Neighbourhood analysis in the savanna palm *Borassus aethiopum*: interplay of intraspecific competition and soil patchiness

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Abstract. A previous study of the spatial patterns of *Borassus aethiopum* (a humid savanna palm tree) led to the following predictions: H1. Trees and termite mounds positively influence all developmental stages; H2. There is intense competition between *B. aethiopum* juveniles; H3. Juvenile and seedling survival and growth rates are higher away from mother plants; H4. Mound positive effect overwhelms the effect of intraspecific competition for very young *B. aethiopum* individuals, the reverse applies to older, non-reproductive individuals. To test for these hypotheses the potential positive and negative neighbourhood effects were analysed. Progression of seedlings into the juvenile stage and juvenile growth were analysed through logistic regression models including the effects of four neighbourhood indices designed to model the respective influence of *B. aethiopum* juveniles and adults, trees and termite mounds. Statistical results explain the observed spatial pattern and reveal two main neighbourhood effects that influence both *B. aethiopum* juveniles and seedlings: a positive effect of mounds due to the fact that they constitute nutrient-rich soil patches, and a negative effect of juveniles due to intraspecific competition. Seedlings would be mostly affected by the mound positive effect, whereas juveniles would be mostly affected by competition.

Keywords: Facilitation; Leaf number increment; Neighbourhood effect; Progression; Seedling; Spatial pattern; Soil heterogeneity; West Africa.

Abbreviations: EL-seedling = Entire-leafed seedling; H = Height. LN = Leaf number, LNI = leaf number increment, PFI = Practical fit index; SL-seedling = Slit-leafed seedling

Introduction

The sessile nature of terrestrial plants ensures that interactions between plants and between plants and their environment are local (Pacala & Silander 1985; Tilman 1994; Lehman & Tilman 1997). Therefore, the place where a seed germinates is of paramount importance for its probability of surviving and becoming adult. The neighbourhood of an individual plant greatly influences its growth (Firbank & Watkinson 1987; Thomas & Weiner 1989), survival (Aguilera & Lauenroth 1993; Condit et al. 1994) and reproduction (Weiner 1982; Silander & Stephen 1985). Neighbourhood suitability is determined by intrinsic soil quality (e.g. nutrients and water-holding capacity) and is further modified by other plants that may have negative effects (competition for light, water and soil nutrients) or positive effects (soil quality improvement through litter incorporation, micro-climate improvement) (Holmgren et al. 1996). Therefore, the neighbourhood of a plant must be described by quantitative assessment of both positive and negative neighbourhood effects and our main goal is to disentangle such effects in a particular field case.

A relatively easy way to detect neighbourhood effects is to analyse plant spatial patterns: if a spatial distribution deviates from a purely random distribution, a neighbourhood effect can be hypothesized. A previous comprehensive study of the spatial distribution of *Borassus aethiopum* (a savanna palm tree) detected several deviations from spatial randomness (Barot et al. 1999a): 1. Seedlings, juveniles and adults are associated with termite mounds and tree clumps; 2. Seedlings and juveniles are aggregated whereas adults are randomly distributed; 3. Seedlings are strongly associated with female *B. aethiopum* (the species is dioecious) but this is not the case for juveniles; 4. There is a discrepancy between the locations of non-reproductive individuals (seedlings and juveniles) and adults, i.e. seedlings and juveniles grow directly on mounds, while adults generally grow off mounds but remain spatially associated to them.

These results suggested a parsimonious set of hypotheses about the neighbourhood effects driving *B. aethiopum* demography (Barot et al. 1999a). To build these hypotheses we used traditional assumptions: competition leads to regular spatial distributions (Pielou 1962), and positive interactions lead to positive spatial associations (Mott & McComb 1974). We also used the results of independent studies which show that tree clumps and termite mounds constitute nutrient-rich soil patches (Abbadie et al. 1992; Mordelet et al. 1993, 1996). The set of hypotheses can be summarized as follows: H1. Tree clumps and termite mounds positively influence all *B. aethiopum* stages, enhancing growth and survival rates as they are nutrient-rich patches: H2. There is intense competition between *B. aethiopum* juveniles; H3. Seedling survival and growth rates are higher away from their mother plants, probably due to competition between juveniles and their mother (Barot et al. 1999b); H4. At a certain stage, the positive effects of mounds on *B. aethiopum* juveniles growing on them is outweighed by the negative effect of intraspecific competition between these highly aggregated individuals.

