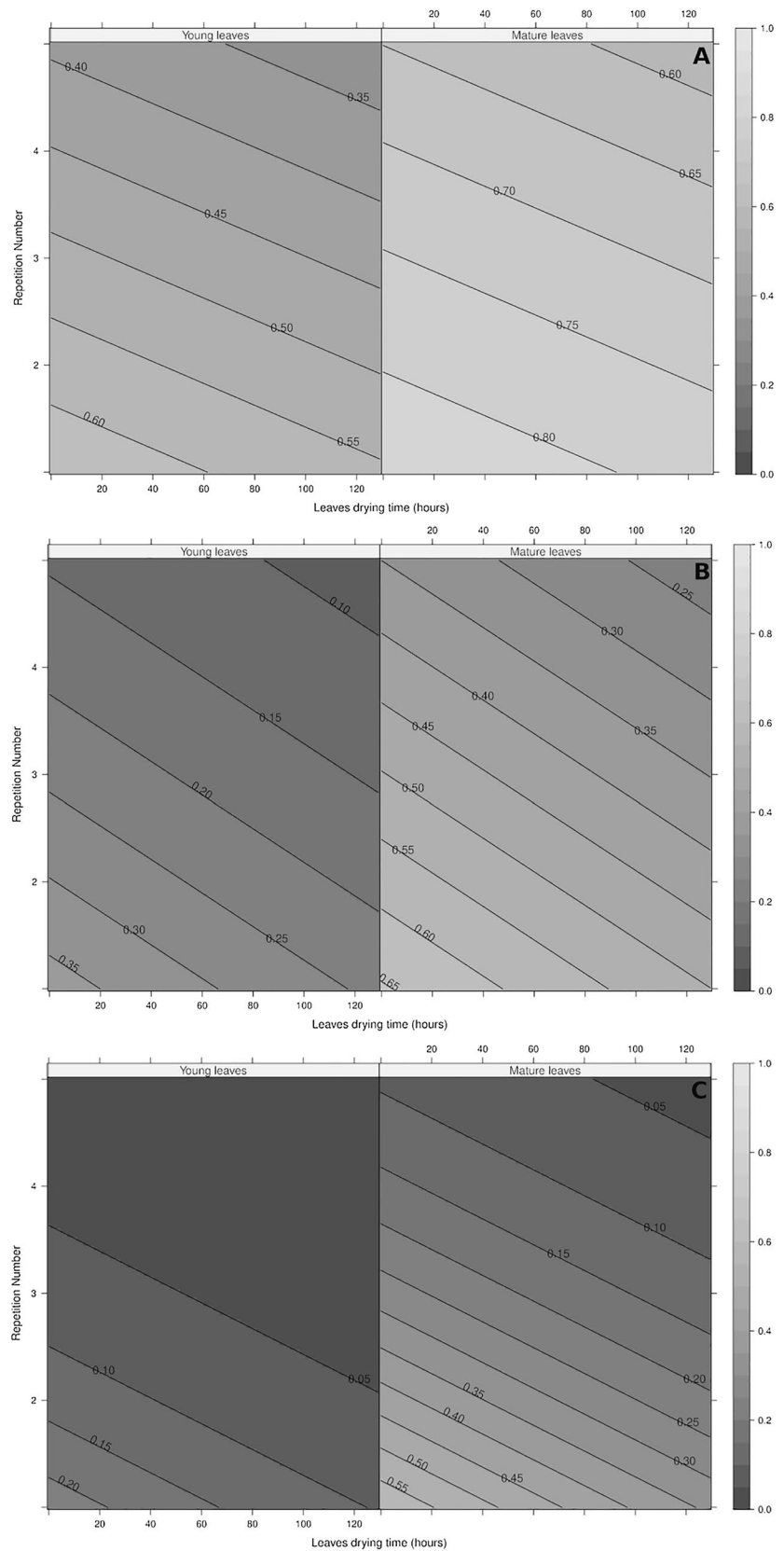
Although *A. sexdens* feed the colony's fungus with *T. glaucocarpa*, the hypothesis in this study was rejected. The drying period was among the variables found in the model selection test. However, this was the single variable absent

from the simplest concurrent models. This result suggests that, even if there is a relationship between probability of consumption and drying period, this is among the weakest statistical relations in the tested models. Moreover, the tendency we found in the analyses suggests a reduction in consumption along with an increase in drying period, an observation that disagrees with our initial working hypothesis.

