Development of an herbaceous cover in a Sudano-Sahelian savanna in North Cameroon in relation to available soil water

J. Seghieri[1] , Ch. Floret[2] & R. Pontanier[3]
[1] *Centre ORSTOM, BP 11416, Niamey, Niger;*
[2] *Centre ORSTOM, BP 1386, Dakar, Senegal;*
[3] *Mission ORSTOM, 7 rue Teimour, 1004 El Menzah, BP 434, Tunis, Tunisia*

Abstract

Dynamics of annual communities are studied in Sudano-Sahelian savannas of the north of the Cameroon. The vegetation composition of three types of soil (a vertisol, a degraded vertisol and a ferruginous soil) under two rainfall conditions is compared. The study supports the idea that intense fluctuations in water availability at the beginning of the rainy season determine which species germinate, grow and survive under conditions of water stress. However soil conditions can accentuate or reduce the influence of the rainfall fluctuations while the land use history of each station tends to buffer the variations of the overall pattern determining potential vegetation.

Nomenclature: follows Hutchinson & Dalziel (1954–1972), *Flora of West Tropical Africa*, London, UK. Herbarium of l'Ecole pour la Formation des Spécialistes de la Faune in Garoua, BP 271, Garoua, Cameroon.

Introduction

The savannas under study belong to the Sudano-Sahelian region (Letouzey 1985). In these shrub- and arboreal savannas of northern Cameroon, vegetation is subject to strong water stresses that vary in time and space (Pontanier *et al.* 1984). These savannas undergo a annual dry period of six to eight months, despite an average annual rainfall of 600–800 mm between May–June and September–October (Olivry 1986). Timing of the first rains is very irregular.

Topography and physical soil properties, including soil surface strata (Casenave & Valentin 1989) have a strong effect on water availability for plants. These soils are highly diverse, both due to natural heterogeneity and human activities, the latter leading to edaphic aridification. We have therefore sought to analyse the way in which rainfall distribution and soil moisture regimes influence the establishment, development and final structure of the herbaceous cover during the rainy season. Although other factors may obviously affect

intraseasonal vegetation dynamics, the hydrological factor is emphased in this study.

Site description and methods

Site description

Three sites were chosen along a soil catena, occurring on a gentle slope (Fig. 1). The site at the top of the catena has a ferruginous soil that is sandy in the first 40 centimetres. With ferruginized gravel scattered on the surface. Sandy clay appears deeper down. Hardpan fragments are present in both these horizons. This site is a recent fallow less than 5 years old. The other two sites are located at the bottom of the toposequence, on old fallows (more than 10–15 years old). One has a typical vertisol composed of very thick horizons with high montmorillonitic clay content (40–50%). The soil has deep shrinkage cracks in the dry season. The third site has a highly degraded vertisol called 'harde', with

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a thin and widespread surface crust that considerably reduces its permeability. It is sandy-silty in texture and is derived from the typical vertisols by anthropic degradation. The rain efficiency coefficients (Ke = water infiltrated or 'efficient' rainfall/total rainfall, Floret & Pontanier 1984) are 80–90%, 75–80% and 20–50% on ferruginous soil, vertisol and harde respectively (Seiny-Boukar 1990).

The woody stratum is always present in these savannas. Ligneous plant cover is 30 to 50% on the ferruginous soil site, as compared to 20 to 30% on vertisol, and 5 to 7% on harde. Roots come down to more than 2 m of depth in ferruginous soil and vertisol, the densest being in the 40–50 first cm, and not under 50 cm in harde. Annual species compose 90% of the herbaceous stratum, with total cover varying between 5 to 80%, depending upon soil type and rainfall conditions. About one-third of the annual species present are forbs, and these are primarily on sandy soils. Grasses occur preferentially on clayey soils (Seghieri 1990).

Methods

On each station, 35 quadrats (30 × 30 cm) were installed under natural conditions in 1986. 15 were conserved in 1987, this last number of quadrats being sufficient to take into account 80% of species (reading abacus of Greig Smith 1964 in Milner & Hugues 1968). We followed the seasonal and inter-annual trends in total cover, floristic composition, richness in species and relative cover of each dominant species during two rainy seasons. The structure of the herbaceous cover at the end of the growing season (August) was described by the proportion of cover of the dominant species (the greatest relative covers which are the ratio specific cover/total cover) and the total number of contributing species. The total cover was not taken into account, because it is not significant in explaining variations between sites at this time of year, as will be explained below.

