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SPATIAL DISTRIBUTION AND ESTIMATION OF FOREST FLOOR COMPONENTS IN A 37-YEAR-OLD *CASUARINA EQUISETIFOLIA* (FORST.) PLANTATION IN COASTAL SENEGAL

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Summary—Forest floor spatial variability was studied in a coastal *Casuarina equisetifolia* plantation in Senegal. Systematic sampling was monitored along a 300 m transect perpendicular to the shore. The forest floor was divided into litter components (leaves, catkins, cones and twigs), fecal pellets and undetermined material. Total accumulation was 106 t ha^{-1}; litter components accounted for 50%; accumulation of fecal pellets averaged 15 t ha^{-1}. Components were not related to the local tree stand. The spatial pattern of each component was investigated by three complementary statistical methods operating at different scales, including spatial autocorrelations and geostatistics. Twigs and leaves were randomly distributed. The fecal pellet semivariogram was characterized by a high nugget effect and a large range of spatial dependence. Cones and catkins exhibited more complicated patterns with a large-scale trend and periodical structures. These results show that forest floor components exhibit particular spatial patterns, probably in relation to their production and decomposition specificity.

INTRODUCTION

Annual litterfall and standing crop must be measured to understand soil dynamics and nutrient cycling in forest ecosystems. Litter accumulation is known to show high spatial variability, resulting from both litterfall and litter decomposition variations (Olson, 1963). Litterfall and accumulation have been measured in numerous temperate and tropical forests (Vogt *et al.*, 1986). Spatial variability was generally estimated by coefficient of variation calculated from more or less random samples. Little or no attention has been paid to spatial structures defined as the multiple spatial scales of heterogeneity (Legay and Debouzie, 1985). In most studies spatial pattern is restricted to departure from random distribution (Taylor, 1984) and is classified as aggregative, random or regular. Such a reduction brings few ecological insights on population structure since more than 90% of the spatial distributions are viewed as contagious (Legay and Debouzie, 1985). Spatial patterns are, thus, more complicated with generally several imbricated scales (Hengeveld, 1987; Thioulouse, 1987).

Systematic sampling provides better estimates of spatial structure while maximizing the area covered that do other designs (Chessel, 1978; Williams *et al.*, 1992). Statistical methods necessary to understand spatial distributions must incorporate the spatial locations of samples (Legendre and Fortin, 1989). Such methods have been used in numerous fields of geology (Matheron, 1965; Journel and Huijbregts, 1978) and biology [agronomy—Ruelle *et al.* (1986); pedology—Burrough (1983) and Webster and Burgess (1984); phytopathology—Chellemi *et al.* (1988); animal ecology—Thioulouse *et al.* (1985) and Williams *et al.* (1992)]. To our knowledge, no attempt has been made to apply these methods to forest floor variability. Regular systematic sampling has been monitored (McFee and Stone, 1965; Arp and Krause, 1984), but results were analyzed without reference to geostatistic methods.

Our general goal is to test, by means of spatial analysis techniques, whether or not components of the forest floor exhibit different spatial patterns related to forest stand pattern. Data were obtained from a systematic sampling of litter along a transect in a 37-year-old *Casuarina equisetifolia* (Forst.) plantation in Senegal. Forest floor was separated into six components and the spatial pattern was described for each component and for total forest floor accumulation. The present paper is concerned only with forest floor accumulation; results for litterfall will be presented later.

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MATERIALS AND METHODS

Study site

Casuarina plantations on the Sengalese littoral began in 1948 and continue to the present for stabilization of coastal sand dunes (Maheut and Dommergues, 1959; Andeke-Lengui and Dommergues, 1983). Nowadays the plantations occupy 9700 ha along the coast between Dakar and St-Louis (180 km).

The study site was located near lake Retba (14°52 N., 17°12 W.), 20 km north of Dakar. The climate is sahelo-soudanean. In Dakar, the mean annual temperature is 24°C (min. 19°C in January, max. 29°C in October). The mean annual rainfall, calculated over the 1961–1985 period, is 411 mm with a rainy season from mid-July to mid-October.