We aim to test these hypotheses using growth and demographic data. This is the only way to test hypotheses derived from purely static data. This is crucial because more studies detect deviations from spatial randomness in natural plant communities (Sterner et al. 1986; Skarpe 1991; Frelich & Graumlich 1994; Haase et al. 1997; Dovciak et al. 2001; Pélissier & Goreau 2001) than test for underlying neighbourhood processes at the scale of natural stands (Condit et al. 1994; Stoll et al. 1994). Note that these two lists are not exhaustive but reflect the real proportion of the two types of study. Moreover, many experimental studies directly prove the existence of neighbourhood effects (Goldberg 1987; Aarsen & Epp 1990; Benjamin 1993; Bergelson 1993), either at the individual scale or at the scale of experimental stands, but few of them allow spatial patterns observed in natural plant communities to be linked to underlying dynamic processes. This is mainly due to the fact that although these experiments provide differences in neighbourhood quality, it is usually not known whether individuals in natural stands really experience differences of such magnitudes.

We want to disentangle the effects of four features of the neighbourhood of immature *B. aethiopum*: other immature plants, adults, trees and termite mounds. As far as we know, this is the first time the neighbourhood approach has been applied to such a complex situation. It is also the first time this approach has been used to detect positive and negative effects simultaneously. For these reasons we used sophisticated statistical methods: 1. We determine the neighbourhood radius of the four neighbourhood indices at the same time; 2. We use a multivariate approach, path analysis, to disentangle the effects of the different neighbourhood indices and to determine the relative direct and indirect effects of the size of *B. aethiopum* individuals; 3. We use a randomization approach for all statistical tests to avoid spurious results that might arise due to spatial auto-correlation and the interdependence of individuals belonging to the same stand.

Material and Methods

Study site and study species

The study was conducted at the Lamto research station, Ivory Coast (6°13' N, 5°02' W) at the edge of the rain forest domain (Menaut & César 1979). Savanna vegetation is composed of grasses and small dicotyledonous trees. Adult *B. aethiopum* form a third stratum above the other two. Two main savanna types have been defined, corresponding to two different soil types and to differences in the dominant grass species (Menaut & César 1979): tree savanna on ferruginous soils and grass savanna on hydromorphic soils. The soil is considered to be particularly nutrient-poor but trees (which are generally aggregated in clumps) and low weathered termite mounds both constitute nutrient-rich patches (Abbadie et al. 1992; Mordelet et al. 1993). These mounds are present in every savanna type (between 8 and 12 mound.ha^{-1}) but represent a maximum of 9 % of the savanna surface (Abbadie et al. 1992). There is some evidence that these patches (mounds and tree clumps) are long-lived relative to *B. aethiopum* (Barot et al. 1999a). *B. aethiopum* is a dioecious, tall, solitary palm. Four developmental stages were defined using leaf morphology and the onset of reproduction (Barot et al. 2000): Entire-Leafed seedlings (EL-seedlings), Slit-Leafed seedlings (SL-seedlings), juveniles and adults.

Data collection

Four plots were mapped: 150 m × 250 m (GS1) and 250 m × 200 m (GS2) in grass savanna, 200 m × 200 m (TS1) and 128 m × 250 m (TS2) in a tree savanna. Basic data about *B. aethiopum* life history have been collected in the same plots (Barot et al. 2000) and *B. aethiopum* spatial patterns were comprehensively analysed in the four plots (Barot et al. 1999a). All *B. aethiopum* except EL-seedlings, all trees with woody parts > 1 yr old (recognizable by the presence of fire scars) and all mound tops were mapped within 50 m × 50 m quadrats with an ultrasonic telemeter and a sighting compass. Trees and termite mounds were classified into two size classes (T1, ca. 1 m tall, shrub-like trees; T2, trees > 1 m;

M1, mounds ca. 20 cm high and < 2 m diameter; M2, bigger mounds). Numbers of *B. aethiopum*, trees and mounds mapped are shown in Table 1.

The fate of each mapped *B. aethiopum* (progression to the next stage, survival or death) was determined between April 1996 and April 1998. *B. aethiopum* adults and juveniles heights were measured in April 1996 and 1998. The number of leaves was counted at the same time. For each *B. aethiopum* a class variable denoted whether it grew directly on a mound or not.

