Chapter

EFFECTS OF ABIOTIC FACTORS ON HERBACEOUS PLANT COMMUNITY STRUCTURE: A CASE STUDY IN SOUTH-EAST CAMEROON

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ABSTRACT

Abiotic factors significantly influence the structure of plant communities, with the effects varying in both space and time. Herbaceous plants belonging to 15 families were monitored in 250 4-m² plots distributed in six habitat types in order to assess the effects of abiotic factors on the abundance of this resource. In each plot, we counted herb stems and determined the total number of species, the total number of normal stems and the total number of dwarf stems. In addition, we determined soil fertility and other environmental variables. Elevation and soil texture varied, but similar levels of chemical fertility were seen across different habitat types. Herb abundance varied within and between patches, reflecting changes in environmental conditions. Stem biomass was highest in light gaps, and decreased in late successional forests. Light seemed to be the most important factor influencing the abundance of herbs from Marantaceae and Zingiberaceae families only. Despite the hydromorphic nature of the soil in swamps, stem biomass did not exceed that of *terra firma* forests. At the temporal scale, rainfall did not seem to influence stem density as herbaceous plants were available year-round. These results suggest that light might limit the abundance of some herbaceous plants in the

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study site. However, a long-term investigation is needed to draw firm conclusions on the effects of abiotic factors on herbaceous plant communities in African rain forest.

Keywords: Dja reserve, forest understory herbs; plant gradients; stem size; soil fertility

INTRODUCTION

Abiotic variables, among other factors, significantly shape the structure of plant communities (Tilman, 1983; Wright, 1992; Malenky et al., 1993; Crawley, 1997a; Van Andel, 2005; Bonnefille, 2010; Matías et al., 2012). Plant productivity depends on abiotic resources such as light, water and nutrients. Light is needed to catalyze chemical reactions that result in accumulation of plant biomass (Leuschner, 2005; Mooney &Ehleringer, 1997). In turn, these reactions require water, and plants use available water in the air and soil to compensate for the associated loss (Mooney &Ehleringer, 1997). In addition, nitrogen, phosphorus and other nutrients are needed to enhance plant chemical reactions (Fitter, 1997; Mooney &Ehleringer, 1997). For example, under high light conditions, there is a positive correlation between leaf nitrogen content and net photosynthesis (Mooney &Ehleringer, 1997). Tropical herbaceous plant communities are very sensitive to shortages in water, nutrients and light (Wright, 1992).

Across tropical Africa, studies on herbaceous plant community structure have revealed variations in diversity, density and biomass within and across sites (Watts, 1984; Rogers & Williamson, 1987; White et al., 1995; Fay, 1997; Brugiere&Sakom, 2001; Doran et al., 2002; Ganas et al., 2004; Harrison & Marshall, 2011). It has been suggested that such variations might result from differences in land use history and forest structure and composition, as well as variations in light and soil conditions and other environmental constraints (Brugiere&Sakom, 2001; Baeten et al., 2011). For example, human disturbance of natural habitats may deplete soil resources and negatively affect the recruitment of plant species (Martin et al., 2004). Describing abiotic factors and assessing their relationship with plant communities may therefore provide information on species which are effective indicators of habitat quality and diversity (Moffatt & McLachlan, 2004).

The majority of studies focusing on herbaceous plants across sites of Central Africa have not investigated the influence of environmental factors on the diversity, density and biomass of these plants (e.g. Rogers & Williamson, 1987; Malenky et al., 1993; Furuichi et al., 1997; Brugiere&Sakom, 2001). In some rare cases, the influence of a few abiotic factors has been assessed (e.g. Rogers et al., 1988; but see also Willie et al., 2012). However, the trends that emerge from such studies are often incomplete because the performance of understory plants is a response to the combined effect of a set of environmental factors which vary in magnitude (Ticktin&Nantel, 2004). As a result, other important factors not previously explored can affect the performance of these herbs. A more complete evaluation of the relationship between herbaceous plant communities and environmental parameters is therefore needed. Such investigations may help to highlight the abiotic factors that determine herb availability to potential users such as forest herbivores.

The objective of this study is to assess the influence of abiotic factors on the growth of forest understory herbaceous plants, and provide insights on the causes of gradients in the

availability of herbs that are used by forest herbivores. We hypothesize that spatial changes in the magnitude of ecological variables translate to variations in density, diversity and biomass of herbaceous plants. We predict that soil fertility and light and water availability will be the variables that have the greatest influence on herbaceous plant community structure, and will correlate positively with plant abundance and diversity. Assessing density, diversity and growth performance of herbs in relation to abiotic factors might help to describe the environmental features which confer suitability of some species for use by herbivores. In addition, such investigations may provide more clues regarding the environmental characteristics of habitats which are more suitable to herbivores, thus allowing a more accurate assessment of their quality.

