Spatial Patterns of Trees and Structuring Factors in a Trachypogon Savanna of the Orinoco Llanos[1]

J. J. San José

Centro de Ecología y Ciencias Ambientales, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela

M. R. Fariñas

Postgrado de Ecología Tropical, Facultad de Ciencias, Universidad de los Andes, Mérida 5101, Venezuela

and

Judith Rosales

Centro de Ecología y Ciencias Ambientales, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela

ABSTRACT

Tree dispersion was evaluated in a *Trachypogon* savanna by measuring the distance from individual trees to their nearest conspecific neighbor. The vegetation is a closed bush island savanna with coexistent isolated trees and small patches of semideciduous forest. The isolated trees were in clumps similar to trees growing in savannas and tropical forests. In our study, adults were less clumped compared to juveniles. Environmental and biotic differences related to edaphic heterogeneity, life history, and reproductive strategy could account for the clumped pattern. Different spatial patterns emerged for stems in groves. Thus, uniform spatial distribution was evident in the individuals of the fire resistant species (*Curatella americana, Byrsonima crassifolia* and *Bowdichia virgilioides*) and a gap filling species (*Casearia decandra*). Changes in the demographic components between different age groups provide evidence for density-dependent mortality. A hypothesis mainly based on two scales of disturbance (human impact and gap formation) acting synergetically with a large scale factor (substrate patchiness) is put forward to explain the dynamics of tree invasion and the maintenance of the *Trachypogon* savanna.

RESUMEN

La disposición espacial de los árboles fue evaluada en una sabana de *Trachypogon,* a través de la medida de la distancia de los individuos arbóreos a su co-específico más cercano. La vegetación es una sabana cerrada donde coexisten árboles aislados y bosquetes semi-deciduos. El patrón de los árboles aislados fue agrupado, tal como ha sido reportado para los árboles que crecen en las sabanas y bosques tropicales. En nuestro caso, los adultos fueron menos agrupados que los juveniles. Diferencias ambientales y bióticas relacionadas a la heterogeneidad edáfica, historia de vida y estrategia reproductiva, podrían determinar el patron agrupado. En relación a los árboles de los bosquetes, diferentes patrones espaciales fueron determinados. Así, una distribución espacial uniforme fue evidente en los individuos de especies resistentes al fuego (*Curatella americana, Byrsonima crassifolia* y *Bowdichia virgilioides*) y en una especie común en los claros de los bosquetes (*Casearia decandra*). Los cambios en los componentes demográficos entre grupos de diferentes edades, suministran evidencias de una mortalidad denso-dependiente. Una hipótesis basada en la sinergía de dos escalas de perturbación (impacto humano y formación de claros), con un factor de gran escala (heterogeneidad del sustrato) fue propuesta para explicar la dinámica de la invasión de los árboles y el mantenimiento de la sabana de *Trachypogon.*

THE ORINOCO LLANOS IS A MAJOR UNIT of homogeneous relief in northern South America. Geostructurally complex, it includes high, pene- and alluvial plains (Zink 1980), which are extensively covered by *Trachypogon* savannas. The large scale vegetation pattern of these savannas has been explained mainly by mesoclimate, geomorphology, soil characteristics, and water relations (Beard 1944, 1953).

At an intermediate scale, the *Trachypogon* savannas include a wide variety of physiognomic types ranging from herbaceous to woody vegetation, with

isolated trees in a herbaceous matrix, intermingled with patches of deciduous forest (San José *et al.* 1985). These patches, embedded in the matrix of grass cover, have stimulated research concerning the dynamics of savanna vegetation. Hypotheses explaining the origin and maintenance of savannas range from savanna being a consequence of natural environmental conditions to it being an unstable system (Sarmiento & Monasterio 1975). Evidence from permanent plots and long-term study is accumulating (Vuattoux 1970, 1976, Menaut 1977; Menaut & Cesar 1979; Coutinho 1982; Huntley 1982; Lacey *et al.* 1982; San José & Fariñas 1983). Understanding general spatial relationships is useful for establishing a context for studies emphasizing perturbation and response of the community.

