

Towards testing the “honeycomb rippling model” in cerrado

Gonçalves, CS. and Batalha, MA. *

Departamento de Botânica, Universidade Federal de São Carlos – UFSCar,
CP 676, CEP 13565-905, São Carlos, SP, Brazil

*e-mail: marcobat@uol.com.br

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(With 4 figures)

Abstract

Savannas are tropical formations in which trees and grasses coexist. According to the “honeycomb rippling model”, inter-tree competition leads to an effect of trees growing and dying due to competition, which, at fine spatial scale, would resemble honeycomb rippling. The model predicts that the taller the trees, the higher the inter-tree distances and the evenness of inter-tree distances. The model had been corroborated in arid savannas, in what appears to be caused by uneven distribution of rains, but had not yet been tested in seasonal savannas, such as the cerrado, which could be caused by the irregular occurrence of fire. A basic assumption of the model is that strong inter-tree competition affects growth (estimated by height) and mortality (estimated by inter-tree distances). As a first step towards testing this model in the cerrado, we tested this assumption in a single cerrado patch in southeastern Brazil. We placed 80 quadrats, each one with 25 m², in which we sampled all shrubs and trees. For each individual, we measured its height and the distance to its nearest neighbour – the inter-tree distance. We did not find correlations between tree height and both inter-tree distances and evenness of inter-tree distances, refuting the honeycomb rippling model. Inter-tree distances were spatially autocorrelated, but height was not. According to our results, the basic assumption of the model does not apply to seasonal savannas. If, in arid savannas, rainfall events are rare and unpredictable, in seasonal savannas, the rainy season is well-defined and rainfall is considerable. We found horizontal structuring in the community, which may be due to soil nutrient heterogeneity. The absence of vertical structuring suggests that competition for light among adult trees is not as important as competition for nutrients in the soil. We tested the basic assumption of the model in a single patch and at a single moment. To test the model effectively, we suggest this assumption to be tested in many patches over time.

Keywords: competition, honeycomb rippling model, patch-dynamics model, savanna, spatial autocorrelation.

Rumo a um teste do “modelo de favos ondulantes” em cerrado

Resumo

As savanas são formações em que os componentes herbáceo-subarbustivo e arbustivo-arbóreo coexistem. Segundo o “modelo de favos ondulantes”, a competição interárvores leva a um efeito de árvores crescendo e morrendo devido à competição, que, em pequena escala espacial, lembra favos ondulando. O modelo prevê que, quanto mais altos os arbustos e árvores, maior a equabilidade das distâncias interárvores e maiores essas distâncias. Esse modelo fora corroborado para savanas áridas, em que parece ser causado por distribuição irregular de chuvas, mas ainda não tinha sido testado em savanas estacionais, como o cerrado, em que poderia ser causado pela ocorrência irregular de fogo. Uma premissa básica do modelo é que uma forte competição interárvores afeta o crescimento (estimado pelas alturas) e a mortalidade (estimada pelas distâncias interárvores). Como primeiro passo para o teste desse modelo em cerrado, testamos essa premissa em uma mancha de cerrado no sudeste de São Paulo. Lançamos 80 parcelas de 25 m², em que amostramos todos os indivíduos arbustivos ou arbóreos. Medimos a altura de cada indivíduo e a distância entre esse indivíduo e outro indivíduo arbustivo ou arbóreo mais próximo – a distância interárvore. Não encontramos correlações das alturas dos indivíduos com as distâncias interárvores ou com a equabilidade delas, refutando o modelo dos favos ondulantes. As distâncias interárvores se mostraram autocorrelacionadas espacialmente, mas as alturas dos indivíduos não. De acordo com nossos resultados, a premissa básica do modelo não deve se aplicar às savanas estacionais. Se, nas savanas áridas, eventos de chuva são raros e imprevisíveis, nas savanas estacionais, a estação chuvosa é bem definida, previsível e comporta um volume de chuva razoável. Encontramos uma estruturação horizontal na comunidade, que pode ser devida à heterogeneidade na distribuição de nutrientes no solo. A ausência de estruturação vertical sugere que a competição por luz entre os indivíduos adultos na comunidade não é tão importante quanto a competição por nutrientes no solo. Testamos aqui a premissa básica do modelo em uma única mancha e em um único momento. Para testar efetivamente o modelo, sugerimos que essa premissa seja testada em várias manchas e ao longo do tempo.