MATERIAL AND METHODS

Study Site and Species

Data were collected in 'La Belgique' research site of *ProjetGrands Singes* (PGS), of the Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), located between 013°07'–013°11' E and 03°23'–03°27' N. The site is situated in the northern buffer zone of the Dja Biosphere Reserve (Cameroon), and is located in the transition zone between the semi-deciduous forests of Equatorial Guinea and the evergreen forests of the Congo basin (Letouzey, 1985). The climate is equatorial and humid and is characterized by seasonal rainfall. During a two-year period (April 2009–March 2011), average rainfall was 1637.9 ± SD 105.1 mm, and mean minimum and maximum daily temperatures ranged between 19.5 ± SD 1.3°C and 26.3 ± SD 2.4°C. The study subjects were herbaceous species belonging to 15 families, namely Araceae, Aspleniaceae, Balanophoraceae, Commelinaceae, Costaceae, Cyperaceae, Marantaceae, Melastomataceae, Poaceae, Pteridaceae, Rubiaceae, Selaginellaceae, Thelypteridaceae, Urticaceae and Zingiberaceae. It is noteworthy that Marantaceae and Zingiberaceae density in the study site is about 3 stems/m² (Willie et al., 2012), whereas overall herb density is estimated at 6 stems/m² (Willie et al., in prep.), therefore meaning that herbs from these two families are an important component of the herbaceous layer in the study site.

Habitat Types

In line with previous vegetation classifications in the area (e.g. Nguenang&Dupain, 2002; Dupain et al., 2004), we distinguished six habitat types: 1) Near primary forest (NPF), where large tree species of height > 30 m predominate (e.g. *Polyalthiasuaveolens*,*Omphalocarpumprocerum*, *Uapaca*spp.and *Piptadeniastrumafricanum*), and there is little undergrowth and a closed canopy; 2) Old secondary forest (OSF), with dominant canopy trees of height 25−30 m (e.g. *Terminaliasuperba*), a more dense understory than NPF, and a discontinuous canopy layer; 3) Young secondary forest (YSF), characterized by a canopy height of < 25 m dominated by early successional trees (e.g. *Myrianthusarboreus*,*Tabernaemontanacrassa*), and a relatively

dense undergrowth; 4) Light gaps (LG), with completely open canopies resulting from elephant activity or tree and branch fall; 5) Swamps (SW), with high densities of *Raphia* spp., rare (< 5%) raphia-free open areas (clearings), and a hydromorphic soil; and 6) Riparian forest (RF), growing in the transition zone between SW and other habitat types, with a highly heterogeneous floristic composition comprising species from all habitat types. NPF, OSF, YSF and LG are referred to collectively as *terrafirma* habitats. SW and RF are (periodically) flooded habitats.

Sampling Design and Characterization of Plots

Stems of all ground-rooted herb species were surveyed in 250 2 × 2plots placed along 10 transects. Each transect was 6 km long and set at a bearing of 45°. Along each transect, 25 plots were set 250 m apart, at the right side of transects, and at a perpendicular distance of 5 m. Habitat type for each plot was noted. Percentage canopy cover above each plot was visually described (Loya& Jules, 2008) by assigning cover classes and light scores as follows: closed (0), half-open (50) and open (100). Soil humidity scores were determined in a 100–300 scale (100 = *terra firma* habitats on well-drained soils; 200 = riparian forest in the transition zone between *terra firma* habitats and swamps; 300 = swamps on hydromorphic soils). Geographic coordinates and elevation for each plot were also recorded using a GPS Map60cx. Soil samples were collected in 50 plots (7–10 randomly selected plots per habitat type) in 10 × 10 × 15 cm (depth) volumes and analyzed in the lab to determine the pH and the content of organic matter, sand, clay and nutrients (e.g. nitrogen, phosphorus, potassium).

To assess the spatial structure of the herbaceous plant community, we identified and counted herb stems in 4-m² contiguous square plots along a 1.5-km transect traversing all habitat types at a bearing of 45°. Average stem density for each habitat patch encountered along the transect was calculated, and results were graphically portrayed to highlight the patterns of variation.