Neighbourhood indices

Here, four neighbourhood indices were defined to model the influence of *B. aethiopum* juveniles (*J*), adults (*A*), termite mounds (*M*) and trees (*T*) on *B. aethiopum* juveniles and seedlings. The four neighbourhood indices were computed as the numbers of neighbours (mound, tree, juvenile *B. aethiopum*, adult *B. aethiopum*) within the neighbourhood radius (r_{max} = the maximum distance between a focal plant and other individuals that may influence it) weighted by the quantity W_{ij} (*i* is the suffix for the focal immature *B. aethiopum* and *j* the suffix for its neighbours, r_{ij} is then the distance from the focal immature *B. aethiopum i* to the neighbour *j*):

$$Index = \sum_{r_{ij} \leq r_{max}} W_{ij} . \qquad (1)$$

W_{ij} is used to model a possible dependence of the neighbourhood effect on the size of focal individuals, and/or the size of the considered neighbours. For mound and tree neighbourhood indices (*M*, *T*), W_{ij} = 1 was used: tree and mound influence was supposed to be independent of their own sizes and of the focal *B. aethiopum* size whenever they are close enough ($r_{ij} \leq r_{max}$). Different r_{max} values were used to take into account the two size classes distinguished for mounds and trees. The final *M* and *T* indices were calculated as the sums of the indices computed separately for each mound or tree size class: i.e. four neighbourhood indices were originally computed and thus four neighbourhood radii had to be determined.

For the juvenile index (*J*), we tested several simple weights (W_{ij}):

$W = 1$; $W = LN_j/LN_i$; $W = LN_j$; $W = H_j/H_i$; $W = H_j$

where *LN* = number of leaves, *H* = height, *j* = influencing juvenile and *i* = focal immature). W_{ij} = 1 corresponds to an absolutely symmetric competition, independent of plant size (Thomas & Weiner 1989).

The four other weights correspond to a neighbourhood effect that depends on the sizes of competing

Table 1. Numbers of trees, termite mounds and *B. aethiopum* seedlings, juveniles and adults mapped in the four plots.

Plot	Seedlings	Juveniles	Adults	Trees	Mounds
TS1	249	228	65	376	48
TS2	90	160	60	407	18
GS1	127	152	111	305	51
GS2	208	132	77	420	39

plants (size-dependent symmetric competition) (Hara & Wyszomirski 1994). This corresponds to the fact that plants are able to use more resources (e.g. light or soil nutrients) when they grow bigger. The following weights were used to introduce some asymmetric competition, i.e. bigger individuals monopolize a disproportionate share of available resources (Thomas & Weiner 1989; Weiner 1990):

(1) if $H_j \geq H_i$ then $W_{ij} = \omega_{ij}$, if $H_{j\dagger} < H_i$ then W_{ij} = 0;
(2) if $LN_j \geq LN_I$ then $W_{ij} = \omega_{ij}$, if $LN_j < LN_I$ then $W_i = 0$
(where $\omega_{ij} \in \{1, LN_j/LN_i, LN_j, H_j/H_i, H_j\}$).

In these cases, W_{ij} introduces completely asymmetric competition, i.e. a juvenile cannot have any negative effect on a larger juvenile (Thomas & Weiner 1989; Weiner 1990). For the adult index (*A*) the following weights were tested:

$W = 1$; $W = LN_j / LN_i$; $W = LN_j$; $W = H_j / H_i$; $W = H_j$.

We did not introduce asymmetry since adults are always taller and have more leaves than juveniles.

Logistic regression

We used a logistic regression to analyse the effects of the four neighbourhood indices (4-index model) on the juvenile Leaf number increment (*LNI*): the change in the number of leaves between 1998 and 1996. Growth in height could have also been used (with classical regression), but imprecision of measurement was too high relative to the small increase observed during the study period. We believe that the number of leaves is a good index of fitness because it is a key-factor determining photosynthesising leaf area.

Logistic regression was relevant because leaf number increment is a discrete variable and the number of leaves is always low for juveniles (between two and ten for most juveniles). It allowed us to express the probability of each observed leaf increment as a function of the four neighbourhood indices (Collett 1991). The cumulative logit link function was used. Computations were made using the SAS LOGISTIC procedure (Anon. 1989). The stepwise regression method allowed choice of a model

incorporating variables selected among the number of leaves (*LN*), height (*H*) and the four neighbourhood indices. It is obviously important to allow for an effect of height or the number of leaves since plant performance generally depends on their size (Stoll et al. 1994; Duncan 1995). For each variable the raw variable, its square and its logarithm were incorporated in the stepwise process.