Although spatial patterns of individual species have been analyzed in grassland and savannas (Goodall 1952; Kershaw 1958, 1959, 1964; Anderson 1965; Lock 1972; Morton 1974; Greig-Smith 1979), few studies measure the distance between plants (Greig-Smith 1983). Recently, biologists have been more concerned with the richness and spatial patterns of trees in tropical forests than with those in temperate forests (Forman & Caldwell Hahn 1980, Armesto *et al.* 1986). A predominance of random spatial patterns has been explained as the result of catastrophic disturbances (Armesto *et al.* 1986); whereas, clumped patterns (Poore 1968, Lang & Anderson 1971, Richard & Williamson 1975, Hubbell 1979, Forman & Caldwell Hahn 1980) have been related to canopy gap phase processes, which are considered to be the major cause of structural changes (Shultz 1960, Poore 1968, Grubb 1977, Bormann & Likens 1979, Putz & Milton 1982, Armesto *et al.* 1986, Newbery *et al.* 1986).

This work compares spatial patterns of trees in order to formulate a hypothesis about processes governing tree invasions and maintenance in a savanna. This hypothesis will be the starting point for further investigations of the causal factors.

METHODS

The spatial distribution of the trees in a *Trachypogon* savanna was assessed by locating and marking all individuals ($\geq$ 0.05 m in height) in 10 plots of 400 × 400 m² each selected at random on the 190 ha permanent grid at the Biological Station of the Plains (Calabozo, Venezuela) (8°56′N; 67°25′W). This area has been protected against fire and cattle grazing since 1960. The selected 400 × 400 m² plots lay within the total area covered by most tree populations (San José *et al.* 1978). Because some tree species spread vegetatively, it was impossible to determine whether new individuals were the result of seedling establishment or vegetative propagation. Therefore, we will refer to them as "tree stems" or "stems."

Two categories were recognized in the savanna: "isolated tree stems" and "groves." The first consists of scattered tree stems on a continuous grass stratum dominated by species of *Trachypogon* and *Axonopus*; the second involves discontinuous patches of mostly woody vegetation with more than one tree stem and a typical understory layer of herbs and shrubs, which grow within the margins of the canopy. These groves occupy an area usually 12 m in diameter, although their area sometimes reaches 1 ha or more (San José *et al.* 1978). Descriptions of this vegetation are given by Blydenstein (1962), Aristeguieta (1966), San José and Fariñas (1971), and San José *et al.* (1978).

The location of all tree stems ($\geq$ 0.05 m in height) was recorded using a theodolite. A pair of mutually perpendicular sides on each of the 4 ha plots were assigned to be the X and Y coordinates in a Cartesian system. The localization was re-evaluated by selecting tree stems at random and using two perpendicular metallic measuring tapes. The horizontal projection of canopy of each grove and each isolated stem was estimated as an ellipse. Thus, the areas occupied by isolated individuals and the groves were calculated and the density of each category was calculated after excluding the other category from the data.

In addition to these measurements, the height of each tree stem between 0.05 m and 4.0 m in height was measured with a measuring tape and taller stems were measured with a Brunton pocket transit. Life history and reproductive patterns of 500 individuals of the dominant species and of all individuals of the low density species were observed monthly during three years in the ten plots at the Biological Station. Thus, a lower boundary on the height of the reproductive plants was established and the stems separated into juveniles and adults. Comparative data were derived from studying a nearby 100 ha burned plot in the *Trachypogon* savanna.