One rain gauge by site was installed. We verified that the total and the distribution of rainfall were the same due to the proximity of the three sites. One season of the study was conducted during a year of average rainfall, with 700 mm of rain distributed regularly (1986). The other was in a dry year, with 580 mm of rainfall distributed very irregularly (1987) (Fig. 2).

Soil moisture content was measured using a neutron humidimeter (Solo 20) until 80 cm of depth. Because of the imprecise measurements of the neutron probe for the first 20 cm of soil, additional data were obtained by

the gravimetric method for this layer. Moisture readings were taken once a week from the time of the appearance of the first shoots until the cover reached its seasonal maximum. It was assumed that water available for the plants was that lying at a potential greater than $\phi = -1.6$ MPa (Hillel 1988).

Results and discussion

Development of herbaceous cover

For a given rainfall condition, differences appeared among sites with respect to the development of the herbaceous cover. These may be related to differences in soil water.

In the year of average rainfall (Fig. 2 1986, and Fig. 3), the development of the cover was similar on sandy-textured (ferruginous) soil and on clay-textured soil (vertisol). Nevertheless, for the same distribution of rainfall vertisol retained more water than ferruginous soil between 0 and 20 cm of depth. That is why in the surface layers there was much less water transfer between two rains in the ferruginous soil than in the vertisol. The vertisol's high capacity for water retention, and the resulting considerable useful reserve in the upper horizons lessened the effect of intraseasonal variations in rainfall on the deeper ones. In the ferruginous soil, by contrast, much water was lost by deep seepage and by lateral drainage (Seiny-Boukar 1990). However, this disadvantage was less important for mature plants whose roots attain the deep clay layer.

Nevertheless, plant covers on the two types of soil had not very different development during regular and abundant annual rainfall (Fig. 2, 1986, and Fig. 3). In the case of the less abundant and highly irregular 1987 precipitation, the vertisol showed a more edaphic aridity than the ferruginous soil (Fig. 2, 1987). Under these conditions, the upper sandy layer became an advantage for plants growing on the ferruginous soil, since even small amounts of infiltrated water were available to them. This contrasts with the slowness of herbaceous plant development on the vertisol, due to a succession of drought periods affecting the first 20 centimetres (Fig. 2, 1987, and Fig. 4).

In terms of coverage, these results agree with those of Frost *et al.* (1986). When there is little rain, primary production on clay soils may be as little as, or even less than that of sandy soils, despite a greater chemical fertility (its CEC is about 35 meq./100 g of soil against 6–9 meq./100 g of soil for ferruginous soil,
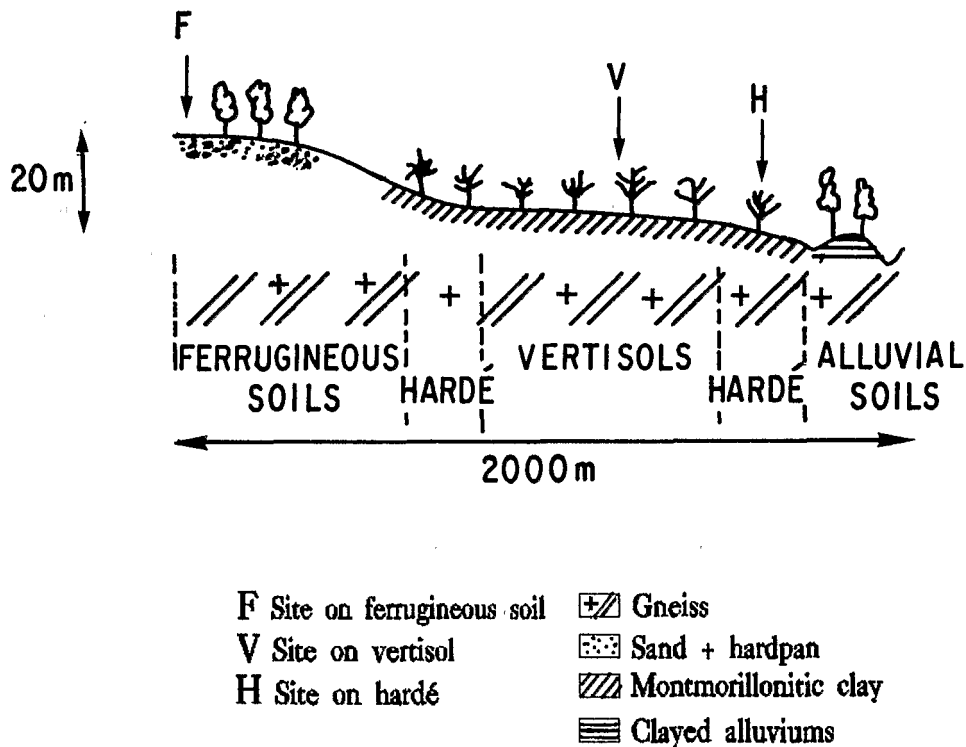
F Site on ferrugineous soil   ⊞ Gneiss
V Site on vertisol   ▦ Sand + hardpan
H Site on hardé   ▨ Montmorillonitic clay
                              ≣ Clayed alluviums