The plantation studied was established in 1955, being 37 years old at the time of sampling (1992). Trees were planted at nodes of a square grid (spacing 2.5 × 2.5 m) with rows perpendicular to the sea shore; the first trees are 120 m from the sea. The plantation formed a 300 m wide band and was 1·km long. The density at planting time was 1600 trees ha^{-1}, but was only 927 ha^{-1} (58% of initial density) in the sampling site in 1992. The mean basal area was 193 cm^2 $tree^{-1}$ (SEM = 35) and the mean height 16.9 m (Mailly and Margolis, 1992). The plantation is a pure *Casuarina* stand with negligible understory vegetation.

Soil description

The dunes were constituted of coarse sand. After 37 years, organic matter under *Casuarina* stands formed a 20 cm thick layer and has been estimated at 120 t ha^{-1} by Mailly and Margolis (1992). A very straight boundary separated organic layers from the sandy substratum.

Litter contained only *Casuarina* remains: leaves (photosynthetic branchlets), male catkins, female cones and twigs. The superficial layer (L) was light-brown recently fallen litter. The F layer was dark and showed important fungal and faunal activities. Cones and twigs were still present in the underlying humus (H) layer, mixed with fine organic matter. In this H layer the accumulation of large amounts of Coleoptera fecal pellets, approximately 1 × 2 mm, was a surprising and characteristic feature.

The pH of the humus was about 5.4–5.7.

Sampling methods

Sampling was done during the dry season in March 1992. A 300 m transect was defined across the plantation perpendicular to the sea shore, along the middle line between two rows. A systematic sample is composed of 120 points, regularly spaced 2.5 m apart. A 10 cm dia core (S = 78.5 cm^2) was taken at each point, the center of each 2.5 × 2.5 m square delimited by 4 neighboring trees (or disappeared tree locations).

Sand was discarded by sieving through a 0.5 mm mesh. Remaining material was sieved through 4–2–1 mm meshes. In each fraction leaves, catkins, cones and twigs were hand sorted and accounted as litter components. So in our study litter components included cone and twig debris found in the L, F and H layers. Fecal pellets were separated from the 1–2 mm fraction by blowing out vegetal remains with a gentle air flow followed by a final hand-sorting. Remaining material, mostly of 1–0.5 mm size, contained amorphous organic matter and some fine vegetal debris; it was reported as undetermined. Leaves, catkins, cones and twigs formed the litter fraction, fecal pellets and undetermined the humus fraction. Each component was oven-dried at 75°C to constant weight before weighing. Results were expressed as g dry matter m^{-2}.

To relate the observed variability pattern of the forest floor components to the forest stand, a living tree index (Arp and Krause, 1984) was determined at each sampling point as the total stem basal area of the surrounding trees (from 0 to 4 trees).

Statistical methods

Pattern was researched by three complementary methods: a non-parametric test to detect different spatial scales, a rank correlation coefficient to find global trends and geostatistics to study the pattern at a finer scale.

The spatial autocorrelation matrix SAM (Chessel, 1981), derived from Geary's index of autocorrelation (Geary, 1954), was used to test the correlation between the values recorded at two adjacent locations on the transect. Core data were progressively grouped to form blocks of increasing size, the principle being to compare the variability (H_v) between two contiguous blocks and the total variability (H_t) in the transect.

Let N_b be the number of blocks and V the matrix of the contiguity relationship between the blocks. $V_{ij} = 1$ if blocks i and j are neighbors, $V_{ij} = 0$ otherwise; x_i and x_j are the values measured inside blocks i and j. $L_i = \Sigma_j V_{ij}$ and $A(V) = \Sigma_i L_i$:

$$H_t = \left[\sum_{i,j} (x_i - x_j)^2 \right] \Big/ [N_b(N_b - 1)]$$

and

$$H_v = \left[\sum_{i,j} V_{ij}(x_i - x_j)^2 \right] \Big/ A(V).$$

Let $Z = H_t/H_v$. The SAM is defined, for each size of block, by

$$Z^* = [E(Z) - Z]/\sqrt{\mathrm{Var}(Z)}.$$

Formulas for $E(Z)$ and $\mathrm{Var}(Z)$ are given in Chessel (1981) and Thioulouse (1987). Z^* approximately follows a Gaussian law for $N_b > 10$. If significant autocorrelation exists, i.e. the value measured inside two adjacent blocks are more closely related than values measured on two blocks selected at random, the observed value of Z decreases and $Z^* > 1.96$ (threshold with a 5% error risk).

