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PLANT - SOCIAL INSECT ASSOCIATIONS IN A HYLEAN SAVANNA: A NON-SPECIFIC INTERACTION

ASOCIACIONES PLANTA-INSECTO EN UNA SABANA DE LA GUAYANA VENEZOLANA: UNA INTERACCION NO ESPECIFICA.

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ABSTRACT

Savannas in the equatorial neotropics may convert to forest, if climatic changes increasing humidity in these areas, such as global warming, take place. This succession may be accelerated by social insects. Termite nests of *Nasutitermes spp.* and those of the grass-cutting ant *Acromyrmex landolti* favor the formation and growth of plant patches through a succession of plant species, by concentrating nutrients and probably by conserving water during the dry season and diminishing the effects of flooding during the rain season. The size distribution of these patches show that large ones are not stable, probably because they are more affected by annual fires than smaller ones.

Key Words: Savannas, insect, associations, ants, termites, ant-plant, insect-plant.

RESUMEN

En climas más húmedos, tales como pueden surgir en las zonas ecuatoriales del neotrópico por un calentamiento global del planeta, las sabanas se convertirían en bosque. En este proceso los insectos sociales, eventualmente juegan un rol escencial. Nidos de termitas *Nasutitermes spp.* y de la hormiga cortadora de grama *Acromyrmex landolti* facilitan la formación de agregados vegetales, a traves de una sucesión de especies, concentrando nutrientes y probablemente reteniendo agua durante la sequia, y disminuyendo los efectos adversos de inundaciones durante la época de lluvias. La distribución de la frequencia de los tamaños de los agregados, muestra que los agregados muy grandes no son estables, posiblemente por ser afectados por el fuego en mayor grado que agregados mas pequeños.

Palabras Claves: Sabanas, insectos, asociaciones, hormiga, termita, hormiga-planta, insecto-planta.

INTRODUCTION

Stable plant-insect interactions are much more frequent than has been reported in the literature (Jolivet, 1986). As ants and termites are considered to contribute most to the biomass of all animals in neotropical ecosystems (Wilson, 1971, Brown, 1973), plant-social insect relations should be common in these ecosystems. In the Orinoco-Amazon basin, savannas are found on sandy soil, surrounded by dense forests. These savannas are thought to be unstable formations, expanding and contracting during recent geological history (Shubert, 1987), giving way to or displacing forests. The process by which these changes occur is largely unknown. This work explores the possible role of plant-insect relations in stabilizing plant patches in savanna which allow for the growth of woody plants, which may eventually lead to expansion of the forest into the savanna.

METHODS

A savanna locally called "Wuaroma-tey", located on the SE of Estado Bolívar, Distrito Piar (62° 32' W and 6° 5' N) at 470 m above see level was chosen for the study. The savanna borders the Acanan river, a tributary of the Carrao river which runs into the Caroni river. The climatic conditions of the area are characterized by strong rains during 9 months, flooding the lower parts of the savanna; and a persistent dry season, which favors annual burns of the grassland from December to February. Annual rainfall is about 2300 mm and annual mean temperatures varies from 24 to 26 °C (Huber, 1986). The savanna studied is relatively small, it occupies about 20 km^2 and is isolated from the nearest savanna by 20 km of forests and rivers. Grasses grow on gray and orange-red sandy soils (low in clay and high in quartz) but with very little draining of water due to absence of a slope and a very shallow ground water table. The grasslands at Wuaroma-tey are subjected to annual fires, initiated by the small local population of Pemon-Kamaracoto Indians which maintain a small number of cows.

Four plots (25 x 2 m) were marked in different parts of the savanna, taking care to include a representative sample of the lower grassland, subjected to annual flooding, and the upper grassland (2-3 m higher), where flooding (according to Pemon indians) does not occur. One hundred meter transects were marked next to each plot, and all plant species growing within 30 cm on both sides, were counted at every meter. In each plot, every patch of two (a shrub or tree + the grass) or more plant species was counted and characterized. A patch was defined as a conspicuous dense plant mass, where plants grew higher than the mean height of the grasses growing in the savanna. The patches were classified as small (less than 30 cm in diameter), medium (between 30 and 60 cm), large (60-90 cm) and very large (over 90 cm in diameter and up to 160 cm). Data from all patches were used to calculate the frequency of occurrence of each species among patches

RESULTS

Wuaroma-tey was dominated by the grasses *Andropogon spp.* and Cyperacae, and was subdivided in upper and lower grassland. The grassland had some scattered trees of *Poecilandra retusa* (Ochnaceae), *Mahurea extipulata* (Guttiferae), *Byrsonima verbascifolia* (Malpighiaceae) and small groups of *Byrsonima crassifloia* (Malpighiaceae) and *Euphronia guianensis* (Trigoniaceae). The most common herbs and grasses found are listed in Table 1. Both type of grasslands could be considered more or less homogeneous and differed among them in the dominant plant species.