Phenological Monitoring of Herbaceous Plants

Herb stems were monitored in all plots (250) along the 10 6-km transects. In each plot, the total number of herb stems and species were determined. Each stem was examined, and only old stems were classified as "dwarf" or "normal" because they had already completed their developmental cycle. Classification was based on size, which affects vegetative propagation (Ticktin&Nantel, 2004). Old stems were distinguished by signs of age, such as the occurrence of many yellow or brown leaves (entirely or partially), sometimes with holes and a dull color. Dwarf and normal stem dimensions were mutually exclusive. In all cases, dwarf stems were less than half the potential plant height. We collected and weighed ten stems of each species (five normal and five dwarf), and only one overlap in weight was found out of 600 measures. Each stem was assessed based on these chosen limits using a small decameter (with millimeter precision). For each species, we recorded the following information: 1) total number of stems; 2) number of dwarf stems; 3) number of normal stems; 4) number of stems with flowers; 5) number of stems with fruits and 6) number of growing

shoots. These data alongside rainfall, humidity and temperature data were collected each month, from August 2011 to July 2012.

Effects of Environmental Factors on Herbaceous Plants

To assess the effects of abiotic factors on herbaceous plant community structure, we performed a nonmetric multidimensional scaling (NMDS) ordination in R using the Euclidian distance on log transformed abundances. The data matrix was composed of herb and environmental data collected on a subset of 50 randomly-chosen plots (7–10 per habitat type). Analyses were done using the Euclidian distance on log transformed abundances. A preliminary principal component analysis (PCA) was performed in XLSTAT in order to assess autocorrelations among environmental variables (Figure 1). For final analyses, four non correlated variables were chosen. Component scores for each plot in the original data matrix were calculated, and correlations between dependent variables and principal axes were assessed using Spearman tests of correlation.
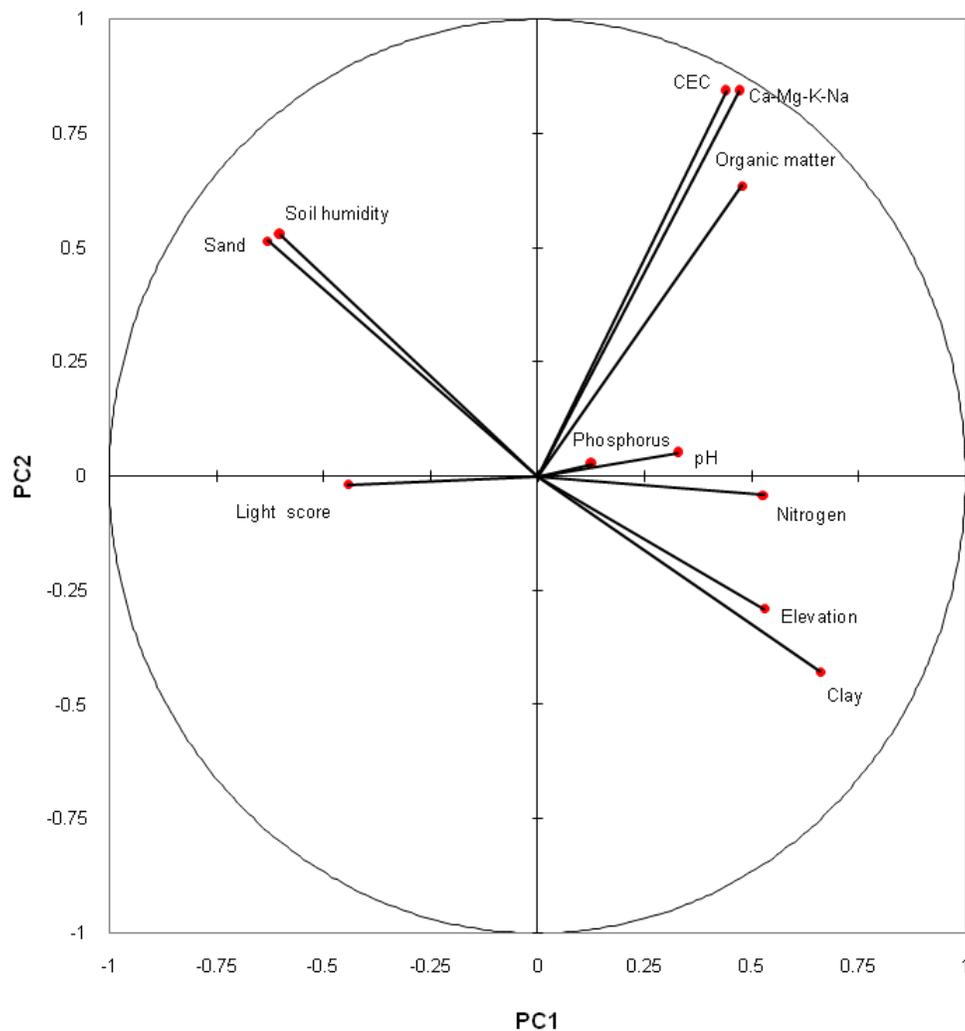
Figure 1. Preliminary principal component analysis (PCA) of environmental variables. Highly autocorrelated variables are more close to each other.