Table 1. Statistical parameters of forest floor components in a 37-year-old *C. equisetifolia* plantation in Senegal

	Mean	SD	CV	Range
Leaves	1327	535	40.3	288–3667
Catkins	194	161	83.0	1–765
Cones	2207	1764	79.9	0–8769
Twigs	770	415	53.8	81–2134
Fecal pellets	1523	1069	70.2	0–5785
Undetermined	4594	2270	49.4	345–13948
Total	10616	3935	37.0	2073–25073

Mean, standard deviation (SD) and range in g m^{-2}, coefficient of variation (CV) in %.

Spatial trends in the transect were searched for according to distance from the shore. Spearman correlation coefficients were computed for each component of forest floor.

Lastly, we used the semivariance statistic, gamma(h) which is the half-mean of squared differences between all possible data pairs for each distance interval h in a sample (Matheron, 1965; Journel and Huijbregts, 1978). An experimental semivariogram is a plot of the sample semi-variance of pair differences vs h; generally it is limited to $h = N/2$ with N = total number of data in the transect (here $N = 120$). Considering the shape of the experimental semivariograms, a spherical model was fitted by a non-linear least-squares iterative method (Marquardt procedure, SAS package):

$$X = C_0 + C_1*(1.5*d/\text{RSD} - 0.5*(d/\text{RSD})^3)$$
$$\text{for } d < \text{RSD}$$

$$X = C_0 + C_1 \qquad \text{for } d \geqslant \text{RSD},$$

where X and d correspond to the semivariance and to the distance between two points. C_0 represents the "nugget" effect (Matheron, 1965) or, in ecological terms, the true aggregation variance (Debouzie and Thioulouse, 1986); $C_0 + C_1$ is the sill and RSD the range of spatial dependence. At the sill the semivariance no longer increases, it becomes random. To compare the semivariograms for each component, we divided the semivariances by the variance calculated as if sampling were random ($s^2 = \Sigma(x_i - \bar{x})^2/N$).

RESULTS

Forest floor standing crop

Means and standard deviations for the different components of forest floor are given in Table 1. The total weight of organic components averaged 10.6 kg m^{-2}. They arranged in descending order as follows:

undetermined > cones > fecal pellets

> leaves > twigs > catkins.

Litter made up about 42% of forest floor weight. Cones accounted for 49% and leaves for 30% of litter weight. Twigs and catkins were minor components. The humus fraction (58% of total forest floor weight) contained 25% of fecal pellets and 75% of undetermined material.

General forest floor variability was described in this paragraph by the coefficient of variation (CV), which ranged from 37% for the total weight to 83% for catkins.

No high correlation was observed between the six components (Table 2); the highest relationship, between fecal pellets and the undetermined component, explains only 17% of variance. Similarly, component variations could not be related to the living tree index (from 1% for leaves to 13% for undetermined material).

Spatial structures

Figure 1 showed the variation of each component along the transect. The observed patterns globally confirmed the high CV. However, a relationship between variance and mean cannot take into account different scales of heterogeneity within the transect. Indeed a high variance may be due to variations in the average value of a component along the transect (at a large scale) or due to a high heterogeneity between two or several successive points (variability at a fine scale).

Trend at the transect scale. Spearman rank correlation was significant for cones, catkins and total material (Table 3). The first two components increased overall from the sea side to the interior. They explained the trend observed for the total weight, since the test was no longer significant when cones and catkins were excluded. In fact, the observed r values did not reflect a true gradient, but an edge effect in the case of cones [$r = 0.18$ (NS) if the 15 first measures were omitted]. For catkins, the correlation was due first to differences between the two halves of the transect and secondly to an edge effect located at the first 11 points [$r = 0.15$ (NS) in the first part after deletion of the edge effect; $r = 0.04$ (NS) in the second part].