Palavras-chave: competição, modelo de dinâmica de manchas, modelo de favos ondulantes, savana, autocorrelação espacial.

1. Introduction

Savannas present a wide physiognomic variation, in which the balance between the grassy and the woody components changes in time and space (Bourlière and Hadley, 1983). Interactions among these two components of the savanna vegetation are remarkable, extensive, and socio-economically important (Archer et al., 2000). The coexistence of grassy and woody plants in savannas has often been attributed to a rooting-niche separation, the so-called “two layer theory” (Walker et al., 1981). However, rooting-niche separation might be insufficient to warrant coexistence of grasses and trees in savannas under a range of climatic situations (Jeltsch et al., 1996).

Wiegand et al. (2006) presented an alternative theory explaining not only tree-grass coexistence, but also woody plant encroachment in arid savannas. According to this theory, at a landscape level, savannas could be patch-dynamic systems, at least arid savannas, where rainfall is often also very patchily distributed, both in time and space (Wiegand et al., 2006). Woody plant encroachment would be part of a cyclical succession between open savanna and woody dominance (Wiegand et al., 2006). This cyclical succession would be driven by two factors, rainfall and inter-tree competition (Wiegand et al., 2006).

According to Wiegand et al. (2006), if we assume that tree seedlings are all of equal size and spatially hexagonally distributed with crowns touching each other, growth and inter-tree competition will convert the tree-encroached patch to an open savanna:

- 1) if one of the seedlings has a competitive advantage over the others, this seedling is able to draw more resources than its immediate neighbours and thereby kills them and grows in size;
- 2) this gives seedlings in the second circle around the focal seedling the opportunity to access more resources and to grow more;
- 3) as long as distances from the focal seedling to the seedlings in the circle of surviving plants are not identical, some individuals in this circle have a disadvantage and will die; and
- 4) the death of these seedlings in the third row gives seedlings in the fourth row access to more water and nutrients, leading to their growth and the death of the next ring, and so on.

The level of competition among trees may be inferred by tree size and inter-tree distance: the taller and the closer two trees, the greater the competition between them (Scholes and Archer, 1997). In the postulated model, one competitively superior seedling can lead, on a fine scale, to a honeycomb-rippling effect. This “honeycomb rippling model” predicts that, due to successive thinning, the arrangement of trees will become more regular or, in other words, evenness of inter-tree distances will increase with the tree size (Figure 1) (Wiegand et al., 2006). It also predicts that inter-tree distances should increase with increasing tree size due to root competition (Figure 1) (Wiegand et al., 2006). The honeycomb rippling model assumes that trees are patchily distributed, and, in this case,

one would expect tree height and inter-tree distance to be spatially autocorrelated. In the honeycomb rippling model, one could expect a small-scale heterogeneity, with many small and more sharply discontinuous patches, reflecting hot and cold spots (Ettema and Wardle, 2002).

Wiegand et al. (2006) postulated the applicability of their theory to fire-dominated savannas, in which rainfall is higher and fire drives spatial heterogeneity, such as the Brazilian cerrado. Nevertheless, the honeycomb rippling model was developed for arid savannas, with an annual rainfall around 100-200 mm and dominated by one tree species, a very different system from the cerrado, where rainfall lies around 1500-2000 mm, tree richness is much higher, and vegetation structure is much more complex (Eiten, 1972). Hence, the applicability of the model to fire-driven savannas may be questioned. A basic assumption of the honeycomb rippling model is that a strong inter-tree competition affects growth (estimated by height) and mortality (estimated by inter-tree distances). As a first step towards testing this model in the cerrado, we tested this assumption in a single cerrado patch in southeastern Brazil. Therefore, we tried to answer the following questions:

- 1) Does evenness of inter-tree distances increase with tree size?;
- 2) Do inter-tree distances increase with increasing tree size?; and
- 3) Are height and intertree distances spatially autocorrelated?

2. Material and Methods

We carried out this study in a woodland cerrado site located in São Carlos, southeastern Brazil (21° 58' 12.7"- 21° 58' 19.0" S and 47° 52' 53.9"- 47° 52' 59.4" W), at 850 m asl, on Oxisol (Oliveira and Batalha, 2005).