Statistical Analyses

Nonparametric statistics were used as data did not meet the assumptions of normality. Median tests (two-tailed) were used for global comparisons of habitat types, and two-sample Kolmogorov-Smirnov tests (two-tailed) were used for pairwise comparisons. We did not apply the Bonferonni correction for pairwise comparisons as sample sizes were too small ($7 \leq N \leq 60$ in most cases; Garamszegi, 2006). Proportions were compared using Chi-squared tests. Statistical analyseswere run in SPSS.

RESULTS

Characteristics of Habitat Types

There was little variation in plot elevation across habitat types, though differences in medians were statistically significant (Table 1). No significant difference in elevation was found among *terra firma* habitat plots or among flooded habitat plots; whereas plots in all *terra firma* habitats, except in young secondary forest, had significantly different elevations compared to plots in swamps (two-sample Kolmogorov-Smirnov tests, $P < 0.01$ in all cases). Sand and clay content of the soil (proxies for soil texture) globally differed across habitat types (Table 1). However, no significant difference was found among *terra firma* habitats and among flooded habitats, and all *terra firma* habitat soils had significantly different sand and clay content compared to swamps (two-sample Kolmogorov-Smirnov tests, $P < 0.05$ in all cases). Levels of soil fertility, estimated using measures of pH, organic matter, cation exchange capacity (CEC) and availability of phosphorus and nitrogen did not significantly differ across habitat types (Table 1).

Spatial Variation in Herb Availability

Along the 1.5 km transect, a mosaic of small-sized patches of various habitat types was encountered. The highest herb densities occurred in light gaps, young secondary forest and swamp patches. Furthermore, there was considerable variation in herb density among patches within each habitat type (Figures 2 and 3).

Abiotic Factors and Herb Community Structure

A preliminary synthesis of environmental parameters using a principal component analysis (PCA) indicated high levels of autocorrelation among variables (Figure 1). To facilitate the interpretation of results, we clustered correlated variables into four groups. Each group was represented by the most meaningful variable, namely clay, organic matter, canopy cover and soil humidity. The NMDS ordination of the herbaceous plant community structure

in 50 plots resulted in a two dimensional solution, and the final stress was 0.24. As shown in

Table 1. Soil Characteristics by Habitat Type

Variable	Near primary forest	Old secondary forest	Young secondary forest	Light gaps	Riparian forest	Swamps	Significant differences
Number of plots	8	7	9	8	8	10	
Elevation (m)	675.25 (17.65)	682.86 (26.30)	674.78 (24.57)	674.63 (12.19)	663.13 (19.25)	650.00 (8.00)	**
Sand content (%)	11.75 (2.05)	10.43 (0.98)	10.56 (2.74)	12.50 (1.60)	25.13 (15.97)	24.40 (8.69)	*
Clay content (%)	66.25 (3.49)	66.00 (3.27)	66.00 (4.15)	67.25 (1.58)	53.00 (15.29)	52.70 (10.30)	*
pH	4.35 (0.43)	4.14 (0.62)	4.54 (0.41)	4.10 (0.30)	4.08 (0.17)	4.13 (0.26)	ns
Organic matter (%)	5.71 (0.93)	5.80 (1.44)	5.56 (1.35)	4.75 (1.67)	6.55 (1.51)	5.22 (0.82)	ns
Cation exchange capacity (milliequivalents/100g)	3.07 (0.66)	3.11 (0.57)	3.11 (0.68)	2.63 (0.61)	3.29 (0.26)	3.08 (0.33)	ns
Assimilable phosphorus (mg/kg)	3.83 (1.01)	3.05 (0.70)	3.65 (0.90)	3.78 (0.87)	3.93 (1.73)	3.45 (0.55)	ns
Total nitrogen (g/kg)	1.99 (0.77)	1.81 (0.31)	1.94 (0.40)	1.75 (0.63)	1.76 (0.44)	1.59 (0.42)	ns