Table 2. Correlation matrix between components of forest floor

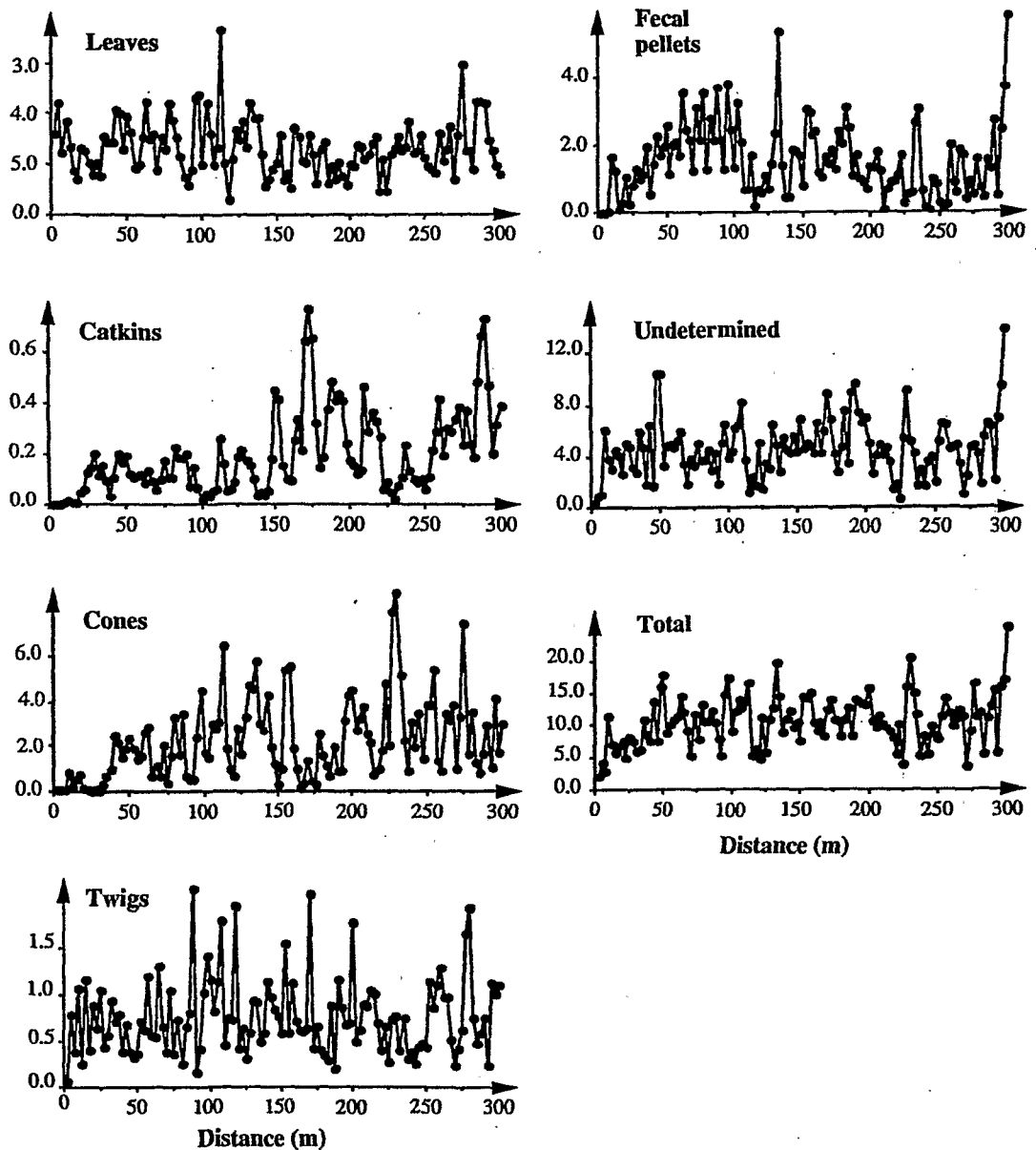|	Leaves	Catkins	Cones	Twigs	Fecal pellets	Undetermined
Leaves	1.00					
Catkins	0.490	1.00				
Cones	0.220	−0.149	1.00			
Twigs	−0.126	0.062	0.077	1.00		
Fecal pellets	0.172	0.095	0.079	0.184	1.00	
Undetermined	0.027	0.335	0.189	0.291	0.438	1.00

Fig. 1. Spatial distribution of forest floor components along the transect from sea shore to the interior; values in kg m^{-2}.

Heterogeneity at intermediate scales. The spatial autocorrelation matrix test gave variable values according to component and block size (Table 4). For

Table 3. Spearman correlation coefficient (ρ) for components of forest floor as a function of distance to shore

	ρ	P
Leaves	−0.105	NS
Catkins	0.532	0.0001
Cones	0.425	0.0001
Twigs	0.061	NS
Fecal pellets	−0.089	NS
Undetermined	0.145	NS
Total	0.248	0.0069
Total—cones and catkins	0.077	NS

P = probability of rejecting the null hypothesis of independence.

twigs the test was not significant whatever the block size, suggesting a random pattern within the transect.