The distance from each individual stem to its nearest conspecific neighbor was calculated from the collected data by using a computer program (DISTANCE) written in FORTRAN for this particular purpose. The calculated distances for each species were re-evaluated by measuring in the field the distance to the nearest neighboring marked indi-

vidual stem and drawn at random in the ten plots using a table of random numbers. The sample size for each species was calculated by using the iterative solution proposed by Sokal and Rohlf (1981). Comparisons between the calculated and the measured distances were not significantly different after applying the Mann-Whitney test (Sokal & Rohlf 1981). When the nearest neighbor of a particular stem was found in the adjacent plot, then the distance was measured as suggested by Clark and Evans (1954) to account for the edge effect on the test results.

The Clark and Evans Index (Clark & Evans 1954, 1979) was calculated using distances to nearest neighbor for all the trees in the population. Thus, the index was based on mean distances and densities which were unbiased estimates corresponding to population parameters (Steel & Torrey 1960, Chou 1985).

The degree to which the distribution of the measured nearest neighbor distances approaches or departs from random expectation was ascertained by using the corrected form of the Clark and Evans test (Clark & Evans 1954) as derived by Donnelly (1978) to account for both edge effects and correlations among nearest neighbor distances. The magnitude of the test bias was evaluated by Sinclair (1985). For purposes of comparison, the Clark and Evans test was applied to the data including the nearest neighbor distances in the adjacent plots. Furthermore, the frequency distribution of observed and expected distances to nearest neighbor were compared by using the nonparametric test (Sokal & Rohlf, 1981).

Spearman correlations (Conover 1980) between the densities of tree species was calculated in order to determine whether the effect of ecological factors on the patterns were the same for different species.

Twelve soil samples of the herbaceous matrix and of the groves were selected at random in each of the ten plots and analyzed as follows: pH, in distilled water (2:5) and in 1 N solution of KCl (2:5), was measured with a Radiometer pH meter; organic carbon percent was measured by the Walkley and Black method (Jackson 1958); total nitrogen (N) by the micro-Kjeldahl method (Bremmer 1965), available phosphorus (P) was extracted by the Olsen method and its concentration was determined by the vanadate-molybdate colorimetric method (Olsen & Dean 1965), exchangable cations (E. C.) were extracted with 1 N-NH$_4$Cl and their concentrations were determined by atomic absorption spectrophotometry with a Varian AA-6 Spectrophotometer.

RESULTS

SPATIAL PATTERN ANALYSIS OF PLANT POPULATIONS.—The Clark and Evans Index (R) for all individuals of the tree species growing in the *Trachypogon* savanna showed values below 0.70 (Table 1), indicating clumped patterns. When only isolated stems were considered (Table 2), clumping was equally pronounced; however, different results were shown when stems growing in the groves were analyzed (Table 3). Thus, even though clumping was the most frequent pattern (72% of the total), an uniform spatial pattern could not be rejected in 18 percent of the total number of species: the fire resistant *B. crassifolia, B. virgilioides,* and *C. americana,* and the gap filling *Casearia decandra.* The other species (9%) were randomly dispersed; these were the understory canopy shrub tree *Genipa caruto* and the resprouting *Cassia moschata.*

Comparison between the results from the corrected Clark and Evans test (Donnelly 1978), using the nearest neighbor distances measured within the plots, and the computed Clark and Evans test (Clark & Evans 1954) for the data including the nearest neighbor distances in the adjacent plots did not detect test bias in favor of regularity.

The average interstem (conspecific) distance for most species ranged from 1 to 10 m, except for three very low density species *Lonchocarpus ernestii, Bactris* sp. and *P. podocarpus* with 10, 5, and 16 stems censused, respectively, which had average interstem distance of 18.7 m. The largest distance between trees growing in the grass layer was almost two fold larger (25.8 m) than that of those censused in the groves (14.1 m). For species in both Tables 2 and 3, the values of R were higher for the censuses of the stems in groves compared to the scattered ones.

The average interindividual distance for stems in relation to the length of the canopy's largest axis of adult stems was approximately from one to two fold.