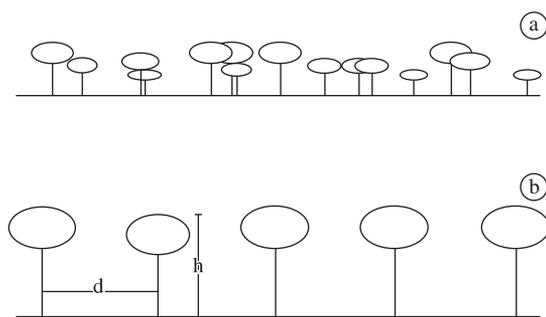


Figure 1. Two opposing situations predicted by the honeycomb rippling model (Wiegand et al., 2006). The model predicts that inter-tree distances (d) should increase with increasing tree height (h) due to root competition. It also predicts that, due to successive thinning, the arrangement of trees will become more regular, that is, evenness of inter-tree distances will increase with tree size. Therefore, in a) trees are short, inter-tree distances are low, and evenness of inter-tree distances is also low; and in b) trees are tall, inter-tree distances are high and evenness of inter-tree distances is also high.

The study site is protected from visitation, patrolled by security guards, and about 0.5 km distant from the nearest gate. Although fires there are usually anthropogenic, fires happen on average every three years, similar to natural fires (Ramos-Neto and Pivello, 2000). Shannon’s diversity is 2.6, within the range found for cerrado sites (Mantovani, 1996). The regional climate is warm temperate, with wet summers and dry winters, classified as Cwa (Köppen, 1931). The annual rainfall and mean annual temperature are approximately 1,339 mm and 22.1 °C, respectively (Oliveira and Batalha, 2005). Therefore, although small, the study site may be considered representative of disjunct cerrado sites. In this site, we placed four transects, 20 m apart one from the other (Figure 2). In each transect, we had 20 contiguous quadrats, each quadrat with 5 × 5 m (Figure 2). In each quadrat, we sampled all woody individuals, that is, all individuals with a woody stem equal to or larger than 3 cm at soil level (SMA, 1997).

We identified all individuals to the species level using an identification key based on vegetative traits (Batalha and Mantovani, 1999) or by comparing them with voucher samples (Hufscar). We used Plantminer (Carvalho et al., 2010) to search for families, authors, and synonyms concerning our species list. For each individual, we measured the height, defined as the lowest distance from the soil to the highest photosynthetic tissues (Cornelissen et al., 2003), and inter-tree distance. We assumed inter-tree distance to be the distance, at soil level, from the center of the focal individual to the center of the nearest woody individual, considering their stem radii.

For each quadrat, we calculated an average height and inter-tree distance evenness. To calculate evenness, we

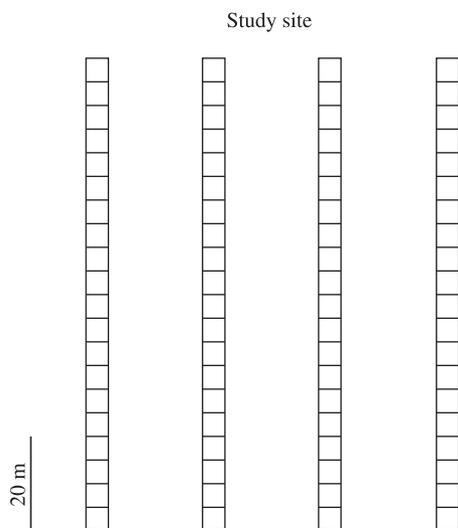


Figure 2. Sample design of the present study. We placed four transects, 20 m apart one from the other. In each transect, we placed 20 contiguous quadrats, each quadrat with 5 × 5 m.

used the coefficient of variation of the inter-tree distances. We did a correlation analysis (Zar, 1999) between these two variables to answer the first question. We also did a correlation analysis between the height and inter-tree distance to answer the second question. According to the honeycomb rippling model, we should find positive relationships in both cases. To answer the third question, we did spatial autocorrelation analyses for the average height and inter-tree distance, using data from each quadrat. We used the semivariance statistics $\gamma(h)$ for a range of distance intervals h with the Equation 1:

$$\gamma(h) = \frac{1}{2n(h)} \sum_{i=1}^{n(h)} (z(x_i + h) - z(x_i))^2 \quad (1)$$

in which $n(h)$ is the number of observation pairs separated by distance h , $z(x_i)$ is the value of either height or inter-tree distance at location x_i , and $z(x_i + h)$ is its value at a location distant h from x_i . If there is a spatial autocorrelation, one may expect the difference $(z(x_i + h) - z(x_i))$ to decrease when h decreases and that closer observations present a more similar pattern than more distant observations (Ettema and Wardle, 2002). For empirical semivariograms, subjective judgement is advisable when selecting a good model, which can be Nugget, Spherical, Exponential, or Gaussian (Bohling, 2005). We selected the Gaussian model, which fitted our data best. To calculate the semivariance statistics, we used the Gstat package (Pebesma, 2004) for R (R Development Core Team, 2008).