Social insects were represented by the grass cutting ant *Acromyrmex landolti* (Formicidae) and by an unidentified mound-building species of *Nasutitermes* (Nasutitermitidae). *Acromyrmex landolti* nests were different from those described previously in the savannas north of the Orinoco (Navarro and Jaffe, 1985). Colonies surrounded their nest entrance, characterized by a typical turret made of dry grass, with wastes from the nest and excavated soil. This waste was disposed some 20 cm away from the turret in all directions, building a soil heap encircling the turret. This contrasted with the nests north of the Orinoco, where a single soil heap was placed preferentially to the SW of the turret at a mean distance of 22 cm (see Navarro and Jaffe, 1985).

Table 1. Frequency of occurrence (%) of plant species, along 100 m transects in different parts of the savanna. All patches were included.

	Sites			
	Lower Grassland		Upper Grassland	
	Plots			
Species	1	2	3	4
Thrasya trinitensis Mez	33	28	6	15
Axonopus pruinosus Henr.	8	2	47	35
Leptocoryphium lanatum (H.B.K.)Nees	20	12	17	0
Panicum savannarum Soderstrom	21	11	19	10
Andropogon leucostachyus H.B.K.	0	8	0	0
Axonopus caulescens (Mez.)Swallen	0	3	0	12
Echinolaena inflexa (Poir.)Chase	0	6	0	0
Byrsonima crassifolia (L.)H.B.K.	9	2	8	4
Rhynchospora globosa R.& S.	5	14	0	0
Lagenocarpus rigidus Nees	0	11	0	10
Fimbristylis capillaris Kunth.	0	0	0	0
Hypolytrum pulchrum (Rudge.)Pfeiff	0	0	0	15
Miconia prasina (SW.)DC.	0	2	0	0
Rhynchospora barbata (Vahl.)Kunth.	0	2	0	0
Rhynchospora rugosa (Vahl.)Gale.	0	2	0	0
Scleria cyperina Kunth.	4	0	3	0
Scleria distans Poir.	1	0	0	0
Echinoleana gracilis	1	1	1	0

There was a positive relationship between number of species and patch size (Pearson correlation coefficient = 0.903, $p < 0.001$), and therefore both type of classifications were equivalent. Small patches were composed of an average of 1.6 ± 0.7 plant species, medium sized ones by 2.7 ± 1.2, on large ones by 5.5 ± 1.8, and very large ones by 9 ± 1.4 plant species.

Plant patches were strongly associated with social insects. Over 75% of all patches had either termites or grass-cutting ants or both (Table 2). *Nasutitermes* spp, were present in the majority of the patches, whereas *A. landolti*

Table 2. Proportion of plant patches with social insect nests according to patch size and experimental site.

Proportion	Patch size: Small	Medium	Large	Very Large
% with termites	74	70	100	100
% with ants	8	39	72	100
% with ants and termites	4	23	72	100
% with ants or termites	78	86	100	100
Total number of patches	44	29	19	7

	Experimental sites: Upper Grassland			Lower Grassland		
	Plot					
	1	2	Mean	3	4	Mean
% with ants or termites	94*	100*	97*	60	86*	73*
% with termites	71*	100*	86*	60	43	52
% with *A. landolti*	47	50	49	40	57	49
Total number of patches	32	23	55	20	24	44
% of nests without a patch						
A. landolti	9	17	13	10	4	7
Termites	9	4	7	0	4	2

* indicates $p < 0.01$ if compared to a binomial distribution with a X^2 test

was present mainly in the large and very large patches. Small patches had very high proportions of termite nests. If patches were classified according to plant species number, patches with 2 plant species had no insect nest in only 29 % of the cases, patches with 3 plant species grew without insect nests in 7 % of the cases, and in 0 % of patches with more than 3 plant species, the probability of such a distribution occurring by chance is $p < 0.001$ ($X^2 = 72.9$, df = 2). Thirty percent of all termite nests and 22 % of the ant nests were found without plant patches, although in the experimental plots, chosen because of patch abundance, these percentages were lower (Table 2).

Not all plants in the savanna were found in patches. *Echinolaena gracilis* for example, a fairly common species, was never found in patches. Among the species found in patches, some were early colonizers (the first 4 listed on Table 3), appearing with high frequency in small patches, whereas others colonized only large patches which had higher species numbers (the last three listed). There was no correlation with patch size, suggesting an opportunist colonization of patches (those listed starting with *A. leucostachyus* to *L. rigidus*, Table 3).

The frequency of occurrence of plant patches of different size (Fig. 1) showed that patches with 4 or 5 species were relatively more common than expected, as the probability of such a distribution occurring by chance is $p < 0.01$ ($X^2 = 22.5$, df = 5). In the dryer savanna, the peak of patch number was 5 species per patch, whereas in the lower savanna it occurred at 4 species.

Table 3. Frequency of occurence (% of the samples) of the main plant species in patches.