ADULT AND JUVENILE SPATIAL PATTERNS.—Calculations of R for all juveniles and adults of species growing in the *Trachypogon* savannas (Table 1) showed a significant clumped spatial pattern. For most species with both adults and juveniles, adult stems were less aggregated than the juvenile ones. Considering only isolated stems, all species were clumped; but 50 percent of the species were less clumped as adult then as juveniles. Considering stems in the groves, different trends were evident when patterns of juvenile and adult species were

TABLE 1.   Census of the total number of stems, average distance to nearest neighbor ($\bar{r}_A$) and ratio (R) of $\bar{r}_A$ to average distance to nearest neighbor expected in random distribution ($\bar{r}_E$) of each tree species in 10 plots of 400 × 400 m^2 at the Biological Reserve (Calabozo, Venezuela).

Species	Occurrence	Relative frequency	Total numbers of stems			$\bar{r}_A$			R		
			Total	Juveniles	Adults	Total	Juveniles	Adults	Total	Juveniles	Adults
Cochlospermum vitifolium (Willd.) Spreng.	IG	100	3970	3472	498	2.087	2.180	6.622	0.448 C	0.445 C	0.415 C
Byrsonima crassifolia (L.) H.B.K.	IG	100	1497	839	658	4.779	6.953	5.901	0.649 C	0.688 C	0.522 C
Bowdichia virgilioides H.B.K.	IG	100	1247	359	915	5.488	9.458	6.625	0.688 C	0.619 C	0.687 C
Curatella americana L.	IG	100	1501	705	796	4.984	6.714	7.214	0.679 C	0.611 C	0.702 C
Cordia hirta M. Johnston	IG	97	1100	1029	71	2.092	2.193	10.809	0.239 C	0.239 C	0.306 C
Casearia decandra Jacq.	IG	92	492	17	475	4.599	0.754	4.726	0.354 C	0.011 C	0.352 C
Genipa caruto H.B.K.	IG	97	454	365	89	4.337	5.407	7.208	0.333 C	0.354 C	0.232 C
Connarus venezuelensis Braill	IG	27	129	54	75	4.137	6.669	4.695	0.170 C	0.169 C	0.136 C
Guettarda elliptica SW.	IG	40	147	8	139	4.055	5.593	4.049	0.178 C	0.050 C	0.162 C
Cassia moschata H.B.K.	IG	87	117	18	99	8.850	12.886	8.644	0.296 C	0.199 C	0.284 C
Godmania macrocarpa Hemsley	IG	65	133	59	74	6.185	7.657	8.191	0.247 C	0.200 C	0.226 C
Annona jahnii Saford	G	52	98	28	70	9.696	11.632	11.268	0.367 C	0.208 C	0.319 C
Platymiscium pinnatum (Jacq.) Dugan	G	52	39	17	22	8.253	1.988	18.900	0.196 C	0.028 C	0.293 C
Copaifera officinalis H.B.K.	G	25	43	6	37	3.025	4.903	3.476	0.069 C	0.044 C	0.070 C
Lonchocarpus ernestii H.B.K.	G	5	10	6	10	14.178	—	14.178	0.155 C	—	0.155 C
Fagara caribea (Lam) K. & Urb.	G	22	9	0	9	3.407	—	3.407	0.037 C	—	0.037 C
Xylosma pallidifolium Sleumer	G	2	18	0	18	3.347	—	3.347	0.047 C	—	0.047 C
Lueha candida (D.C.) Mont.	G	7	6	0	6	2.350	—	2.350	0.021 C	—	0.021 C
Bactris sp.	G	12	5	0	5	26.088	—	26.088	0.165 C	—	0.165 C
Pterocarpus podocarpus Blake	G	20	16	0	16	15.888	—	15.888	0.225 C	—	0.225 C
Bauhinia benthamiana Tanb.	G	2	6	0	6	1.182	—	1.182	0.011 C	—	0.011 C
Ouratea guildingui (Planch.) Ur.	G	2	2	0	2	1.705	—	1.705	0.008 C	—	0.008 C

IG = Species which grow in groves and isolated individuals.
G = Species which grow as isolated individuals.
C = Clumped spatial distribution.
R = Random spatial distribution.