In this study, the random variable colony was present in all selected models and a strong variation in response across nests was observed. This strong intraspecific variation among nests might be the reason why the overall behavior of high collecting of leaves after they were dried (as reported by MMC *pers. commun.*) was not observed (although few colonies showed this pattern—see supplementary materials figures 1–3). This strong intraspecific variation might reflect the high capacity of leaf-cutting ants, as well as other eusocial insect species, to make collective decisions based on emergence property of interactions of workers, during which the whole colony is able to solve complex problems (Bonabeau et al. 1997; Lourenço et al. 2019). However, each nest faces its own idiosyncrasies and may therefore learn to solve problems in different ways from other colonies (Bonabeau et al. 1997), the collective capacity that probably reflects the reported behavior of cutting and collecting drier leaves (Vasconcelos and Cherrett 1996; Wetterer et al. 2000). The drying process probably leads to the decay of secondary compounds, but also reduces other chemical compounds such as water, proteins and lipids (Lugo and Murphy 1986; Aerts 1997; Xuluc-Tolosa et al. 2003). Therefore, we hypothesize there must be an ideal moment between the adequate loss of secondary compounds and the maintenance of nutritional compounds, which might have interfered in the



**Fig. 2** Probability of removal of *Thiloa glaucocarpa* discs by *Atta sexdens* considering leaf types, drying hours and the number of repetitions in experiments in leaf-cutting ants nests in the Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista. Isoclines: gradient of probability role between repetition number and drying hours. Gray color spectrum: probability levels, high levels ( $x \rightarrow 1.0$ ): light gray; low levels ( $x \rightarrow 0.0$ ): dark gray. **a** at least one disc; **b** more than half the number of discs; **c** all discs



**Table 3** Model selection for the acceptance of more than half the number of leaf discs of *Thiloo glaucocarpa* by *Atta sexdens* in experiments in leaf-cutting ants nests from the Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista

N	Models	Deviation	df	AIC	$\Delta$ AIC	wAIC
1	DR + LT + R + (1 Colony)	414.94	415	446.70	0.00	0.6516
2	LT + R + (1 Colony)	418.27	416	447.97	1.27	0.3453
3	DR + LT + (1 Colony)	428.84	416	458.34	11.64	0.0019
4	LT + (1 Colony)	432.05	417	459.49	12.79	0.0011
5	DR + R + (1 Colony)	438.64	416	467.95	21.25	0.0000
6	R + (1 Colony)	441.76	417	469.02	22.32	0.0000
7	DR + (1 Colony)	451.70	417	478.78	32.08	0.0000
8	(1 Colony)	454.72	418	479.75	33.05	0.0000
9	DR + LT + R	507.31	416	515.31	68.61	0.0000
10	LT + R	509.91	417	515.91	69.21	0.0000
11	DR + LT	518.19	417	524.19	77.49	0.0000
12	LT	520.72	418	524.72	78.02	0.0000
13	DR + R	525.90	417	531.90	85.20	0.0000
14	R	528.39	418	532.39	85.69	0.0000
15	DR	536.31	418	540.31	93.61	0.0000
16	NULL model	538.73	419	540.73	94.03	0.0000

DR drying hours; LT leaf type; R repetition number; (1|Colony) Colony as random variable

**Table 4** Model selection for the acceptance of all leaf discs of *Thiloo glaucocarpa* by *Atta sexdens* in experiments in leaf-cutting ants nests from the Laboratory of Myrmecology in Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista

N	Models	Deviation	df	AIC	$\Delta$ AIC	wAIC
1	DR + LT + R + (1 Colony)	280.57	415	309.83	0.00	0.8475
2	LT + R + (1 Colony)	286.12	416	313.26	3.43	0.1525
3	DR + R + (1 Colony)	307.34	416	334.03	24.20	0.0000
4	R + (1 Colony)	312.40	417	336.98	27.15	0.0000
5	DR + LT + (1 Colony)	317.90	416	344.38	34.55	0.0000
6	LT + (1 Colony)	322.78	417	347.16	37.33	0.0000
7	DR + LT + R	345.32	416	353.32	43.49	0.0000
8	LT + R	349.78	417	355.78	45.95	0.0000
9	DR + (1 Colony)	341.59	417	365.65	55.82	0.0000
10	(1 Colony)	346.11	418	368.09	58.26	0.0000
11	DR + R	367.17	417	373.17	63.34	0.0000
12	R	371.37	418	375.37	65.54	0.0000
13	DR + LT	376.00	417	382.00	72.17	0.0000
14	LT	380.10	418	384.10	74.27	0.0000
15	DR	396.28	418	400.28	90.45	0.0000
16	NULL Model	400.18	419	402.18	92.35	0.0000

DR drying hours; LT leaf type; R repetition number; (1|Colony) Colony as random variable

results found here, since finding this ideal moment requires a long learning process. In this sense, colonies that are in frequent and lasting contact with leaves of *T. glaucocarpa*, as seen in nature, will more likely learn the cutting and drying behavior.

Young leaves of *T. glaucocarpa* were less consumed by *A. sexdens* than mature ones. This result contradicts more common literature in several aspects since levels of herbivory are expected to be higher in young than in mature leaves, once young leaves tend to have more structural compounds needed for growth and less secondary compounds, which act

as defense against herbivory (Coley 1983; Cooke et al. 1984; Coley and Kursar 1996; Dirzo and Boege 2008). Young leaves are more tender and nutritive, with higher water content and nitrogen than mature leaves, facilitating chewing and digestion by herbivores (Coley 1983; Kursar and Coley 2003), so damage from herbivores and pathogens in young leaves are higher than mature leaves (Coley 1983).

Usually, leaves of deciduous species are more consumed than evergreen species (Dirzo and Boege 2008; Silva et al. 2015; Dourado et al. 2016), once deciduous species have lower defensive leaf traits (Coley 1983; Aerts 1995; Dirzo

and Boege 2008; Leal et al. 2014). In tropical wet forests, leaf production is constant throughout the year because the majority of the species are evergreen (Aerts 1995; Dirzo and Boege 2008). In dry forest, deciduous species are up to 90% of the plant species (Barbosa et al. 2003; Dirzo and Boege 2008) and there is an almost synchronic production and development of leaves, determined by the beginning of rainy season (Givnish 2002; Silva et al. 2017a, b). This period of leaf expansion is marked by higher intensity of herbivory for all plant species (Coley 1983; Coley and Kursar 1996; Dirzo and Boege 2008; Silva et al. 2017a, b).

Here we report, for the first time, the pattern of *T. glaucocarpa* as a delayed greening species. In this sense, our results are in line with Gong et al. (2020), which report that young leaves of delayed greening species have more tannin and consequently, are less consumed by herbivores. Then, for *T. glaucocarpa*, the protection of young leaves with a high investment of secondary compounds (Oliveira 2012; Itakura et al. 1987), which sprout in narrow time windows, no more than 15 days after the earliest rains (RJSN pers. observation) and typical behavior of greening species (Gong et al. 2020), may guarantee a better strategy to reduce the intensity of herbivory during leaf expanding, the most exposed phase of leaf development, and reduce the leaf production to compensate for the loss of the first young leaves for the herbivores. Thus, the pattern found in *T. glaucocarpa* might be an adaptive mechanism for survival in the Caatinga dry biome.

The interaction between *Thiloo glaucocarpa* and *Atta sexdens* described here, reinforces the importance of further studies about herbivore-plant interaction and chemical ecology in Caatinga, in order to verify whether the results registered are specific to those species or an evolutionary pattern resulting from convergent evolution that might be present in several others plant species within Seasonally Dry Tropical Forests. For instance, Gong et al. (2020), in Asian forests registered a non-monophyletic pattern for delayed greening. In this sense, delayed greening associated with tannin may be a pattern of evolutive convergence to increase the success in avoiding leaf herbivory in dry forests.

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## Declarations

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

**Consent to participate** Consent is granted.

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