The neighbourhood radii r_{max} could not be determined *a priori*. For *J* and *A* indices, all integer values between one and 12 were tested. Preliminary results showed that these were the optimum values. For *M* and *T* we determined an r_{max} value for each size class (T1, T2 for trees; M1, M2 for mounds). Consequently, 169 combinations were tested for each index

$$(r_{max} \in \{0, 1, 2, \dots, 11, 12\}).$$

Thus $169 \times 169 \times 12 \times 12$ combinations of neighbourhood radii were tested. Values of r_{max} that yielded the smallest deviances were retained following earlier authors who retained the neighbourhood radius that minimizes the residual sum of square (Silander & Stephen 1985). Focal juveniles were chosen only in central parts of the plots, excluding those in a 12 m wide area around the plots to correct for any boundary effect (juveniles located in this area have neighbours that have not been mapped). To reduce the amount of computation the effect of each index was first analysed separately (1-index models). These preliminary analyses allowed for the selection of the best weight for each index, i.e. the ones that minimized the deviance. These weights were retained for the 4-index model.

Each juvenile was considered both as a focal individual and as a neighbour of other juveniles. Spatial autocorrelation due to unmeasured sources of environmental heterogeneity (particularly soil heterogeneity) is likely (Legendre 1993). For these reasons observations could not be considered as independent so that usual χ^2 tests were not reliable (Meagher & Burdick 1980; Thomas & Weiner 1989; Mitchell 1992). Therefore, a randomization approach was used (Manly 1991). The null hypothesis was that *LNI* are independent from the four neighbourhood indices. For each randomization, and for each neighbourhood index, each juvenile retained its real *H*, *LN* and *LNI* values, but was attributed the four neighbourhood index values of another juvenile, as if their spatial locations were permuted. The statistic used was deviance (*D*); the probability (*P*) for the test significance was calculated as the proportion of randomizations resulting in a lower deviance than the deviance calculated with the same model for the real data, 1000 randomizations were always used.

The same method was used to study the progression of SL-seedlings into the juvenile stage. The model did not include the height (always 0) of SL-seedlings or their leaf number. After selection of the best model (determination of r_{max} values), randomization was used to test the null hypothesis of the absence of influence of SL-seedling neighbourhood on their progression to the juvenile stage. Survival rates of juveniles and SL-seedlings were so high, and progression rate of juveniles into the adult stage so low, that there was no value in testing for a neighbourhood effect (unpubl.). Both selection of the parameters and randomization were implemented using SAS.

A practical fit index (PFI) was used to compare qualitatively (without any test) models which may or may not have the same degrees of freedom. It is computed as the difference between the deviances of the two compared models divided by the deviance of the null model (no effect tested). It allowed us to select among different models. Preliminary analyses involved logistic regressions where the effects of the four neighbourhood indices were analysed separately (1-index model). The PFI enabled us in particular to assess the improvement in the model goodness-of-fit resulting from the inclusion of the four neighbourhood indices in the same regression (4-index model) or from the inclusion of more sophisticated weights (W_{ij}). This selection process is not detailed here, only the results of the finally selected models are presented.

Path analysis: indirect effects of neighbourhood indices on juvenile LNI

Following Stoll et al. (Stoll et al. 1994) a multivariate approach, path analysis (Mitchell 1992), was used for two reasons: first, neighbourhood indices are correlated (results not presented) due to the spatial patterns of trees, seedling, juvenile and adult *B. aethiopum* that are spatially associated (at various distances) to mounds (Barot et al. 1999a), second, this approach takes into account a possible indirect effect of the neighbourhood of a juvenile on its *LNI*, by testing for the direct influence of the neighbourhood indices on *H* and *LN*. All calculations were made using SAS CALIS procedure (Anon. 1989).

The path diagram (Fig. 1) is based on previous studies of *B. aethiopum* and simple biological hypotheses. We did not analyse the direct causal links between the indices (double-headed arrows in Fig. 1) because available data were not sufficient to derive strongly founded hypotheses about these links. We tested for the direct effect of the four neighbourhood indices, *H*, and *LN* on juvenile *LNI* (single-headed arrows in Fig. 2). We also incorporated indirect effects of the indices on *LNI* and direct effect of the indices on *H* and *LN* into the model. Only the juvenile index had significant indirect
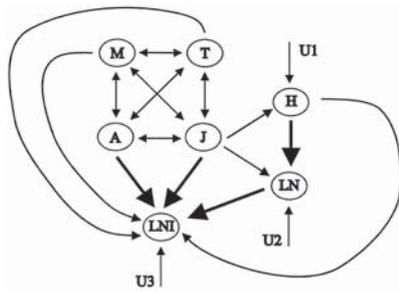
Fig. 1 Path diagram for juvenile leaf number increment (*LNI*). Single-headed arrows reflect causal relationship. Double-headed arrows represent unanalysed correlations (correlations without causation). U_1, U_2, and U_3 are error variables that measure the variability due to unmeasured factors of variability.

effects in preliminary analyses and was kept in the presented analysis. *H* should have had an effect on *LN*, and not the reverse as the two variables are strongly correlated. Height will determine the expected number of leaves although the actual number is expected to vary considerably.