Species	Patch size (No of plant species) 2	3	>3
Thrasya trinitensis	70	86	86
Axonopus pruinosus	31	50	39
Leptocoryphium lanatum	31	54	54
Panicum savannarum	39	29	75
Andropogon leucostachyus	0	19	19
Axonopus caulescens	3	21	22
Byrsonima crassifolia	11	19	25
Rhynchospora globosa	3	11	32
Lagenocarpus rigidus	6	14	15
Hypolytrum pulchrum	3	0	22
Echinolaena inflexa	0	0	22
Scleria cyperina	0	0	15

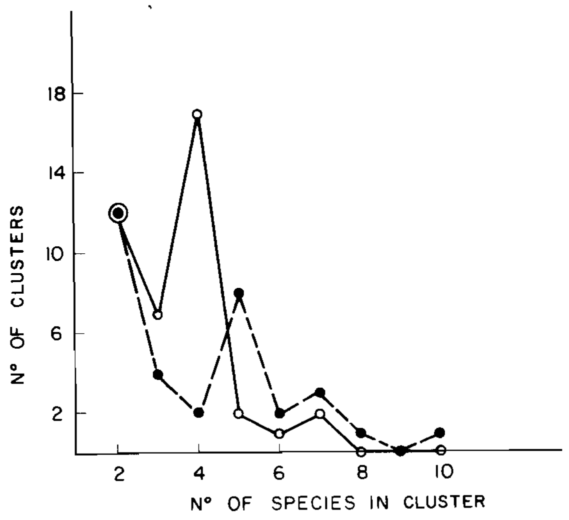

FIGURE 1. Frequency distribution of the number of species per patch (cluster). Upper and lower grasslands in discontinuous and continuous lines respectively.

DISCUSION

Ant and termite colonies were strongly associated with plant patches in the savanna. Nevertheless, it is not clear, whether plant patches attracted insect nests or whether termite and ant nests favor the establishment and growth of plant patches. Probably both phenomena occur. In dryer savannas, *Nasutitermes spp.* build their nests among grasses (San Jose et al., 1989) showing no preferences for plant patches. Although in the laboratory, *A. landolti* founding queens searched for conspicuous plant trunks or grass masses in the terrarium to initiate nest building (Navarro and Jaffe, 1985), suggesting that founding queens will prefer plant patches rather than open land to initiate new colonies.

On the other hand, the presence of either *A. landolti* nests or termite nests, should increase availability of nutrients (Lopez-Hernandez et al., 1989), favoring survival and growth of plant species. Salik et al. (1983) for example, found that soil under termitaria along the Rio Negro were up to 20 times richer in nutrients than the surrounding soils and that the high turnover of mounds at 11% per year contributed to seedling establishment in the enriched soil. Sylvester et al. (1978) also report high levels of nitrogen fixation by *Nasutitermes* species in the Amazon region. In Wuaroma-tey savanna, termites were more common than grass cutting ants, and had a greater frequency of occurrence in small plant patches compared to *A. landolti*, which in turn were more frequent in the dryer parts of the grassland.

Our results suggest that plant-insect patches in this savanna may improve the chances of survival of some of its members. This increase could be due to one or various factors: a) improved chances for seedling growth, b) increased capture of seeds, c) improved concentrations of nutrients in the soil accelerating growth of the plants or d) because communities are more resistant to extreme climatic changes than isolated species. Our results indicate the existence of succession of plant species as the patches increased in size. No species-specific plant- insect relation could be found, indicating that insect colonies work as plant patch catalysts through a non-specific interaction with plants. This type of non-specific inter-species interaction probably plays an important but unrecognized role in the modulation of selective forces during evolution (Lewin, 1985) giving ample opportunity for coevolution processes to work. Coevolution processes have always been related to specific inter- species interaction. This work shows that non specific interactions are also very efficient in creating self-generated microclimates which can increase stability of certain communities.

Among the abiotic factors possibly favoring patch formation are improved "water management". patches provide certain protection against prolonged flooding during the rain season, as the patches are elevated 10 to 20 cm from the savanna surface due to the accumulation of organic matter and excavated earth carried by termites and *A. landolti* nests (see also San Jose et al. 1989). On the other hand, during the dry season, patches may retain humidity due to increased shade and increased accumulation of organic matter, protecting the organisms against excessive drought. This seems evident after a low intensity fire, when most of the patches were not affected by the flames.

Very large patches are rare, suggesting the existence of a forces acting against large patches. We propose that large concentration of organic matter eventually sustain longer and more intense localized fires during the annual savanna burns, which increase the soil temperature to a degree that kills most of the plants. Observations in savannas in the Estado Monagas showed that woody plant species burned for 1 to over 3 days, depending on the diameter of the trunk, heating the soil directly under it; whereas open grassland burned in less than 5 min, heating only the most upper surface of the soil (unpublished observations). This may explain why in the dryer grassland, where plants are smaller and thus fires burn faster, the most common patch size is larger (Fig. 1). We suggest that under a more humid climate in a different geological era, such as that proposed under prolonged global warming (Shubert 1987) the frequency of annual burns should be reduced, increasing the chances of very large patches to survive, starting the process of forest formation in these savannas.

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