TABLE 2. Census of the number of isolated stems, average distance to nearest neighbor ($\bar{r}_A$) and ratio (R) of $\bar{r}_A$ to average to nearest neighbor expected in random distribution ($\bar{r}_E$) of each species in 10 plots of 400 × 400 m² each one at the Biological Reserve (Calabozo, Venezuela).

Species	Number of isolates stems			$\bar{r}_A$			R		
	Total	Juveniles	Adults	Total	Juveniles	Adults	Total	Juveniles	Adults
Cochlospermum vitifolium (Will.) Spreng.	2171	2137	34	2.818	2.870	23.629	0.473 C	0.476 C	0.496 C
Byrsonima crassifolia (L) H.B.K.	622	500	122	8.457	9.574	14.714	0.771 C	0.766 C	0.518 C
Bowdichia virgilioides H.B.K.	896	267	629	6.466	11.707	7.836	0.701 C	0.687 C	0.704 C
Curatella americana L.	868	549	319	6.772	7.623	11.927	0.736 C	0.640 C	0.762 C
Cordia hirta M. Johnston	43	41	2	8.416	8.990	3.280	0.199 C	0.205 C	0.016 C
Casearia decandra Jacq.	22	0	22	25.558	—	25.558	0.428 C	—	0.428 C
Genipa caruto H.B.K.	35	33	2	8.995	10.888	17.965	0.197 C	0.218 C	0.088 C
Connarus venezuelensis Baill	2	2	0	1.045	1.045	—	0.005 C	0.005 C	—
Guettarda elliptica SW.	2	0	2	2.830	—	2.830	0.014 C	—	0.014 C
Cassia moschata H.B.K.	24	18	6	10.108	12.866	10.922	0.181 C	0.199 C	0.098 C
Godmania macrocarpa Hemsley	31	19	12	17.382	14.981	27.823	0.365 C	0.232 C	0.352 C

compared. The proportion of species with clumped, random, and uniform spatial patterns for the juvenile stage were 61, 7, and 30 percent, respectively, vs 46, 7, and 46 percent for the adult stage. Thus, the proportion of the patterns changed with the maturity stage. Data from the groves indicated that the species *Guettarda elliptica, Godmania macrocarpa, A. jahnii,* and *Copaifera officinalis* presented clumped juveniles and less clumped adults. The juveniles of the species *Cochlospermum vitifolium, B. crassifolia* and *C. americana* presented the same patterns as the adults, but in this case, both were uniform. Differences between juvenile and adult dispersion pattern occurred in the rest of the species censused in the groves. Thus, *Cordia hirta* and *Casearia decandra* were clumped in the juvenile stage and uniform in the adult one; by contrast, *G. caruto* has uniform juveniles and clumped adults. Only juveniles of *B. virgilioides* were random and the adults presented uniform dispersion pattern.

PATTERN INTENSITY.—Values of R for each species were compared among the ten plots using the F test as proposed by Clark and Evans (1954). The test was not significant for the total number of stems counted for each species in the herbaceous layer and in the groves. An exception to this trend was found for adults of *C. vitifolium*, growing in the herbaceous layer. Thus, isotropy patterns were apparent over the Biological Reserve, since a directional effect in the patterns was not evident.

COMPARISONS OF THE SOIL NUTRIENT CONTENT BETWEEN THE HERBACEOUS LAYER AND THE PATCHES OF FOREST.—Soil fertility of the stands is presented in polygonal graphs (Fig. 1) using a modification of the system proposed by Alvim and Rosand (1974). The area of these graphs is directly proportional to soil fertility. The hexagonal formats indicate that the soil in the herbaceous layer was more acid and lower in exchangeable cations (1.46 vs 1.95 meq/100 g soil) compared to those of the groves. Both soils studied can be considered highly infertile, with the herbaceous layer being more so than that in groves.