Displayed figures for all measured parameters are average values and corresponding standard deviations (in parentheses); soil parameters were measured in 50 plots selected in all habitat types. All global comparisons were done using Median tests; df = 5 in all cases; ns: non significant; **significant at $P < 0.01$; *significant at $P < 0.05$.
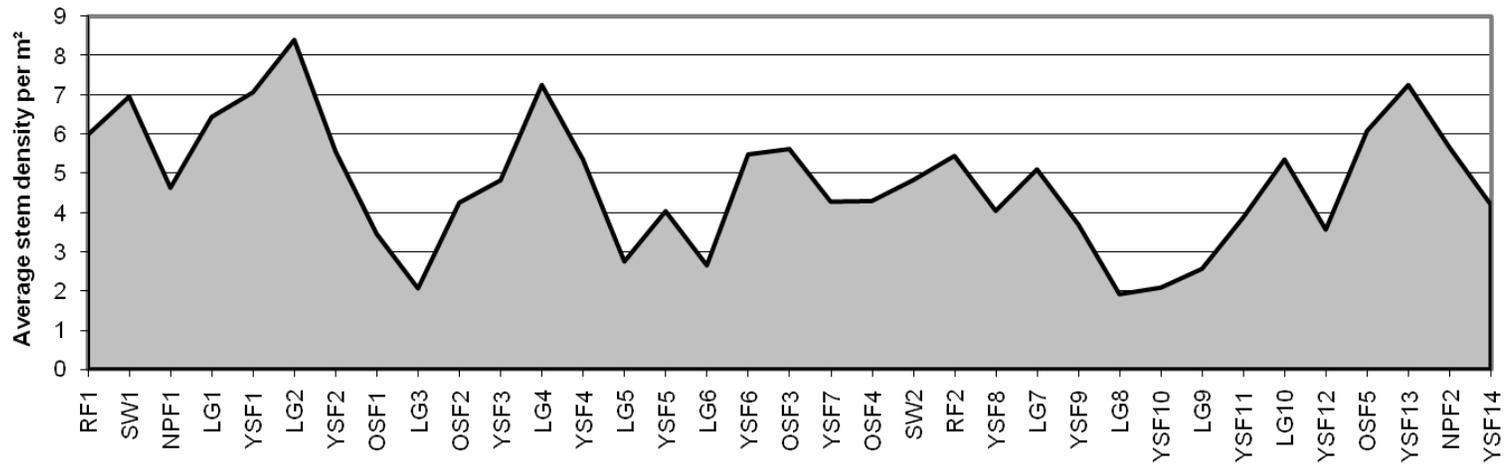
Figure 2. Habitat type sequence and spatial variation of herb stems along a 1.5 km transect (RF: Riparian forest; SW: Swamp; NPF: Near primary forest; LG: Light gap; YSF: Young secondary forest; OSF: Old secondary forest).
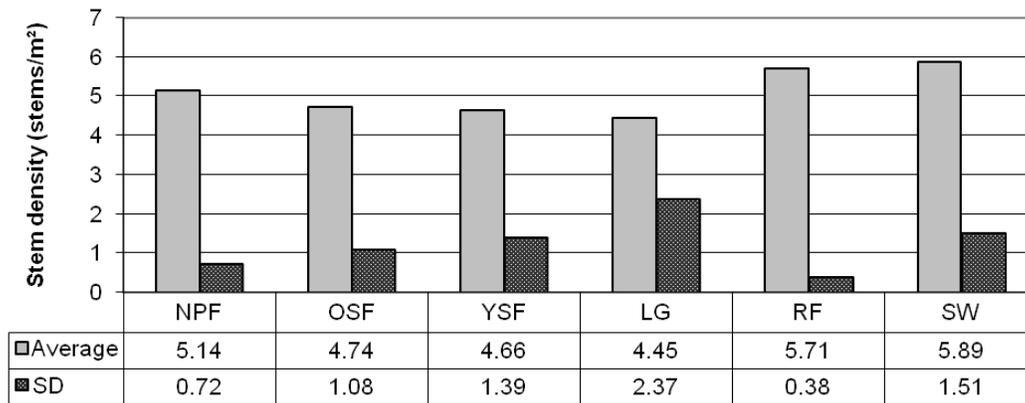
	NPF	OSF	YSF	LG	RF	SW
□Average	5.14	4.74	4.66	4.45	5.71	5.89
▨SD	0.72	1.08	1.39	2.37	0.38	1.51