Fig. 1. Catena of the soils and position of the three sites.

Seiny-Boukar 1990). In a water-poor year, this better trophic level could increase the risk of aridity, causing more rapid water consumption (i.e., greater water use efficiency by the plants). This agrees also with the results of Fournier (1990), who compared the herbaceous productions of savannas on sandy and on clay soils in very dry regions of West Africa. For savannas on sandy soil, water is available very soon after rainfall, due to greater permeability and, especially, very low soil moisture, equivalent to the permanent wilting point (−1.6 MPa). The risk of high inter-annual variations in herbaceous cover is thus greater on soils with high clay content (vertisol) than on sandy soils (ferruginous soil) (Dye & Spear 1982). With regard to harde (Fig. 2, 3 and 4), edaphic aridity explains perfectly the maintenance of the cover at very low levels during both the 1986 and 1987 years, because of the surface impermeability of the soil (Floret & Pontanier 1984).

The period of low water availability following the end of June 1987 caused a high rate of plant mortality, and hence a drop in cover both in ferruginous soil and in vertisol (Fig. 2). 'Continuous growth' (Cisse 1986) or 'linear growth' (Penning de Vries 1982) was unable to begin at the moment of 'heavy rains' (Hiernaux 1984), as was the case in 1986. In 1987, new germination and development followed the drought stress at the end of June. Thus, the period during which plant growth was possible was much shorter during the second year, leading to lower final cover on the three types of soil. The poor development in 1987 compared to 1986 was all the more marked in that the rainfall following the period of establishment of the plants (July–September) was lower in 1987 than in 1986. That is why it is recognised that, in both the semi-arid and the arid environments, grass development in a given season is determined not only by the onset of rainfall, but also by the amount of the first rains and by the
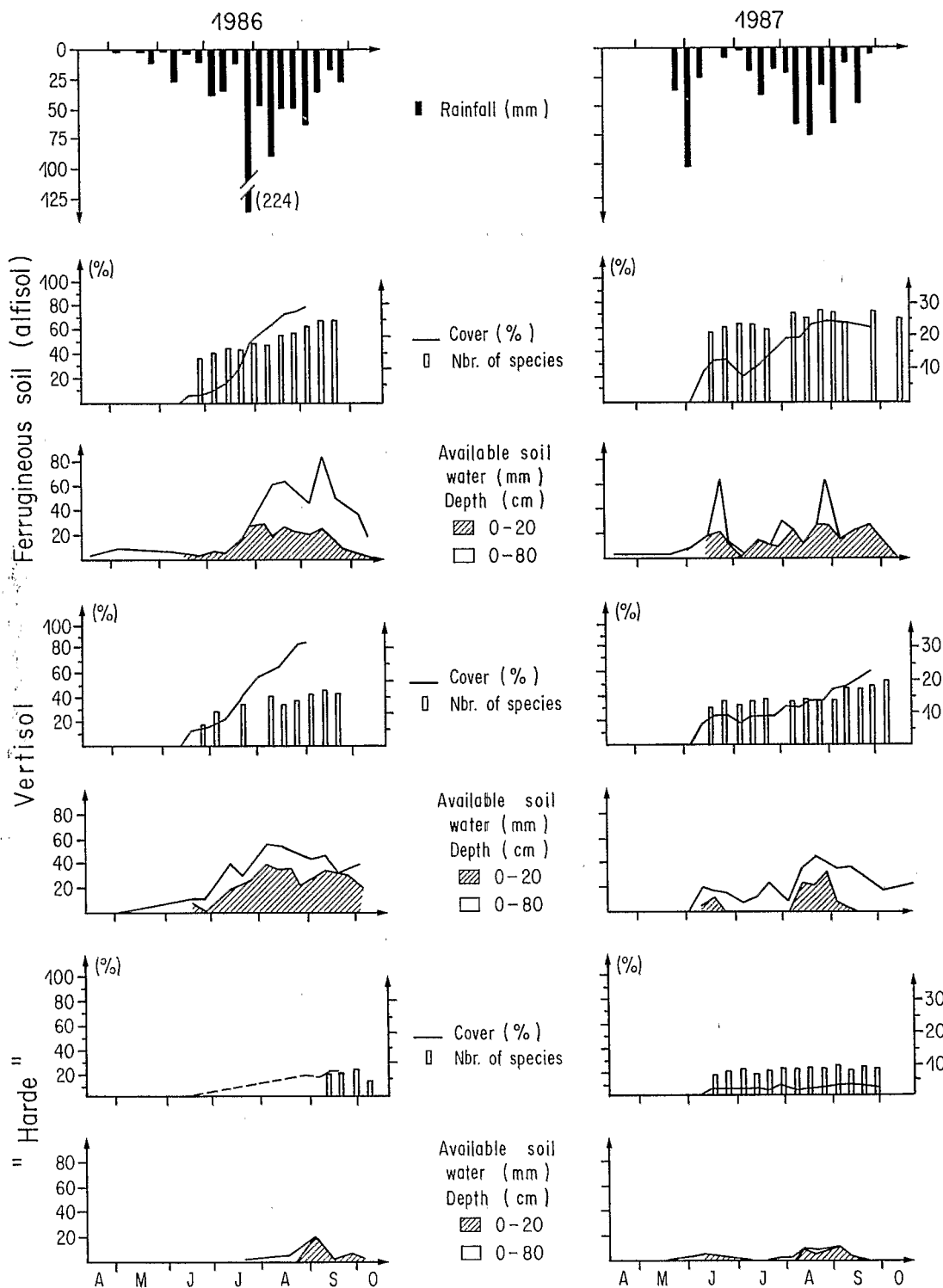