DISCUSSION

The dominant spatial pattern for the tree populations of the *Trachypogon* savanna was clumped as has been reported for other savannas (Greig-Smith 1983). Understanding this pattern as it relates to ecological factors could contribute to forming hypotheses on the causes of this pattern as well as on

TABLE 3. Census of the number of stems in groves, average distance to nearest neighbor ($\bar{r}_A$) and ratio (R) (Clark and Evans index) (R) of $\bar{r}_A$ to average distance to nearest neighbor expected in random distribution ($\bar{r}_E$) in 10 plots of 400 × 400 m² each one at the Biological Reserve (Calabozo, Venezuela).

Species	Number of stems in groves			$\bar{r}_A$			R		
	Total	Juveniles	Adults	Total	Juveniles	Adults	Total	Juveniles	Adults
Cochlospermum vitifolium (Will.) Spreng.	1799	1335	464	1.774	3.976	6.381	0.937 C	1.135 U	1.177 U
Byrsonima crassifolia (L.) H.B.K.	875	339	536	3.897	7.614	5.419	1.477 U	1.747 U	1.561 U
Bowdichia virgilioides H.B.K.	378	92	268	6.191	8.261	8.350	1.585 U	0.986 R	1.757 U
Curatella americana L.	633	156	477	4.969	10.912	6.967	1.620 U	1.696 U	1.893 U
Cordia birta M. Johnston	1057	988	69	2.014	2.106	14.074	0.828 C	0.824 C	1.455 U
Casearia decandra Jacq.	470	17	453	4.088	0.754	4.196	1.116 U	0.039 C	1.111 U
Genipa caruto H.B.K.	419	332	87	4.083	5.102	7.505	1.095 R	1.157 U	0.871 C
Connarus venezuelensis Braill	127	52	75	4.179	6.917	4.695	0.627 C	0.620 C	0.506 C
Guettarda elliptica SW.	145	8	137	4.277	5.593	4.314	0.680 C	0.197 C	0.628 C
Cassia moschata H.B.K.	93	0	93	8.094	—	8.094	0.971 R	—	0.971 C
Godmania macrocarpa Hemsley	102	40	62	5.261	5.238	7.926	0.694 C	0.412 C	0.777 C
Annona jahnii Saford	98	28	70	8.192	4.563	9.930	0.967 C	0.171 C	0.940 C
Platymiscium pinnatum (Jacq.) Dugan	39	17	22	8.221	1.998	18.900	0.691 C	0.103 C	1.102 R
Copaifera officinalis H.B.K.	43	6	37	3.025	4.903	3.476	0.251 C	0.149 C	0.263 C
Lonchocarpus ernestii Harms.	10	0	10	14.178	—	14.178	0.560 C	—	0.560 C
Fagara caribea (Lam) K. & Urb.	9	0	9	3.407	—	3.407	0.127 C	—	0.127 C
Xylosma pallidifolium Sleumer	18	0	18	3.347	—	3.347	0.041 C	—	0.041 C
Lueba candida (D.C.) Mont.	6	0	6	2.350	—	2.350	0.071 C	—	0.071 C
Bactris sp.	5	0	5	26.088	—	26.088	0.719 C	—	0.719 C
Pterocarpus podocarpus Blake	16	0	16	15.888	—	15.888	0.791 C	—	0.791 C
Bauhinia benthamiana Tanb.	6	0	6	1.182	—	1.182	0.036 C	—	0.036 C
Ouratea guildingui (Planch.) Urb.	2	0	2	1.705	—	1.705	0.031 C	—	0.031 C