Figure 3. Average values of herb stem density among habitat patches along the 1.5 km transect (NPF: Near primary forest; OSF: Old secondary forest; YSF: Young secondary forest; LG: Light gaps; RF: Riparian forest; SW: Swamps).
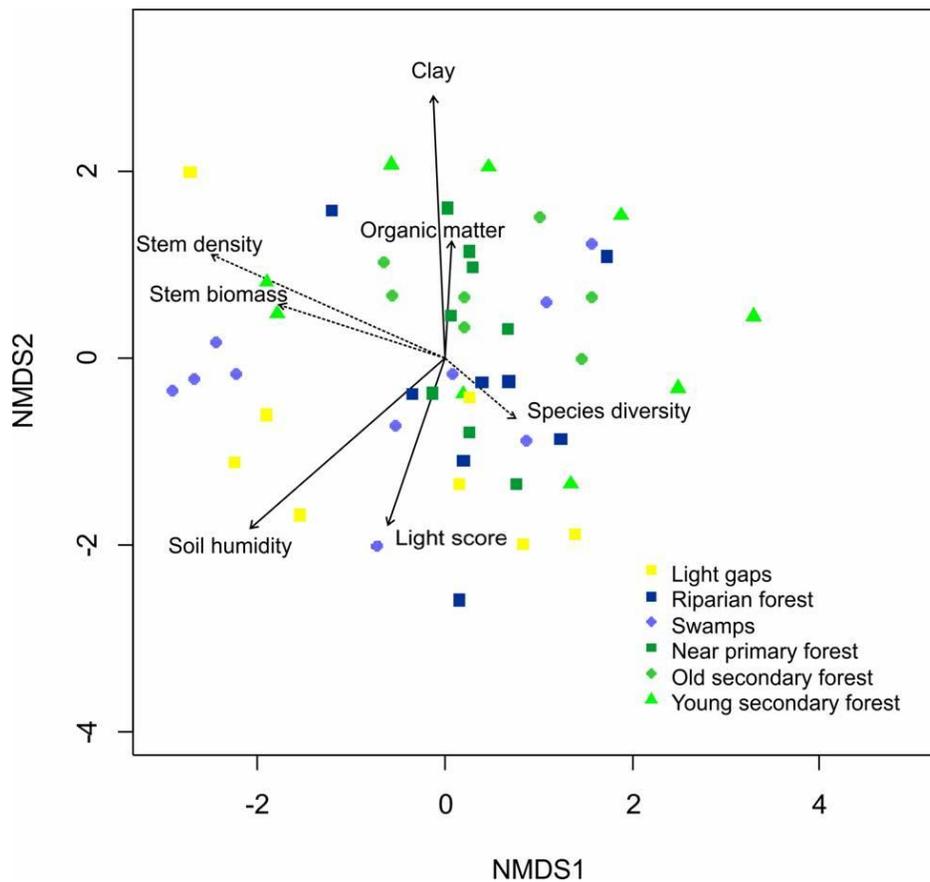

Figure 4. Nonmetric Multidimensional Scaling ordination showing the relationship between habitat type, abiotic factors and herbaceous plant community structure. The symbols represent plots in each habitat type grouped relative to the floristic similarity. The arrows indicate strength and direction of correlations among habitat characteristics and ordination scores (r^2 ranged between 0.02 and 0.2).

Figure 4, no clear relationship between predictors (clay, organic matter, light score and soil humidity) and dependent variables (stem density, stem biomass and species diversity) was detected. Plots from light gaps, riparian forest and swamps were separated from the others along the second axis. The first axis was roughly related to dependent variables while the second axis was mainly related to the predictors. Correlations with ordination scores were significant only between stem density and axis 1 ($r_s = –0.31$; $P = 0.027$). To corroborate these results, we assessed the relationship between measured environmental variables, namely sand, clay, pH, organic matter, nitrogen, phosphorus, CEC, light score, soil humidity and elevation, and dependent variables using the Spearman test of correlation: correlation was significant only between species diversity and elevation ($r_s = 0.31$; $P = 0.029$).
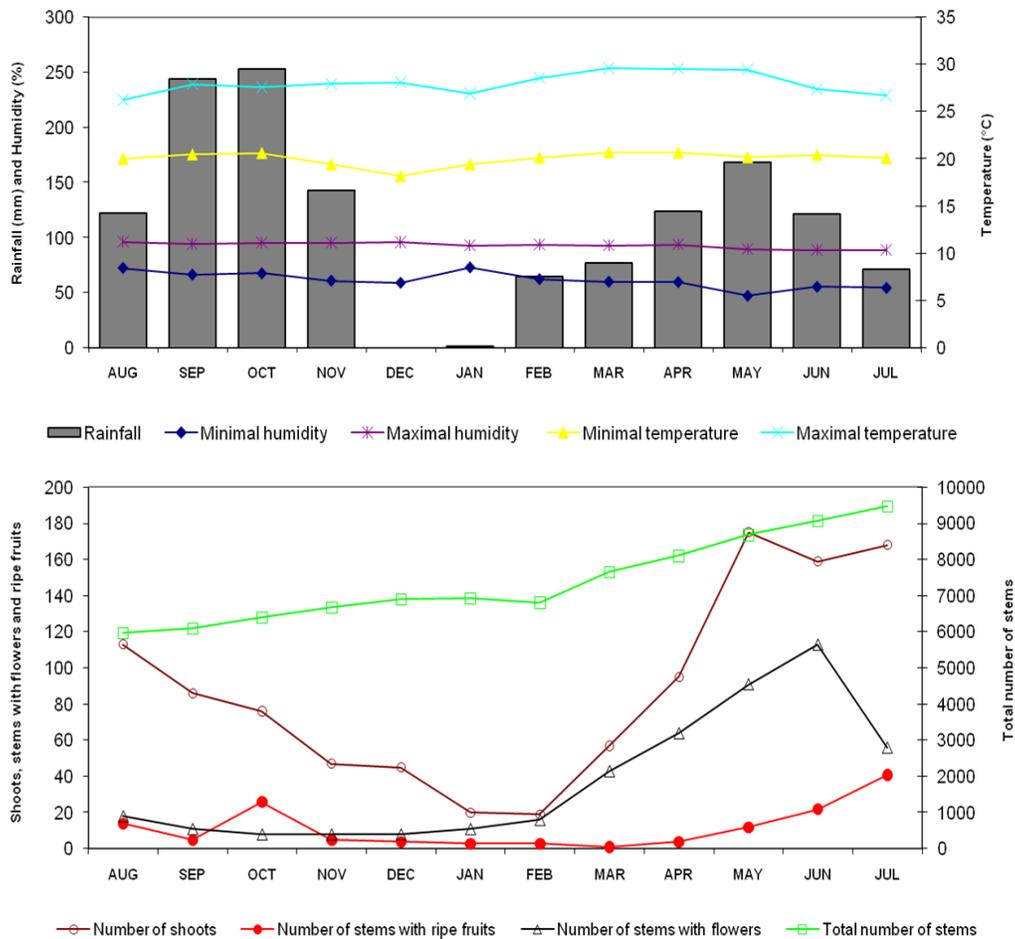