Indices were calculated with the set of r_{max} values that minimized the deviance in the four neighbourhood indices models (previous section). When an index had no effect in a plot, we retained the neighbourhood radii selected in another plot and that led to a significant effect of the corresponding index.

Observations on juveniles are not independent. We used a randomization approach to build a statistical test, as was done in a path analysis context by Mitchell-Olds (1987). Significant paths ($V_1 \rightarrow V_2$) (as indicated by *t*-tests) were re-tested through randomization tests. The null hypothesis was that the influencing variable (V_1) of the considered path had no effect on the other (V_2), so that V_1 values were randomly permuted among juveniles. A path was considered to be significant when less than 5 % of the 1000 permutations led to higher *t*-values than the *t*-value calculated for the real data (one-tailed test).

Results

Occurrence of Borassus aethiopum on mounds

Percentage of non-reproductive *B. aethiopum* growing on termite mounds, classified according to their demographic status, were compared through log likelihood ratio tests (Sokal & Rohlf 1981; Table 2). The four plots displayed the same pattern: higher proportions of juveniles (A) than SL-seedlings (C) growing on mounds; higher proportions of newly recruited juveniles (B) than SL-seedlings (C) on mounds, higher proportions of SL-seedlings (C) than newly recruited SL-seedlings (D) on mounds. The (A/B) proportion difference was never significant. The (A/C), (B/C) and (C/D) proportion differences were significant in three, two and four plots respectively (Table 2). The significance of the (B/C) comparison is questionable because of the low numbers of new juveniles. However, the comparison is significant when individuals of the four plots are pooled.

Difference (C/D) suggests that SL-seedling survival is higher on than off mounds. Differences (A/C) and (B/C) suggest that SL-seedlings are more likely to recruit to the juvenile stage when they grow on mounds. Yet, juveniles are not more likely to survive when they grow on mounds (no clear difference between the proportion of new juveniles and other juveniles that grow on mounds (A/B)).

SL-seedlings progression

The use of weights (W_{ij}) introducing asymmetric competition did not improve the statistical models for either *J* or *A*. We retained $W_{ij} = 1$ as weight (preliminary analyses using PFI). In the four plots, more than one neighbourhood index had a significant effect in the 4-index model (Table 3). All significant effects on SL-seedlings progression were positive except for the effect of *T* in the tree savanna plots. *J* and *M* had a positive

Table 2. Percentages of non-reproductive *Borassus aethiopum* plants growing on termite mounds and classified according to their current and former stage (2 years earlier). Absolute numbers of *B. aethiopum* are displayed in parentheses. The last column displays the pooled results for the individuals of the four plots. The differences in the proportions of individuals growing on and off mounds were tested between the following pairs of lines: A/B, B/C, C/D and A/C. Results of these tests are displayed in the lower part of the table. * = $P < 0.05$, log likelihood ratio (*G*) statistic (Sokal & Rohlf 1981).

	TS1	TS2	GS1	GS2	All plots
Juveniles (A)	59.2 (223)	77.9 (154)	88.2 (144)	49.5 (105)	68.8 (626)
New Juveniles (B)	50.0 (22)	94.1 (17)	77.8 (9)	40.0 (15)	60.3 (63)
SL-seedlings (C)	46.5(230)	68.1 (69)	32.4 (139)	26.1 (176)	39.9 (614)
New SL-seedlings (D)	15.4 (104)	35.0 (20)	11.8 (17)	8.1 (37)	15.7 (178)
A/C	*	ns	*	*	*
A/B	ns	ns	ns	ns	ns
B/C	ns	*	*	ns	*
C/D	*	*	*	*	*
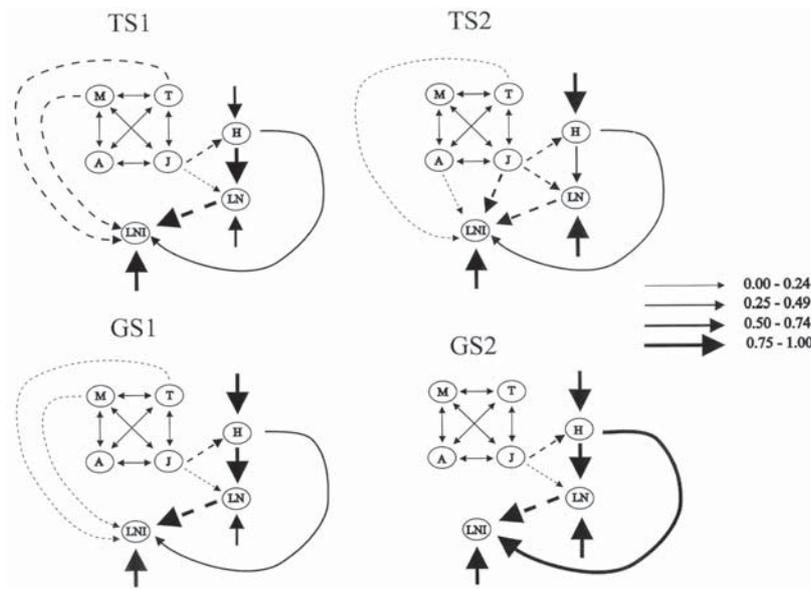
Fig. 2 Path diagram for the four plots. Width of arrows are proportional to the standardized path coefficient; dashed lines indicate negative paths, while solid lines indicate positive ones. Only significant (randomization test, 1000 permutations, see text for details) paths are displayed. Double-headed arrows represent unanalysed correlations (correlations without causation).