The spatial pattern of leaves was very weak. Maximum heterogeneity was observed between blocks composed of 30 points (75 m); leaves were less abundant in the third block (mean of 1058 g m^{-2}) than in the other three (1396–1454 g m^{-2}).

Fecal pellets and undetermined material showed very similar patterns, with significant heterogeneity at small and medium scale for blocks of 2 (5 m) to 15 (about 40 m) or 8 points (20 m); their distribution was random at larger scale.

The SAM test took its highest values for the reproductive vegetal remains, cones and catkins. The

Table 4. SAM test values for each component of forest floor in blocks of increasing size (number of points)

Block size	Leaves	Catkins	Cones	Twigs	Fecal pellets	Undetermined	Total
2	1.55	5.77	3.96	−0.14	3.83	**3.91**	3.02
4	2.00	7.26	4.54	0.03	3.46	2.96	2.48
8	2.15	10.79	6.06	−0.34	4.83	2.84	2.78
15	2.97	12.80	7.01	−0.49	**6.43**	0.47	**4.04**
30	**3.09**	13.53	**8.63**	0.21	0.08	0.30	2.69
60	2.17	**23.45**	4.21	−0.71	−0.10	1.82	2.11

Bold figures correspond to the maximum value, when significant, per component.

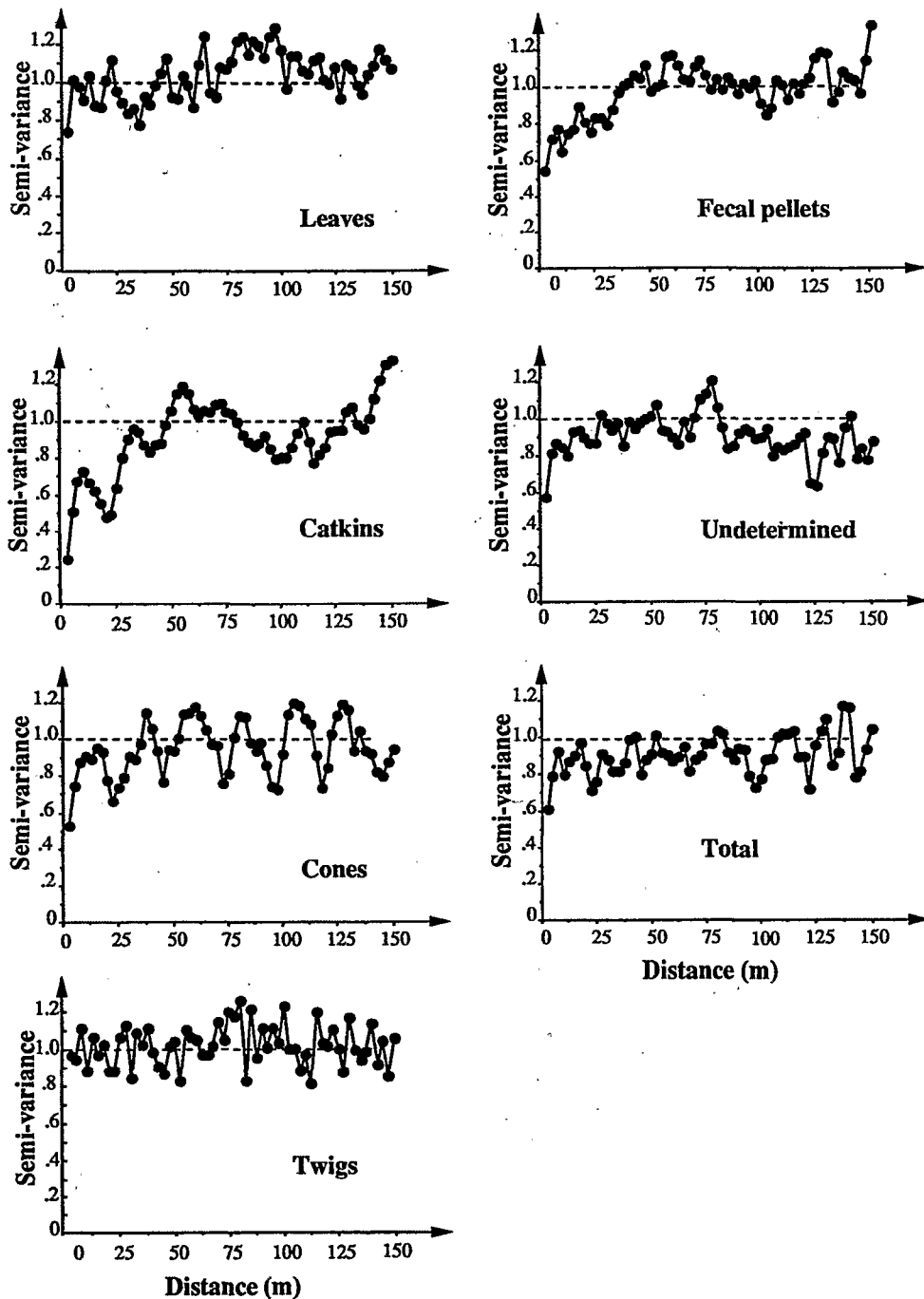Fig. 2. Normalized semivariogram for each forest floor component; the dashed line corresponds to the expected value of semivariances.