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Fig. 2. Seasonal changes in percentage cover and the number of herbaceous species on ferruginous soil, vertisol and harde, in relation to rainfall and available soil water during 1986 and 1987.
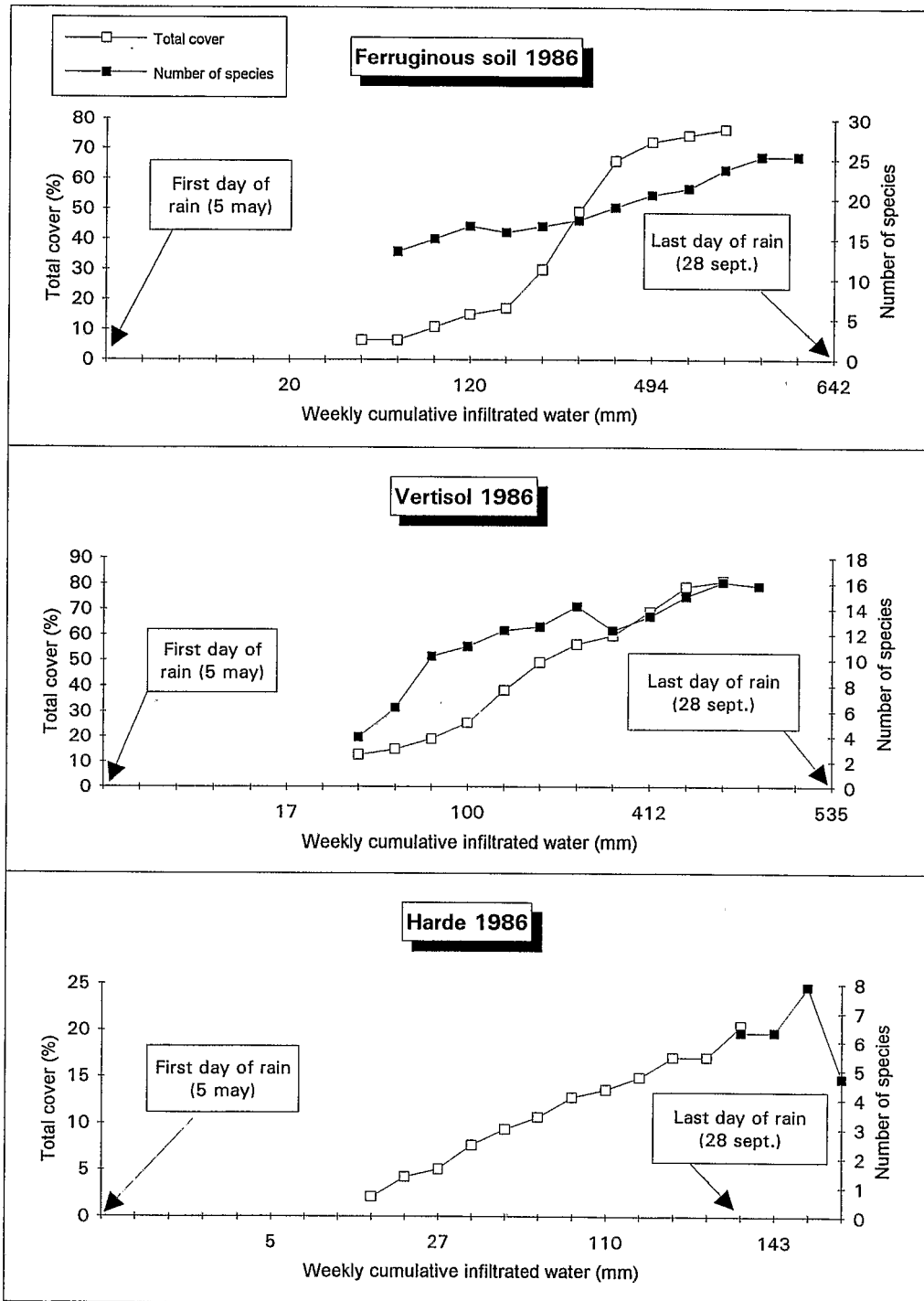
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Fig. 3. Total cover (%) and number of herbaceous species in relation to weekly cumulative infiltrated water on ferruginous soil, vertisol and harde in 1986.
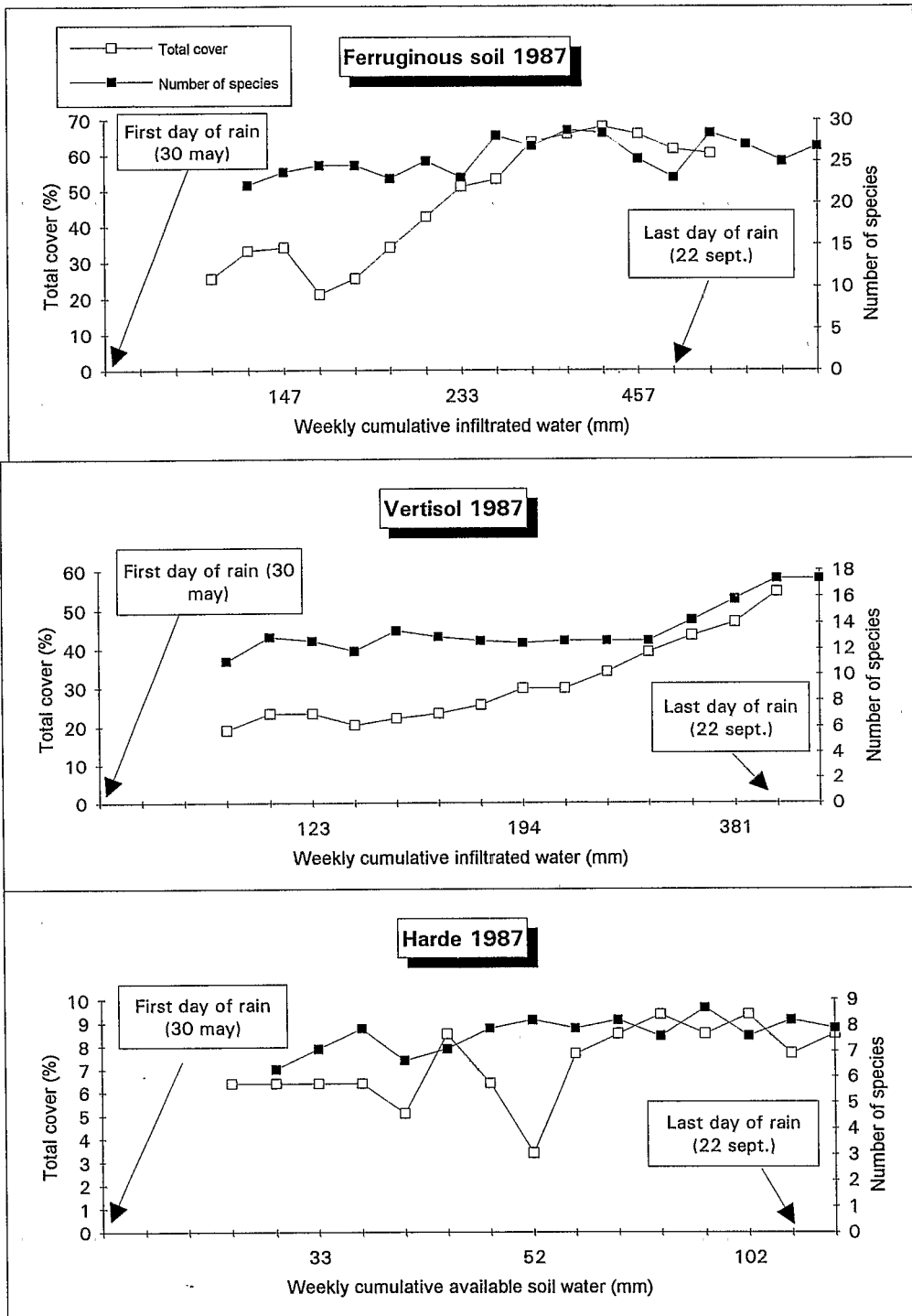
Fig. 4. Total cover (%) and number of herbaceous species in relation to weekly cumulative infiltrated water on ferruginous soil, vertisol and harde in 1987.