3. Results

We found 54 tree species and 803 individuals in the sampled quadrats. For each quadrat, we calculated the average tree height, average inter-tree distance, and inter-tree distance evenness (Table 1). The tree height was 2.57 ± 1.14 m (mean \pm sd) and inter-tree distance, 0.59 ± 0.49 m (mean \pm sd). The tree height was not correlated either with inter-tree distance evenness ($r = -0.117$, $p = 0.32$) or with inter-tree distance ($r = 0.147$, $p = 0.20$). On the one hand, inter-tree distance was spatially structured, with the range of patch size at 60 m (Figure 3); on the other hand, tree height was not spatially autocorrelated, as indicated by the very small difference between the nugget and the sill (Figure 4).

4. Discussion

The honeycomb rippling model assumes that a strong inter-tree competition affects growth (inferred by height) and mortality (inferred by inter-tree distance). Based on this assumption, Wiegand et al. (2006) postulated that (1) the arrangement of trees will become more regular, that is, evenness of inter-tree distances will increase with tree size and (2) inter-tree distances will increase with increasing tree size. We refuted these postulates, since we did not find relationships between tree height or evenness of the inter-tree distances or inter-tree distances. The honeycomb rippling model was initially postulated to explain arid savanna

Table 1. Average height (h, in meters), average inter-tree distances (d, in meters), and inter-tree distances evenness (E) in the 80 quadrats sampled in a cerrado site in southeastern Brazil (21° 58' 12.7"- 21° 58' 19.0" S and 47° 52' 53.9"- 47° 52' 59.4" W).

Quadrat	h	d	E
1	2.13	0.91	0.78
2	4.95	0.60	0.00
3	3.17	0.43	1.65
4	1.97	0.74	0.98
5	2.19	0.34	1.14
6	2.88	0.53	0.96
7	2.00	0.66	1.12
8	2.76	0.71	0.97
9	2.82	1.09	0.63
10	2.03	1.30	0.27
11	2.13	0.77	0.80
12	2.84	0.91	0.50
13	2.63	0.79	0.77
14	1.57	1.33	0.31
15	2.07	0.72	0.85
16	1.83	0.57	0.86
17	2.10	0.83	0.66
18	3.52	0.96	0.40
19	1.94	0.69	0.85
20	2.01	1.06	0.47
21	3.40	0.36	0.91
22	3.02	0.60	0.46
23	2.37	0.86	0.49
24	2.44	1.05	0.45
25	1.94	0.83	0.66
26	2.09	0.77	0.55
27	3.15	0.54	0.96
28	2.05	0.83	0.41
29	2.43	0.93	0.64
30	2.63	0.53	0.84
31	3.26	1.02	0.59
32	3.42	0.92	1.00
34	1.88	3.16	0.41
35	2.31	2.08	0.06
36	2.85	2.64	0.00
39	6.25	2.02	0.65
41	2.83	0.40	0.76
42	2.97	0.19	1.07
43	2.82	0.30	0.81
44	2.95	0.44	0.93
45	2.89	0.33	1.05
46	3.12	0.49	0.53
47	2.49	0.58	0.60
48	2.91	0.54	0.58
49	3.11	0.53	0.78
50	2.35	0.61	0.37

Table 1. Continued...

Quadrat	h	d	E
51	2.49	0.68	0.58
52	2.22	0.61	0.57
53	2.50	0.45	0.79
54	2.21	0.43	0.80
55	1.74	0.64	0.63
56	2.58	0.80	0.40
57	3.11	0.47	0.51
58	3.18	0.45	0.66
59	2.15	0.43	1.05
60	4.75	1.81	0.20
61	2.66	0.30	0.96
62	2.76	0.54	0.49
63	3.42	0.64	0.72
64	2.21	0.52	0.80
65	1.90	0.62	0.38
66	2.18	0.37	0.92
67	2.07	0.61	0.75
68	2.36	0.55	0.74
69	2.33	0.84	0.26
70	2.26	0.51	0.88
71	2.41	0.63	0.76
72	1.81	0.55	0.65
73	2.39	0.45	1.16
74	1.98	0.63	0.88
75	2.45	0.47	0.79
76	1.81	0.77	0.56
77	2.57	0.64	0.87
78	2.38	0.50	0.64
79	2.07	0.50	0.87
80	2.32	0.48	1.66