C = Clumped spatial distribution.
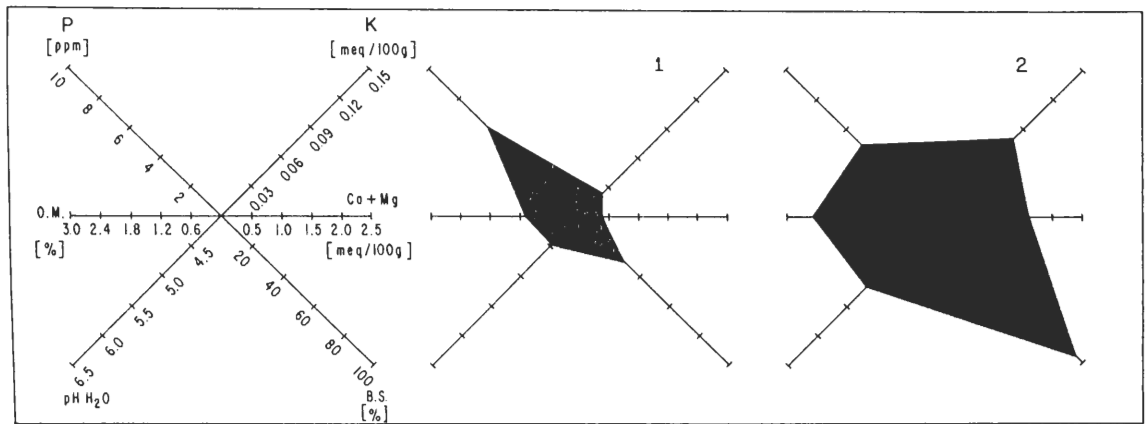R = Random spatial distribution.
U = Uniform spatial distribution.

FIGURE 1. Polynomial graphs of soil fertility in a *Trachypogon* savanna of the Orinoco Llanos, Venezuela. 1 = soil from the herbaceous layer and 2 = soil from the groves.

the dynamics of tree invasion and maintenance of these savannas. Among these factors, physical and chemical heterogeneity of soil seems to determine the spatial configuration of "soil suitable sites" for causing seedlings to grow in a clumping fashion. Thus, the superficial indurated ironstone layer in *Trachypogon* savannas limits tree colonization (San José & Fariñas 1983). Furthermore, even though the soil of the *Trachypogon* savanna is highly infertile, the relatively higher nutrient content in the soil of the groves could be differentially perceived by highly responsive species.

Seed dispersion seems to play a minor role in determining clumping, because our observations showed that these species were widely dispersed by animals and wind.

Nurse trees seem to favor seedling establishment in this savanna. Tree shade in groves is apparently harmful to the grass layer, which is replaced by a herbaceous layer. Positive associations between tree species indicated that abundant species increase the abundance of other species and impose their clumped patterns; for instance *G. elliptica,* a clumped species, was associated with species exclusively exhibiting clumped patterns (*C. officinalis, Luhea candida,* and *Lonchocarpus ernestii*). Furthermore, findings could also be related to recent past history as the result of the presence of species which compose the groves. It is possible for individual species to alter soil conditions and the enriched microsites beneath the trees may provide nuclei for the invasion of savannas (Kellman 1979). Enhancement of soil conditions by termites and its influence on tree invasion has been documented for savanna vegetation (Egler & Haridasan 1978). Based on the species in the savannas, the species *C. americana, B. crassifolia,* and

B. virgilioides were most likely to initiate grove formation under the described conditions.

The aggregated spatial pattern of the species growing as isolated stems could be also related to their capability for vegetative regrowth, which is stimulated by the physical injury of the root systems such as was observed in the burned individuals occurring in the adjacent plot to the Biological Station. Thus, the reproductive strategy in *C. officinalis* and *A. jahnii* could be responsible for the clumping fashion of the isolated and grove trees and *a fortiori* of the pattern in juveniles and adults. The growth of stems found around the site of the "mother plant" has often been held responsible for overdispersion (Goodall 1952).