regularity of those which follow them (Beatley 1974; Hiernaux 1984).

On the other hand, there is an arrest in growth of the cover before the end of the rainy season in most of the types of soil during the two years: maximum cover is reached at the end of August on ferruginous soil and vertisol in 1986, and on ferruginous soil and harde in 1987 (Fig. 2); on ferruginous soil and vertisol in 1986 (Fig. 3), and on ferruginous soil and harde in 1987 (Fig. 4), total cover has stopped to increase whereas cumulative infiltrated water goes on. These results show the limited duration of plant growth among communities of annual species. It argues in favour of their adaptation to environments in which high amounts of water are available for only a short time (Cornet 1981; Jackson & Roy 1986; Grouzis 1987). This confirms that in the herbaceous communities of the southern part of the Sahel, dominated by annual grasses, it is almost never water shortage which determines the end of growth (Stroosnijder & Kone 1982).

Trends in species richness

The intra-seasonal dynamics of the number of species on a given station strongly depends on the distribution of rains during the growing season. A gradual increase in cumulative rainfall, as in 1986, makes possible an equally gradual increase in the number of species recorded per month (Fig. 2, 1986 and Fig. 3). Appearance of the species is spread out over time, and there is a fairly slow occupation. If the beginning of grass development is triggered by heavy rains, as was the case in 1987, the number of species is nearly at its maximum from the beginning of the rainy season, and then fluctuates around a average without any high global increase (Fig. 2, 1987 and Fig. 4). The late appearance of new species is only possible if part of the stand already in place dies. The irregularity of the rains at the beginning of the season contributes greatly to this renewal, by acting on the species least resistant to water stress. In a semi-arid environment a species' establishment and relative importance in the community depend not only on the rapidity of its germination and early growth (i.e., its competitiveness) but also on the proportion of its population surviving successive intra-seasonal water stresses, especially at the beginning of the rainy season. It is primarily by this type of selection that the interannual variability of rainfall distribution acts on the inter-annual variability of the composition and final structure of the grass car-

pet (Frost *et al.* 1986; Grouzis 1987; Walker & Menaut 1988; Fournier 1990).

Variations in the final pattern of the community

Results are summarised in Table 1. Briefly, on harde, the water deficit was reflected in the establishment of a small number of species (7–9) all of which are marked by a considerable dwarfing peculiar to this type of station. This is a typical drought adaptation of many species to the Sahel (Bille 1975). Species resistant to water stress (e.g., *Schoenefeldia gracilis, Microchloa indica*) predominate. The herbaceous stratum on harde is thus dominated by plants which are related to the 'S' (stress) strategy of Grime (1982). Plants of this type have a very low vegetative development imposed by the shortage water. Few species can coexist, in comparison with typical vertisol and ferruginous soil (Table 1). We observed that *Microchloa indica* is nearly eliminated from the other two sites. It is a species adapted to open environments (Breman & Cisse 1977). It remains very small in size even in the most favourable conditions (Seghieri 1990) which leads to its high decrease because other species prevent its light access. This is a process of competitive exclusion (Keddy 1989). For *Microchloa indica*, there is thus a negative correlation between water- and light availability. This shows how variations of a resource-ratio such as water/light can control the dynamics of communities (Tilman 1987). *Schoenefeldia gracilis* is much more abundant than *Microchloa indica*, but not dominant, on ferruginous soil and vertisol. It has bigger size on them than on harde. This illustrates the importance of plasticity for species survival in an heterogeneous and changing environment (Tilman 1987).

In contrast to the harde site, the composition and the structure of the community growing on vertisol retain the characteristics acquired during numerous years of abundant soil water conditions. The station is dominated, the two years, by two species more widespread in the Sudanian than in the Sahelian region – *Loudetia togoensis* and *Andropogon pseudapricus* (Table 1). Also found in noticeable quantities are species that thrive on an excess of water (*Sporobolus festivus, Panicum laetum, Fimbristylis hispidula, Spermacoce filifolia*). The high homogeneity of the soil favours the dominance of the same three species each year, determining a very stable floristic composition (exactly the same dominant species and the same total number of species each year, composed with nearly the same species).

Table 1. Vegetation pattern in mid August in relation to year and type of soil Ap = *Andropogon pseudapricus*; Bs = *Brachiaria stigmatisata*; Da = *Dactyloctenium aegyptium*; Lt = *Loudetia togoensis*; Mi = *Microchloa indica*; Se = *Schizachyrium exile*; Sg = *Schoenefeldia gracilis*; Sp = *Setaria pumila*; Tc = *Tetrapogon cenchriformis*; Fe = Ferruginous soil; Ve = Vertisol; Ha = Harde.

		1986	1987
Fe	Total number of species	22	28
	Relative cover (%) of	Bs (43)	Sp (44)
	dominant species	Se (27)	Da (25)
		Sp(27)	Bs(15)
Ve	Total number of species	14	14
	Relative cover (%) of	Lt (34)	Lt (44)
	dominant species	Se (20)	Se (28)
		Ap(15)	Ap(15)
Ha	Total number of species	7	9
	Relative cover (%) of	Sg (64)	Sg (48)
	dominant species	Mi (34)	Tc (23)
			Mi (18)