test was significant for all block sizes and its value usually increased with block size, except for cones at the largest scale. At fine scale, two successive measures greatly differed, especially for catkins. At large scale, the SAM test confirms Spearman rank correlations for catkins but showed a significant scale of 30 points (75 m) for cones; this resulted from low abundance of cones in the first 15 points and at the beginning of the second part of the transect (Fig. 1).

·Finally, significant variations were observed in regrouping the total forest floor weight whatever the block size. Maximum heterogeneity occurred at scale 15 points (about 40 m).

Heterogeneity at small scale. Semivariograms were computed for each component from the raw data (Fig. 2). Stabilization of the semivariance around a 1:1 ratio indicated that the total length of the transect was sufficient to account for all the variance of the process. This was true for all the components, except catkins. The parameters of spherical models adjusted to the semivariograms were given in Table 5. The model fitted the data rather well except for catkins; the latter semivariogram showed a periodical aspect with probably two different frequencies and a sharp increase in its last part. When the global trend was removed by subtracting mean values per block of 30 measures from the raw data (see the preceding sub-section), the spherical model was accepted (Table 5).

We restricted the analysis of semivariograms to the occurrence of a significant value of C_0 (the nugget effect) and to the value of RSD (range of spatial dependence). Nugget effect allows us to test the adequacy of lag value to small-scale variability. A significant nugget effect suggests that some source of variance occurs at a scale smaller than the lag value. Non-significant RSD values had similar interpretation. Forest floor components could be classified into three groups according to their semivariograms and their fit to a spherical model:

(a) fecal pellets departed strongly from all other components by a high and significant nugget effect and a large RSD value (56 m);

(b) leaves and twigs showed small RSD values (2 and 3 m) and random variations around the sill; and

(c) catkins and cones had intermediate RSD

values (9 and 11 m) but their semivariograms showed a periodic structure for distances larger than the RSD.

The large standard errors of parameters (Table 5) for all components except fecal pellets, suggested that the spherical model might be probably improved but it would lead to more complicated statistics.

DISCUSSION

Comparison with literature data

The only published work on forest floor accumulation under *Casuarina* plantations is Mailly and Margolis (1992) in Senegal. In 34-year-old stands, including our study site, they reported $120\,t\,ha^{-1}$ ash-free organic matter accumulation, higher than our $106\,t\,ha^{-1}$ estimation (not corrected for ash). Large differences in sampling methods did not allow a more precise comparison. Vogt et al. (1986), after Rodin and Basilevitch (1967), have reviewed numerous data concerning litterfall and forest floor accumulation through the world. Forest floor accumulation depends on climate, vegetation and time (see also Olson, 1963; Gosz et al., 1973; Meentemeyer et al., 1982). Accumulation observed in Senegal under *Casuarina* plantations ranged among the highest forest floor weights, over $100\,t\,ha^{-1}$, which generally occur with cold temperate broad-leaf deciduous and boreal evergreen needle forests. On the contrary, tropical forests usually exhibited small forest floors. Mailly and Margolis (1992) suggested that the particular combination of species characteristics and ecological conditions could explain the unusual high accumulation observed under *Casuarina* in Senegal.

The 1:1 ratio between litter and humus probably resulted from a slow rate of fragmentation of litter by soil fauna (Louisier and Parkinson, 1976). This hypothesis was in good agreement with Mailly and Margolis's (1992) report that no humus formation was observed in the plantations during the first 17 years.