Figure 5. Climatic variables and phenological monitoring of herbs. Data were collected monthly in 250 4-m² plots.

At the temporal scale, abiotic factors such as rainfall, temperature and air humidity, as well as the phenology and dynamics of herbaceous plants showed variations throughout the year (Figure 5). Rainy seasons spanned from August–November and April–June, and dry

season periods occurred in July and from December–March. Highest and lowest temperatures were noted in March and April, and in August and December, respectively. Air humidity peaked in August, and the minimal level was observed in May. Small variations in the total number of stems inventoried were noted, with the highest values in July and lowest in value in August. The number of stems recorded showed little variation from August–February, and significantly increased from March–July.From May–July, high numbers of herb shoots were counted, and low numbers were recorded in January and February. Maximal numbers of herb stems with flowers were observed from March–July, and minimal numbers from August–February. Numbers of herb stems with ripe fruit were high July and October, and minimal values were recorded from January–April.

We used a Spearman test of correlation to assess possible relationships between herbaceous plant density and climatic variables. No significant correlation was detected between the total number of stems recorded each month and rainfall ($r_s = -0.315$; $P = 0.319$; N = 12) or average temperature ($r_s = 0.266$; $P = 0.404$; N = 12). However, there was a negative correlation with average air humidity ($r_s = -0.853$; $P = 0.0004$; N = 12). Similarly, the number of shoots and the number of stems with flowers and ripe fruits did not show clear relationships with climatic variables, and a significant correlation was detected only between the number of stems with flowers and average air humidity ($r_s = -0.649$; $P = 0.022$; N = 12).

Herb Size Categories

There was a significant difference in the proportion of dwarf and normal stems between habitat types (Chi-squared test: $\chi^2 = 119.6$, df = 5, $P < 0.0001$). These proportions significantly differed while only considering herbs from Marantaceae and Zingiberaceae families (Chi-squared test: $\chi^2 = 89.23$, df = 5, $P < 0.0001$; Table 2). The global chi-square value was partitioned to investigate specific differences. For all herbs, detailed results indicated significantly different proportions only in young secondary forest and light gaps ($\chi^2 = 22.14$ and 92.77, df = 1, $P < 0.001$ in all cases). For Marantaceae and Zingiberaceae, significant differences occurred in young secondary forest, light gaps and riparian forest (Chi-squared test: $\chi^2 = 9.65$; 38.07 and 40.38, respectively; df = 1 in all cases; $P < 0.001$ in all cases).

DISCUSSION

Flooded habitats were located in small depressions, and this resulted in lower elevations as compared to *terra firma* habitats (Table 1). Although soil texture varied between these major groups, the chemical characteristics of soils were similar in all habitat types, as also observed by Peh (2009) inside the Dja Reserve (Cameroon). This may be an indication that litter accumulation and decomposition rates and litter nutrient release do not significantly vary across habitat types, despite textural and hydromorphic differences. However, values of standard deviation of the measured environmental variables were sometimes high (Table 1), highlighting spatial variability in the magnitude of these factors. Furthermore, in the study

