

Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon

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ABSTRACT. Phenological patterns of herbaceous and woody plants well represented in the Sudano-Sahelian savannas of northern Cameroon were studied in relation to water availability in three contrasted soil types. Mean annual precipitation in this region is 800 mm, entirely restricted to the period May-June to September-October, but redistribution of rainwater by varying soil substrates leads to considerable heterogeneity in available water resources for plants. Results are discussed in terms of probable competition for water resources among co-occurring plants and the adaptations shown by observed patterns to prevailing environmental conditions. Water stress is seen to be a limiting factor to plant growth but does not constitute the sole trigger for the phenological phases observed, nor is it the principal factor responsible for the preponderance of annual species in the herbaceous stratum.

KEY WORDS: adaptation, northern Cameroon, phenological strategies, savanna, water resources, water stress.

INTRODUCTION

Phenological studies exist for tropical plants, especially in Africa (Duranton 1978, Fournier 1990, Grouzis & Sicot 1980, Merlier 1972, Prins 1988). As phenology is a valuable way for understanding the co-occurrence of species (Frankie *et al.* 1974), studies must be multiplied to draw general laws which govern vegetation patterns. Le Floch (1969) defined phenology as 'the study of the relations between the periodicity of morphological and physiological phenomena of plants and that of ecologically active, particularly climatic variables'. Lieth (1974) elaborated on this definition by stating that phenology studies '(1) the rhythm of repetitive biological events, (2) the biotic and abiotic causes for these rhythms and (3) the relations between phenophases of different species or of a single species'.

In an environment where the limiting factor is water, competition is inevitable among plants occupying the same above-ground stratum and the same soil

horizons. This forces each species to optimize its use of water in both time and space (Granier & Cabanis 1975). Moreover, co-occurring species that show similar phenological rhythms in the vegetative phase often differ in the timing of their reproductive phase. This allows a categorization of phenological patterns or strategies at different levels of similarity (Monasterio & Sarmiento 1976). In the present study, we pay particular attention to flowering phenology. Furthermore, phenological studies of plants with forage potential – as is the case for most of our species – is an indispensable element for a proper evaluation of each one's forage value (Piot *et al.* 1980, Prins 1988).

Shrub and tree savannas of northern Cameroon receive an average of 800 mm annual precipitation from May–June to September–October, yet undergo severe water stress for 6–8 months of each year (Pontanier *et al.* 1984). Additionally, soil heterogeneity is high, as is variability in the stages of soil profile and surface degradation (Casenave & Valentin 1989). Both these factors play an important role in determining water availability for plants. Finally, over-exploitation of soils for agriculture leads to severe malfunctioning of water cycles and increasing surface impermeability (Pontanier *et al.* 1984, Seiny-Boukar 1990, Seiny-Boukar *et al.* 1992).

In our study area, the savannas of the Sudano-Saharan zone of northern Cameroon, the herbaceous stratum consists of 90% annual species occurring under a ubiquitous woody stratum of tall shrubs or trees (Donfack 1991, Letouzey 1985). The irregular distribution of water appears to be the principal determining factor for plant growth throughout the study area (Letouzey 1985). By analysing the phenology of the principal species of these two strata, we sought to determine how different species distribute their life cycle over the course of two rainy seasons on three different types of soil, each of which shows very distinct hydrological characteristics.

The hypotheses we sought to test were: (1) on soils where water is available only briefly and in small quantities, plant life cycles will be adaptively shortened (Cissé 1986, Fournier 1990); (2) the co-occurrence of woody and herbaceous species in Sahelo-Saharan savannas is made possible by the phenology of the first group being out-of-phase with that of the second (Ovalle & Avendano 1987); and (3) the relative independence of phenology of savanna woody plants to rainfall is due to their root systems having access to ground water lying at great depths (Aronson *et al.* 1994, Noy-Meir & Walker 1986, Walker & Noy-Meir 1982).