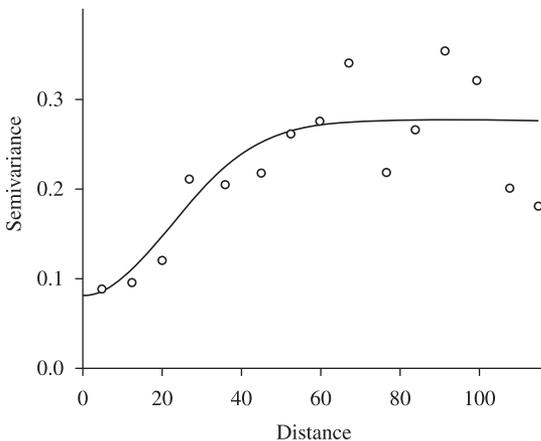


Figure 3. Gaussian semivariogram model of mean inter-tree distance in a cerrado site in southeastern Brazil (21° 58' 12.7"- 21° 58' 19.0" S and 47° 52' 53.9"- 47° 52' 59.4" W).

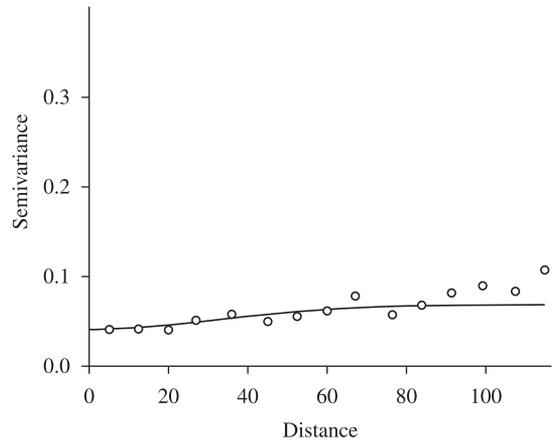


Figure 4. Gaussian semivariogram model of mean tree height in a cerrado site in southeastern Brazil (21° 58' 12.7"- 21° 58' 19.0" S and 47° 52' 53.9"- 47° 52' 59.4" W).

dynamics, in which (1) one or few woody species dominate the community and (2) rainfall is patchily distributed in time and space (Wiegand et al., 2006). The applicability of the honeycomb rippling model in seasonal savannas was suggested by Wiegand et al. (2006).

Contrary to other savannas, including the arid savannas studied by Wiegand et al. (2006), the cerrado is a species-rich savanna (Sarmiento, 1984). Consequently, different woody species could differ in resource requirement, growth rate, and potential height (Köhler et al., 2000), maybe making it difficult to interpret tree size under the honeycomb rippling model, which presumes individuals of similar age and species composition. Moreover, cerrado trees are less sensitive to rainfall distribution patterns (Gardner, 2006), they present differences in site requirements for seedlings (Sarmiento, 1984; Vetaas, 1992), and they invest more into bark thickness than in growth (Archibald and Bond, 2003; Hoffmann et al., 2003; Hoffmann and Franco, 2003). If so, the model should not be applicable to the cerrado vegetation.

In the cerrado we studied, patch size was of 60 m, that is, the study site was slightly larger than one patch. In this patch, if the honeycomb rippling model applies, one would expect the vegetation to change over the years, with increasing tree height, inter-tree distances, and inter-tree distance evenness. To test the honeycomb rippling model in the cerrado effectively, future studies should follow patches over time. One could also use a space-for-time substitution and study many patches in a given area. In this case, if the honeycomb rippling model applies, the average tree height should be negatively correlated across the patches with both inter-tree distance evenness and inter-tree distances.

Nevertheless, even if we tested only the basic assumption of the honeycomb rippling model, we may postulate, based on our results, that this model is not suitable for seasonal savannas. Plant species from arid savannas have a high sensitivity of the soil-plant system to temporal rainfall intermittency, and the area covered by vegetation, opposed to bare soil, is larger when there is intermittent precipitation than when rainfall is constant (Kletter et al., 2009). In arid savannas, intermittent rainfall is supposed to lead to levels of soil moisture that are much higher, even if only locally and for short times, than constant precipitation (Kletter et al., 2009). However if, in arid savannas, rainfall events are rare and unpredictable, in seasonal savannas, the rainy season is well-defined and rainfall is considerable, up to 2000 mm (Eiten, 1972; Gardner, 2006).