Table 2. Frequencies of Herb Stem Categories in Different Habitat Types

Stem size	Near primary forest	Old secondary forest	Young secondary forest	Light gaps	Riparian forest	Swamps
Marantaceae and Zingiberaceae only						
Dwarf	152	415	257	66	55	289
Normal	154	461	363	184	10	287
% dwarf	49.67	47.37	41.45	26.40	84.62	50.17
All herb species						
Dwarf	300	696	494	116	259	361
Normal	392	897	559	249	114	384
% dwarf	43.35	43.69	46.91	31.78	69.44	48.46

site, the amount of light varies within and between habitat types (Willie et al., 2012). As a result, spatial variations in stem density between and within habitat types (Figures 2 and 3) probably resulted from this environmental variability, especially as tropical terrestrial herbs are very sensitive to such variations (Wright, 1992). This is consistent with the fact that plant germination, recruitment and mortality across forest patches are likely to be affected by variability in environmental conditions (Martinez-Ramos et al., 1989).Our results highlight that while idiosyncratic differences between habitat types or sites may explain observed differences in levels of ecological factors (Brugiere&Sakom, 2001; Loya& Jules, 2008; Baeten et al., 2011), within-habitat variation in abiotic factors results in uneven biological patterns.

However, no strong correlation was detected between abiotic variables and herb abundance and diversity (Figure4). Hydromorphic and textural differences between flooded and *terra firma* habitats did not seem to result in variations in herbaceous plant community structure. Moreover, no relationship existed between light score and herbaceous plant density, diversity and biomass. This may be an indication that these abiotic factors did not limit the growth of the herbaceous plant community. However, while only considering herbs from Marantaceae and Zingiberaceae families, the proportion of dwarf stems was lowest in light gaps, and consistently increased from young secondary to near primary forest (Table 2). In the study site, the amount of light drastically decreases as the forest progresses from early to late successional stage (Willie et al., 2012). In addition, as shown by the analyses, variations in soil fertility levels across habitats were not significant. Therefore, it is possible that light strongly limits the growth and development of Marantaceae and Zingiberaceae herb species in the study site. It is shown that the stem density of herbs from these two families peaks in light gaps, with minimal values in near primary forest (Willie et al., 2012). These trends are consistent with the observations of White et al. (1995) who found differences in growth formsof *Haumanialiebrechtsiana* between Marantaceae and mature forest, with shorter stems occurring in the latter habitat type where shade conditions predominate in the understory. Stems of other plant life-forms such as saplings have displayed similar negative correlations between 'slenderness' and light availability (Van Breugel et al., 2012). In the ecological literature, it is well established that light is a major determinant of plant growth (Mooney &Ehleringer, 1997; Leuschner, 2005). Our analyses, however, did not reveal a clear effect while considering all herb species probably because some of the studied herb species are generalists (Willie et al., in prep.), meaning that they can thrive in a range of habitat conditions. For example, ferns, an important component of the herbaceous layer in the study site, can adapt and persist in shade conditions (Crawley, 1997b). Hence, we can suggest that although light had no major influence on the herbaceous plant community as a whole, some species appeared to be more dependent.

Water availability did not seem to limit herbaceous plant growth in the study site. One would have expected the highest stem density and biomass in flooded habitats if water was a liming factor to herbs in *terra firma* habitats. Stem density seemed to be highest in swamp patches (Figure3), but differences in stem density between this habitat and others are not significant (Willie et al., in prep.). In addition, riparian forest and swamps had high proportions of dwarf stems compared to other habitats (Table 2), implying that other factors may be important. Moreover, at the temporal scale, no clear pattern was detected between rainfall and density of herbaceous plants (Figure 5). This result must be interpreted with caution because between consecutive surveys, other factors such as herbivory, trampling by

animals and humans and other biotic influences might have removed some stems, including shoots, fruits and flowers, thus biasing the results. Nevertheless, these results suggest that herbs are available year round. It has been noted that tropical herbaceous plants are very sensitive to water shortage which can cause mortality and inhibit the germination of some species (Wright, 1992; Crawley, 1997b). In spite of this, the herbaceous plant community of the study site did not seem to be affected by seasonal rainfall as well as variation in temperature. However, further investigation is needed to draw firm conclusions.

CONCLUSION

Soil nutrients for plant growth are randomly distributed across habitats. Contrary to our predictions, abiotic resources were not limiting factors to the herbaceous plant community of the study site as a whole, though light seemed to be the most important factor influencing the abundance of a number of species. The effect of climatic variables was unclear, although it is suggested that rainfall is a major limiting factor to plant growth in the tropics (Bonnefille, 2010), and that herbaceous plants are very sensitive to climatic stress (Wright, 1992). Further investigations over a longer period are needed to provide a more accurate assessment of the impact of climatic variability on herbaceous plant communities in African forests.

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