effect in four and two plots respectively. Indices with a significant effect in 1-index models had also a significant effect in the 4-index models, and *vice versa* (only two exceptions). Incorporating the four indices in the same model little improved the explanation of SL-seedling progression. This is linked to the fact that the four indices are correlated (results not shown).

Juvenile leaf increment

The 1-index model for juvenile *LNI* was slightly improved (preliminary analyses using PFI) when W_{ij} expressed asymmetry in the competition between juveniles: for *J* we retained $W_{ij} = 1$ if $H_j \geq H_i$ and $W_{ij} = 0$ otherwise. For *A*, we kept $W_{ij} = 1$. These weights were also used in the 4-index models. In the four plots more than one neighbourhood index had a significant effect in the 4-index models (Table 4). All neighbourhood effects on juvenile *LNI* were negative. *A* and *M* had a significant

negative effect in two plots each, *J* and *T* in three plots each. Most neighbourhood effects pointed out in 1-index models were also significant in 4-index models. Yet, in two plots, a neighbourhood index had a significant effect in the 1-index model that was no longer significant in the 4-index model: the four indices contain some of the same information about juvenile *LNI* and are correlated (correlation analysis not shown). *LN* had a negative effect on juvenile *LNI* in the four plots and *H* had a positive effect in three plots (Table 4).

Path analysis

Although standardized path coefficients for error variables were high (> 0.90 for U_1, 0.33 - 0.75 for U_2 and 0.75 - 0.86 for U_3), path models globally fitted the data. This is indicated by the goodness of fit indices which were > 0.95 in the four plots and by χ^2 tests for which $P < 0.05$ in all plots. In all cases, the randomization test

Table 3. Logistic regression of the progression of SL-seedlings into the juvenile stage (1996-1998) as a function of all neighbourhood indices. *P* was calculated through a randomization test (see text). r_{max}, = neighbourhood radius; D = deviance of the model; ns = no significant result was found for the variable corresponding to the r_{max} value. *M* and *T* were both calculated as the sum of the indices calculated separately for two size classes so that two r_{max} values are given for mounds and trees of increasing size (see text). The model column displays the variables that had significant effects in the retained models; + = positive effect; – = negative effect.

| Plot | N | r_{max} | | | | D | Model | P |
		M_1/M_2	T_1/T_2	J	A			
TS1	209	ns	8/2	5	ns	102.7	*T*– *J*+	< 0.001
TS2	82	ns	9/3	12	ns	60.3	*T*– *J*+	0.004
GS1	119	5/12	ns	2	ns	23.2	*M*+ *J*+	0.007
GS2	132	8/3	0/6	3	9	51.0	*M*+ *T*+ *J*+ *A*+	< 0.001

Table 4. Logistic regression of the leaf increments (1996-1998) as a function of the four neighbourhood indices. *P* was calculated through a randomization test (see text). r_{max} = neighbourhood radius; *D* = deviance of the model; ns = no significant result was found for the variable corresponding to the r_{max} value. *M* and *T* were both calculated as the sum of the indices calculated separately for two size classes so that 2 r_{max} values are given for mounds and trees of increasing size (see text). The model column displays the variables that had significant effects in the retained models; + = positive effect; – = negative effect.