MATERIALS AND METHODS

Over 20 months, including two rainy periods (April 1986–November 1987), we recorded the appearance of leaves, flowers and fruits for the majority of herbaceous species and the most abundant woody species occurring on three soil types of the Mouda watershed, 30 km south of Maroua, in the Diamaré plain, in northern Cameroon (north of the 10th parallel, 20 km on east of the 14th

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degree of longitude). The watershed has been the subject of a map at 1/40,000 scale, showing ecosystems and soils which compose it (Donfack 1991, Seghieri 1990, Seiny-Boukar 1990). On this map we chose a typical toposequence and we placed the three sites to be able to generalize the results to soil types well described in the literature on West Africa (Brabant & Gavaud 1985, Pontanier *et al.* 1984).

The three soil types are:

- (A) a ferruginous soil, situated at the top of the toposequence. The top 40 cm are sandy, with poor nutrient and water retention capacity. The underlying clayey-sandy stratum shows high permeability. The coefficient of rainfall efficiency, K_e (infiltrated water/total rainfall, in percentage, Floret & Pontanier 1984) measured on the ferruginous soil of the same toposequence over a period of 5 y is 80–90% (Thébé 1987), but it has a low potential water reserve (WR) (*c.* 73 mm in 80 cm of soil). Generally, this type of soil is burnt by people in December–January to prepare it for rainy season cultivation;
- (B) a typical vertisol, on the lower slope, with a high percentage of montmorillonitic clays, rather low permeability ($K_e = 75\text{--}80\%$), and high WR (*c.* 178 mm in 80 cm of soil). Large, deep surface cracks permit deep water infiltration at the beginning of each rainy season. This type of soil is always burnt by the people in October, just after the rainfall has stopped, to bed out the 'muskuari' which is a sorghum species cultivated in part of the dry season;
- (C) a badly degraded, over-exploited vertisol, locally known as 'hardé', with sandy-silty texture and without surface cracks. A thick surface crust inhibits permeability ($K_e = 20\text{--}50\%$), which in turn causes rapid and intense surface run-off. Notwithstanding, this soil has rather high WR (*ca.* 155 mm for 80 cm of soil) (Seiny-Boukar 1990).

Potential Water Reserve (WR) of a soil is the difference between its water content at the field capacity and its water content at the permanent wilting point multiplied by the soil depth considered.

Soil water contents were measured with a Solo 20 neutron scattering device, placed one per site. We assumed that soil water is available for plants when soils show water potential above -1.6 MPa (Hillel 1988). Thus, phenology is related to soil water content above -1.6 MPa in the three sites, i.e. Soil Water Availability $SWA = \Sigma$ (water content at time t – water content at -1.6 MPa) \times depth in decimetres. SWA has been calculated every 10 cm of depth up to 80 cm. Rainfall was recorded with permanent rain gauges installed at each study site. Relative humidity and temperature data were provided by the near-by meteorological station at Maroua-Agro, representative of the study area.

Weekly observations of herbaceous plant phenology were carried out throughout each rainy season on populations of each study site according to the method

proposed by Duranton (1978). Only on 'hardé', observations started later in 1986 because of very sparse vegetation and small plants which led us astray and made us delay the first observations. After burning, no herbaceous plants survived; that is why there were no observations. On each site, in 1986, 35 quadrats 30 × 30 cm in size were randomly marked in a circle of 10 m radius around one neutron scattering device. Only 15 quadrats were retained in 1987 to represent the variability of soil conditions. This number of quadrats was sufficient to take into account 80% of species (reading abacus of Greig-Smith 1964 in Milner & Hugues 1968). For each species in each quadrat, leafing, flowering and fruiting were recorded. We noted the beginning, peak and end of each phenological phase as the percentage of the population.