The honeycomb rippling model assumes that there is competition among seedlings. However, positive local interactions among individuals may shape community dynamics (Pueyo et al., 2008). “Nurse plants”, which can establish seedlings under their canopies due to more favourable environmental conditions, are essential for the survival and recruitment of young individuals (Meyer et al., 2008; Pueyo et al., 2008). Positive forces operating in communities have usually been neglected, in such a way that models for plant dispersal have been based

solely on competition among individuals. However, several types of facilitation have been recorded in plant communities, including savannas. For instance, trees and shrubs contribute to an uneven distribution of water and nutrients in dry savannas (Vetaas, 1992). This uneven distribution may favor some herbs when growing under canopies of trees and shrubs due to the accumulation of nutrients, the presence of nitrogen fixing bacteria, and a sub-canopy fauna (Sarmiento, 1984; Vetaas, 1992). The capture of precipitation by the trees and shrubs leads to the formation of mineral enriched microsites, where litter and herbage weight increase above the amounts found in treeless spaces of the savanna (Sarmiento, 1984).

Walker et al. (1981) postulated that the coexistence of herbaceous and woody species in savannas is possible due to rooting depth separation, the former having shallow roots and the latter deep roots. In cerrado communities, trees can access water all year long, which is highlighted by leafing and flowering at the end of the dry season (Goodland and Pollard, 1972). Seedlings of dry forest species invest a large part of their biomass in their root system, allowing them to access water in deeper soil layers and increase water conservation (Markesteyn and Poorter, 2009). Since seedlings of cerrado tree species also invest in their rooting systems to reach the water table as soon as possible (Hoffmann and Franco, 2003), the competition for water postulated by Wiegand et al. (2006) is not as intense in seasonal savannas as to result in the honeycomb rippling model.

Nutrient availability is a key factor for savanna species, especially in more humid regions (Gardner, 2006). The importance of nutrients for horizontal structuring in the studied cerrado can be inferred by the spatial autocorrelation in the inter-tree distances. Spatial patterning in plant communities can be a response to heterogeneity in the abiotic environment, such as topographic gradients or the result of local biological processes, such as competition, seed dispersal, or clonal growth (Perry et al., 2009). The spatial patterns of distribution of soil resource availability for plants play a crucial role in the structure, composition and productivity of many terrestrial communities (Rodríguez et al., 2009). The more clustered pattern in soil nutrients leads to a more clumped spatial pattern in plant distribution, with higher spatial dependence (Rodríguez et al., 2009), up to 60 m in the community we studied. Fire may cause extreme changes in the concentrations and distribution of nutrients, which become more clumped because of ash accumulation and deposition of litter around individual trees (Rodríguez et al., 2009). Moreover, the importance of the effect of trees on spatial distribution of nutrients was recorded (Rodríguez et al., 2009).

Contrary to intertree distance, tree height was not spatially structured, suggesting that competition for light among adult individuals in the community studied is not as important as competition for soil resources. This is expected, since in savannas, trees are sparsely distributed (Sarmiento, 1984; Archibald and Bond, 2003) and light interception is not limiting (Archibald and Bond, 2003). In

plants, investment in height improves access to light, and potential height is an important aspect of the ecology of a plant species (Falster and Westoby, 2003; Archibald and Bond, 2003). Nevertheless, there is greater competition for light in forests than in savannas, which should select greater investment in height growth in the former than in the latter (Archibald and Bond, 2003; Hoffmann et al., 2003; Hoffmann and Franco, 2003). Savanna trees are expected to invest more in bark thickness than in height (Jackson et al., 1999; Hoffmann and Franco, 2003), since this environment suffers with the threat of frequent fires (Hoffmann et al., 2003; Hoffmann and Franco, 2003). Savanna trees invest heavily in root biomass, enabling carbohydrate and nutrient storage, necessary for surviving frequent fire, and providing greater rooting depth, which permits access to deeper soil water during the 5-month dry season (Hoffmann and Franco, 2003).

To conclude, one of the models that attempts to predict spatial patterns of savannas is the honeycomb rippling model, which assumes that strong inter-tree competition will affect tree height and inter-tree distance (Wiegand et al., 2006). According to our results, this basic assumption does not seem to apply to seasonal savannas. However, we tested this assumption here in a single patch and at a single moment. To test the model effectively, we suggest that this assumption should be tested in many patches over time at different sites and on different scales.

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