Plot	N	r_{max}				*D*	model	*P*
		M_1/M_2	T_1/T_2	*J*	*A*			
TS1	175	0/9	12/0	6	ns	526.3	*LN*– *H*+ *M*– *T*– *J*–	< 0.001
TS2	130	ns	3/0	6	3	283.3	*LN*– *T*– *J*– *A*–	< 0.001
GS1	113	0/12	12/0	ns	ns	400.6	*LN*– *H*+ *M*– *T*–	0.005
GS2	62	ns	ns	3	5	121.0	*LN*– *H*+ *J*– *A*–	0.001

supported the results of the raw path analyses, i.e. the same paths were found to be significant.

In the four plots (Fig. 2) *J* had a significant negative effect on both *H* and *LN*; *H* had a positive effect on *LNI*, while *LN* had a negative effect on *LNI*; *H* had a positive effect on *LN*. Direct effects of neighbourhood indices on *LNI* displayed a less consistent pattern across the four plots: negative effects of *T* and *M* in TS1 and GS1, negative effects of *T*, *A* and *J* in TS2, and no direct effect of the indices in GS2 (Fig. 2). This pattern is the same as that found through the logistic regression models including the four indices except for GS2 in which a significant effect of *A* and *J* was found only through logistic regression. The only other difference between path analysis and logistic regression results was that no significant effect of *H* on *LNI* was found through logistic regression in the TS2 plot.

Overall, path coefficients between *H-LN* and *LNI* are higher than paths reflecting direct relationships between the neighbourhood indices and *LNI*. Standardized path coefficient for the relationship between *J* and *H* ranged between 0.25 and 0.50 in the four plots, while the coefficients between *J* and *LN* only exceeded 0.25 in the TS2 plot.

Discussion

Detecting neighbourhood effects

Our goal was to detect the positive and negative neighbourhood effects that could explain previously identified spatial patterns (Barot et al. 1999a). This goal has been achieved. Specifically, the positive effect of mounds and juveniles on seedlings explains the aggregation of juveniles on mounds, while the negative effect of juveniles and mounds on juveniles explains why adults have a random pattern and grow further from mounds than juveniles. The negative effect of adult *B. aethiopum* on juvenile *LNI* (detected in one

plot) explains potentially why seedlings are spatially associated to females, but not juveniles. The interpretation of the spatial association between mounds and juvenile/adults is warranted because mound dynamics are slower than *B. aethiopum* dynamics (cf. study site and study species).

However, statistical analyses reveal some problems: 1. The introduction of juvenile height and number of leaves improves the models much more than the introduction of neighbourhood indices; 2. The introduction of the four indices in the same logistic regression improves the models (in seven cases out of eight) only faintly relative to the 1-index models (preliminary analyses using the PFI, and path analyses); 3. The use of particular weights (W_{ij}) to take into account juvenile and adult size (*H* or *LN*) improves the model inconsistently across plots (except for *J* in the juvenile *LNI* model), and only slightly (preliminary analyses using PFI); 4. The neighbourhood indices which have a significant effect and the neighbourhood radii are not consistent across the plots. These points frequently lead to poor predictive power of neighbourhood models (Firbank & Watkinson 1987; Bergelson 1993; Bonan 1993), whereas size by itself is a good predictor of plant growth since it reflects the capacity of a plant to absorb resources.

The poor predictive power of neighbourhood models arises fundamentally from a time-scale problem (Bonan 1993): the spatial distributions and associations to be explained result from decades of *B. aethiopum* dynamics, while our study only encompasses a 2-yr interval. This problem should not discourage investigation of neighbourhood effects in natural communities because such studies are an indispensable complement to models that show that the accumulation in time of short-term neighbourhood interactions may have important consequences for the long-term dynamics of plant communities (Bonan 1988; Law & Dieckmann 2000) and ecosystem functioning (Pacala & Deutschman 1995).

Inferring biological processes from the neighbourhood effects

Logistic regressions using neighbourhood indices suggest that SL-seedlings are mostly positively influenced by the presence of mounds and juveniles, while juveniles are mostly negatively influenced by the presence of mounds and other juveniles. The analysis of the percentages of individuals growing directly on mounds supports these results. Yet, the logistic regression models did not enable us to distinguish clearly between the effects of juveniles and mounds. Do juveniles and mounds both really have a positive effect on seedlings and a negative effect on juveniles?

J and *M* are positively correlated (analyses not shown) since juveniles and mounds are spatially associated in all plots (Barot et al. 1999a). Consequently, it is not possible to determine *a priori* which of the neighbourhood features (juveniles, mounds or both) influences seedling progression and juvenile *LNI*.