Finally, on ferruginous soil, the considerable heterogeneity of the substrate determines the coexistence of a larger number of species than on the other two stations (between 19 and 28). The discontinuous presence of surface cuirass leads to soil depth being highly variable. Moreover, the density of ligneous plants is greater here than on the other soils. This determines the differentiation on this site of a large number of micro-sites, distinguished by soil moisture conditions, nutrient contents, and the depth of root occupancy. These are potential niches for resource use and 'refuge' for annual species less well adapted to the average seasonal conditions of the station (Godron *et al.* 1981; Frost *et al.* 1986). The low chemical fertility of the soil on the surface (accentuated by a recent and intensive agricultural exploitation) contributes to the appearance of a large number of species by limiting the growth and the reproduction of the plants, and therefore the rate at which the species reach competitive equilibrium (Frost *et al.* 1986). It also limits the contribution made to the cover by the species which dominates each year, hence its relative stability (43 and 44% of the cover), despite a quasi-annual renewal of the species occupying this rank (Table 1). The diversity of micro-sites always makes it possible for the species which are disadvantaged one year on any one of them to install

themselves on another. From one micro-site to another, the species 'avoid' competition and coexist thanks to a very marked spatial differentiation of available resources. This pattern is maintained at the site scale by spatial micro-heterogeneity ('non-coexistence equilibrium', Van der Maarel 1988). Spatial heterogeneity thus combines with temporal variability of water availability to modify the hierarchy every year, on the basis of the complementarity of species (Rice 1989).

Conclusion

In arid and semi-arid land it is useful to say that water availability strongly determines vegetation (Floret & Pontanier 1984; Frost *et al.* 1986; Fournier 1990). It is confirmed that the inter-annual dynamics of the herbaceous stratum of the Sudano-Sahelian savanna studied is determined above all by the distribution of precipitation at the beginning of the season. Irregular rainfall in a region of high evapotranspiration creates a succession of constraints and opportunities for the establishment and development of any given species. From the time when rainfall becomes regular (July), periods of drought, which are edaphic on the upper horizon and climatic during the season, become extremely rare. Rainfall is no longer a limiting factor and the plants already established mature. This is why the selection of species constituting the community intervenes essentially during the stages of germination and establishment. The edaphic characteristics exercise a much longer term form of selection, and give rise to a certain inertia in the system. The relative abundance of plants present as seeds in the soil, the flora spectrum of which is inherited from the preceding years, amplifies or reduces the effect of rainfall distribution on the relative importance of a species in the final community (Seghieri 1990). In addition, the edaphic conditions (chemical fertility, structure and texture, heterogeneity) evolve only very slowly, and can be considered as constant in our case (a period of two years). In the short term, for a specific type of soil, they tend to dampen the effects of interannual rainfall variations on the fluctuations of the final organisation of the herbaceous cover. As a result, no important changes occur from one year to the next in the species which predominate on a site. On the other hand, the redistribution of precipitation along a toposequence, due to micro topography, heterogeneity of the surface states (Casenave & Valentin 1989), and the physical and water characteristics of the substrate, cause a marked spatial differentiation in soil

moisture regime. This is expressed in the form of mild variations in the final structure of the herbaceous cover and in reactions of the plant community (peculiar to each site) in the face of annual changes in rainfall. With respect to the soil, the effects of within-season water stresses are accentuated or attenuated by the edaphic characteristics at each site (Floret & Pontanier 1984). Thus a deep clay soil such as vertisol accentuates the seasonal contrasts that cause more marked aridity in dry season or intra-seasonal dry periods, and greater quantities of available water over a longer period in wet years. Harde reinforces climatic drought by limiting the proportion of water infiltrating the soil (Thebe 1987) even in a favourable year. Lastly, the ferruginous soil constitutes the substrate which reacts most directly to rainfall variations.

This gradient of water availability gives rise to a hierarchy of predominant species. The most competitive species for water resources (e.g., *Loudetia togoensis*) predominates at the most favourable end of the spectrum (vertisol), while species that are less competitive but can withstand the lack of water (e.g., *Schoenefeldia gracilis*, *Microchloa indica*) predominate at lower levels of water availability (harde). On ferruginous soil, the accessibility of available water to plants is modified by the heterogeneity of the site and by low surface chemical fertility of the soil. These two characteristics lead to a more complex community structure, and high annual variations described above. This last result confirms previous ones obtained by other authors (Godron *et al.* 1981; Gibson & Hulbert 1987).

Acknowledgments

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