There was a tendency for species found both in groves and as isolated individuals to have a higher percentage of adults in the groves as opposed to isolated stems. Also, the individuals which were found only in groves usually did not present juveniles. These results indicated a relative homoeostasis in the groves where seed and seedling predation or extinction may be higher than beneath the isolated trees, and/or reproduction decreased.

Small disturbance in the groves due to gap formation caused by falling of a tree or trees could reinforce the savanna resource patchiness as a transient environment. This process seems to lead to a predominantly clumping spatial pattern as detected in the censused plots for *C. officinalis* and *C. moschata*. In tropical forest, patchy seed deposition, seedling emergence of pioneer and primary species, combined with gap formation, have been regarded as determinants of clumped populations (Brokaw 1986).

Even though clumping was the dominant spa-

tial pattern of tree species growing in the groves, the proportion of species with uniform spatial distribution was higher than the number of species with random distribution. Clumping has been reported as the common pattern for tree species in tropical and subtropical forest; whereas, uniform patterns are considered rare (Sakai & Oden 1983). Thus, Armesto *et al.* (1986) found the proportion of clumping ranged from 75 to 100 percent in tropical and subtropical forests with similar climatic and topographic conditions. In these forests the proportion of species with random spatial distributions was as high as 24 percent, and only one out of 96 species surveyed in Guanacaste (Costa Rica) had a uniform pattern.

Special attention has to be given to the fact that the spatial pattern of the tree species *C. americana, B. crassifolia,* and *B. virgilioides* which grow in the herbaceous layer of the burned savannas, was uniform in the groves. These fire tolerant species are evergreen and may take advantage of morphological and physiological adaptations to maintain a positive CO_2 metabolism during stressful savanna conditions (San José 1977). Observations in the burnt plot adjacent to the Biological Station indicates that a net sequential dispersion of trees occurs from the grass layer to the grove edges and that they persist at the edge as seeds, seedlings, and saplings until their growth is activated after fire sensitive species are removed and competition is reduced. Thus, grove edges are maintained at the outer edge of canopy trees forming an ecotonal belt (Blydenstein 1962, San José *et al.* 1978) and resulting in a canopy dripline edge as defined by Ranney *et al.* (1981). Uniform spatial distribution of trees could have an effect in the transfer of mass and energy between the adjacent systems since turbulence should be relatively lower (San José & Berrade 1983); therefore, the nutrient and sediment retention is enhanced (Cáceres 1983, Montes & San José 1989). Furthermore, the clumped spatial distribution as determined by using the groves as independent units of the species composition could also play an important role in the development of a new boundary layer.

Intraspecific competition and mortality in the limited surface of the ecotone seems to occur as evidenced by comparing the mean density of the newly established plants with that of plants in the interior of the groves. These results seems to indicate that the uniform pattern of the aforementioned species was associated with a density-dependent factor. Comparisons of the patterns between juvenile and adult stems seem to reinforce that regular spatial distribution of these species was apparently due to an intraspecific competition resulting in mortality of small individuals. Similar shifts between different age groups have been detected in dynamic studies of plant populations (Antonovics & Levin 1980). Slatkin and Anderson (1984) proposed a model of competition for space, implicating self-thinning of even aged trees and the generation of overdispersed spatial patterns following growth of a population with an initially underdispersed spatial distribution. The self-thinning rule for plants (Yoda *et al.* 1963) has been documented for populations growing together (Harper 1977). Another explanation about the uniform spatial distribution of the fire tolerant species growing in the groves could be based on predation. Thus, Janzen (1970) and Wilson and Janzen (1972) hypothesized that a number of specific predators of species could cause high seedling mortality close to the parent trees. We found that density of stems of fire tolerant species measured from juvenile to adult age and average intertree distance was lower in adult trees as compared to juvenile stems. Further evidence of the effect of competition and predation on the spatial distribution of the populations needs documentation for the *Trachypogon* savannas, where interadult distance between the groves was relatively short.

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