In the path analyses, the local density of juveniles (*J*) always negatively affected both juvenile height and number of leaves whereas the direct effect of this neighbourhood index on *LNI* was only found in one plot. This is due to the time scale issue mentioned in the preceding section: juvenile height and number of leaves at one time is due to the growth in height and *LNI* that accumulated during many years, whereas our study takes into account the *LNI* of a 2-yr period. Thus, *J* has to be considered as the main factor influencing juvenile *LNI*, even if this influence is mainly exerted through the height and the number of leaves. It shows that in the four plots there is some intraspecific competition between closely clumped juveniles. The fact that the index selected to model the interaction between juveniles introduced some height based asymmetry supports this interpretation and suggests that competition between juveniles is mainly for light, since such competition is asymmetric (Weiner 1990).

As already emphasized, both *J* and *M* have positive effects on seedling progression and a negative effect on juvenile *LNI*. However, according to the parsimony principle, (1) mounds are responsible for the positive effect (H1) since they have been proved to be nutrient-rich patches (see hypotheses in the Introduction) and since *B. aethiopum* has been shown to be sensitive to these nutrient-rich patches (Mordelet et al. 1996), whereas (2) juveniles cause the negative effect (H2) due to some intraspecific competition for light, as suggested by the path analysis (see previous paragraph). Juveniles could have their own positive effect on seedlings (facilitation by improvement of microclimatic or edaphic conditions) and mounds could have their own negative effect on juveniles, yet invoking such new mechanisms is not parsimonious. Mounds are likely to have a positive effect both on juveniles and seedlings, while juveniles are likely to have a negative effect both on seedlings and juveniles. For seedlings, the effect of competition with conspecific immature individuals is overwhelmed by mound positive effect, while for juveniles, mound positive effect is overwhelmed by the negative effect of the presence of nearby juveniles (H4 in the Introduction).

T has a negative effect on juvenile *LNI* and seedling progression in five out of six significant cases in the 4-index models. Since *T* is the only neighbourhood index with a negative effect on seedlings, trees are likely to negatively affect seedling recruitment to the juvenile stage. This partially contradicts hypothesis H1. Trees compete with young *B. aethiopum* for light, as well as being nutrient-rich patches. Adults tend to have a negative effect on juveniles as predicted in hypothesis H3. This supports the results showing that seedling survival and progression increase with the distance to their mother plants (Barot et al. 1999b).

Interpretation of the causes of seedling and juvenile different spatial distributions

So far it has been deduced from the neighbourhood analysis that seedlings are most sensitive to the presence of termite mounds which are nutrient-rich patches while juveniles are mostly affected by other juveniles that are competitors, probably for light. These differences in seedling and juvenile responses to environmental factors are probably due to differences in the factor that limits their growth and survival. Seedlings are most likely to be nutrient limited while juveniles are most likely to be light limited because the relative size of their root and aerial systems are very different. All SL-seedlings have either one or two leaves, which represents approximately the same photosynthetic surface. Their capacity to recruit must depend on their capacity to take up nutrients and thus on the development of their root systems which are initially extremely reduced (Barot pers. obs.). Juveniles have probably already developed an effective root system, but they have to increase the number of leaves (i.e. photosynthetic surface) to become adult, and to grow taller to avoid shading by their neighbours. In fact, some juveniles (on mounds) are so densely clumped that they seem to compete for the very space required to develop leaves (Barot pers. obs.). Thus, the relative size of the above and below-ground systems is likely to determine the succession of constraints that limit growth capacity and survival throughout the life cycle.

Although the interplay between competition and facilitation has already been widely discussed (Aguiar et al. 1992; Holmgren et al. 1996; Callaway & Walker 1997) this is, as far as we know, the first time that the

neighbourhood index approach has been used to test for both positive and negative interactions simultaneously, while it was originally meant to distinguish competition. This approach might be very useful both to analyse field studies and to implement positive interactions in individual based spatially-explicit models.

The outcome of this interplay depends on the stage considered, such phenomena have already been identified (Grubb 1977; Grace 1985; Callaway & Walker 1997). Here, the younger (and smaller) *B. aethiopum* stage, SL-seedling, is more sensitive to ecosystem heterogeneity, while the next stage, juvenile, is more sensitive to competition. This competition arises, at least partly, because the sensitivity of the first stage to ecosystem heterogeneity leads to a concentration of individuals in the favourable patches (Barot et al. 1999a). The same pattern was found by Stoll (1994) in a temperate *Pinus* forest. This probably constitutes a very general trend in plant demography: first, survival and growth of young individuals depend only on the quality of their immediate physical environment (foraging phase), because their root and aerial systems are very poorly developed. Second, older individuals have better developed root and aerial systems and become increasingly independent of their immediate physical environment but increasingly dependent on the local density of competitors (competition phase).

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