Cones were the major component of *Casuarina* litter, whereas leaves accounted for more than 70% of litterfall in most studied forests (Meentemeyer et al., 1982). Observations of cones in the H layer

Table 5. Parameters of the spherical model of semivariogram for each component

	C_0	C_1	$C_0 + C_1$	RSD
Leaves	−0.11	1.16	1.05	1.8 (0.3)
Catkins				
Raw data	0.26	0.75	1.01	53.2
Detrended data	−0.11	1.15	1.04	8.9 (2.6)
Cones	0.33 (0.26)	0.64	0.97	11.2 (4.1)
Twigs	−0.16	1.19	1.03	3.1 (0.7)
Fecal pellets	0.56 (0.05)	0.48	1.05	55.7 (7.1)
Undetermined	0.28 (0.30)	0.63	0.92	7.9 (3.0)
Total	0.35 (0.28)	0.57	0.92	8.0 (3.1)

C_0 = nugget effect; $C_0 + C_1$ = sill; RSD = range of spatial dependence (meters); ( ), standard error, not given for negative values of C_0 (no biological meaning) or for catkins raw data (no convergence of the iterative procedure).

where leaves had disappeared showed that cones decomposed very slowly.

Accumulation of fecal pellets has been rarely reported and quantified. To our knowledge, the only similar accumulation was described by Seastedt (1983), who observed 28–463 g m^{-2} *Xyloryctes jamaicensis* (Drury) (Coleoptera, Scarabaeidae) fecal pellets accumulation in a temperate forest in Kansas. In the studied *Casuarina* forest floor, this accumulation reached up to 1523 g m^{-2} and 95% of the fecal pellets could be related to *Pachnoda interrupta* (Olivier) (Coleoptera, Scarabaeidae) larvae activity (F. Gourbière, unpubl. results).

Spatial patterns

The three methods of analysis showed that the five well-defined components fell into three types of spatial patterns:

—leaves and twigs were approximately randomly distributed along the transect;

—fecal pellets showed no trend at large scale, but high nugget effect and RSD values, in good agreement with small and medium scales of heterogeneity found by SAM test; and

—cones and catkins exhibited more complicated patterns, with significant SAM values at all scales tested, large-scale trend and periodic structures.

The undetermined component probably was a mixture, in unknown proportions, of finely divided litter, small fecal pellets and fine organic matter. As no correlation existed between components, the spatial patterns of undetermined and total only reflected the relative contribution of their constituents. Discussion is restricted to the five well identified components.

At each sampling point litterfall depended on the four surrounding trees. As two contiguous points had two trees in common, we could expect that two contiguous measures were not independent. This hypothesis agrees well with the RSD values for leaves and twigs but higher RSD values requires another explanation.

The spatial pattern and the average value of each component are functions of its production and decomposition rate. Production depended on tree populations for primary litter components and on more complex mechanisms for secondary components (fecal pellets, humus). We assume, as the simplest hypothesis, that local accumulation of primary components was determined by local litterfall and then by local forest roughly estimated as the living tree index (LTREE index). Lack of correlation between LTREE and accumulation, a result also found by Arp and Krause (1984), could mean (1) that litterfall was not correlated to LTREE or (2) that decomposition rate was more important than production rate in spatial pattern formation.

Most decomposing processes have patchy structures. For example, litter decomposing basidio-

mycetes occurred in patches 0.25–1 m^{2} (Swift, 1982). Interactions between spatial patterns of litterfall and litter decomposers could result in a composite pattern not related to tree biomass distribution.

This simple hypothesis cannot completely explain cone and catkin patterns. Some additional field observations suggested that (1) *C. equisetifolia* was monoecious but most of the trees exhibited a tendency to dioecy, resulting in predominantly male or female trees; and (2) in each of the three categories (male, female and monoecious), production varied greatly between high and low producers of cones or catkins. Moreover, production of these components was reduced at the sea side of the transect.

Fecal pellet distribution was probably more related to *Pachnoda* larvae than to tree distribution. This could explain the very distinctive spatial pattern of the pellets. A more detailed study of *Pachnoda* population biology and distribution will be published elsewhere.

We conclude that the different components of a forest floor exhibit different spatial patterns not directly related to forest stand pattern. Systematic sampling associated with regionalized variables opens a new field of investigation in litter and forest floor studies. As accumulation results from both production and disappearance, more studies are needed on related spatial patterns (tree, litterfall, populations of microbial and animal decomposers) for a better understanding of forest floor variability.

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