For each phenological phase:

Leafing:	Beginning	Young leaves appear;
	Peak	The plant has plenty of leaves;
	End	Leaves lose their green colour, wither and fall;
Flowering:	Beginning	Floral buds clearly appear; for graminaceous plants, inflorescence comes out from the last leaf;
	Peak	Flowers are open and all organs are turgescient;
	End	Fecundation has taken place and male and sterile organs wither;
Fruiting:	Beginning	Fruits are growing;
	Peak	Fruits ripening;
	End	Diaspores dissemination;

For woody plants, we employed the method of Grouzis & Sicot (1980), whereby the number of individuals observed for each species is proportional to its relative importance at the study site. Only the most abundant species were included (Table 1). Sample size was also limited to exclude individuals too far from the place of measurement of soil water to ensure good estimates of soil water potential in each individual's root zone. In contrast with herbaceous species, phenological phases of each individual woody plant were recorded at six stages: 0 – absent, 1 – beginning, 2 – weak, 3 – peak, 4 – declining, 5 – end.

For leafing, the following stages were selected:

1. Swelling buds, no leaf development;
2. Leaf buds and open buds (over 10% and less than 50% of these organs in each individual);
3. Leaves mostly open;
4. Leaves and dry leaves, or leaves which have changed colour (over 10% but under 50%);
5. Over 50% in each individual with dry leaves and falling leaves; this is a difficult stage to monitor since it may extend over several months according to the species.

Table 1. 1
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Species

Sclerocarya bi
Acacia hockii
Acacia senega
Acacia gerrardii
Dichrostachys
Lannea humilis
Acacia seyal
Balanites aegy
Sterculia setigera
Ziziphus maurandia
Entada africana
Combretum fruticosum
Combretum glaberrimum
Ptilostigma retortifolium
Anogeissus leiocarpa
Ptilostigma thurberi
Bridelia ferruginea
Annona senegalensis
Strychnos spinosa
Dombeya quinquefolia
Combretum colobifolium

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Table 1. Number of individuals of the selected woody species found on three soil types in a circle of 30–50 m radius around place of measurement with neutron humidimeter. Nomenclature follows Hutchinson & Dalziel (1954–1972).

Species	Soil types		
	Ferruginous soil (A)	Vertisol (B)	'Hardé' (C)
<i>Sclerocarya birrea</i>	3	2	1
<i>Acacia hockii</i>	10	5	5
<i>Acacia senegal</i>	—	—	5
<i>Acacia gerrardii</i>	—	—	10
<i>Dichrostachys glomerata</i>	—	—	6
<i>Lansea humilis</i>	—	5	10
<i>Acacia seyal</i>	—	11	5
<i>Balanites aegyptiaca</i>	—	5	5
<i>Sterculia setigera</i>	2	—	3
<i>Ziziphus mauritiana</i>	—	10	—
<i>Entada africana</i>	—	6	—
<i>Combretum fragrans</i>	—	6	—
<i>Combretum glutinosum</i>	10	5	—
<i>Piliostigma reticulata</i>	3	10	—
<i>Anogeissus leiocarpus</i>	10	5	—
<i>Piliostigma thonnigii</i>	7	—	—
<i>Bridelia ferruginea</i>	10	—	—
<i>Annona senegalensis</i>	10	—	—
<i>Strychos spinosa</i>	5	—	—
<i>Dombeya quinqueseta</i>	5	—	—
<i>Combretum collinum</i>	5	—	—

For flowering, the following stages were monitored:

1. Floral buds only;
2. Floral buds and open flowers (over 10% and less than 50%);
3. Over 50% of organs carrying open flowers;
4. Open flowers and dry flowers (over 10% and less than 50%);
5. A majority of dry flowers and shedding of floral elements.

Fructification was characterized by the following stages:

1. Early setting stage;
2. Development of fruits to normal size;
3. Maturity;
4. Ripe fruits and onset of dissemination (opening of pods or falling of fruits);
5. Fruits dried and fallen.

In rainy seasons, observations were carried out weekly, in dry seasons, only once a month.

RESULTS AND DISCUSSION

Figure 1 shows the distribution of temperature, rainfall and soil water availability during 1986 and 1987 on the three sites. In 1986 the total rainfall for the

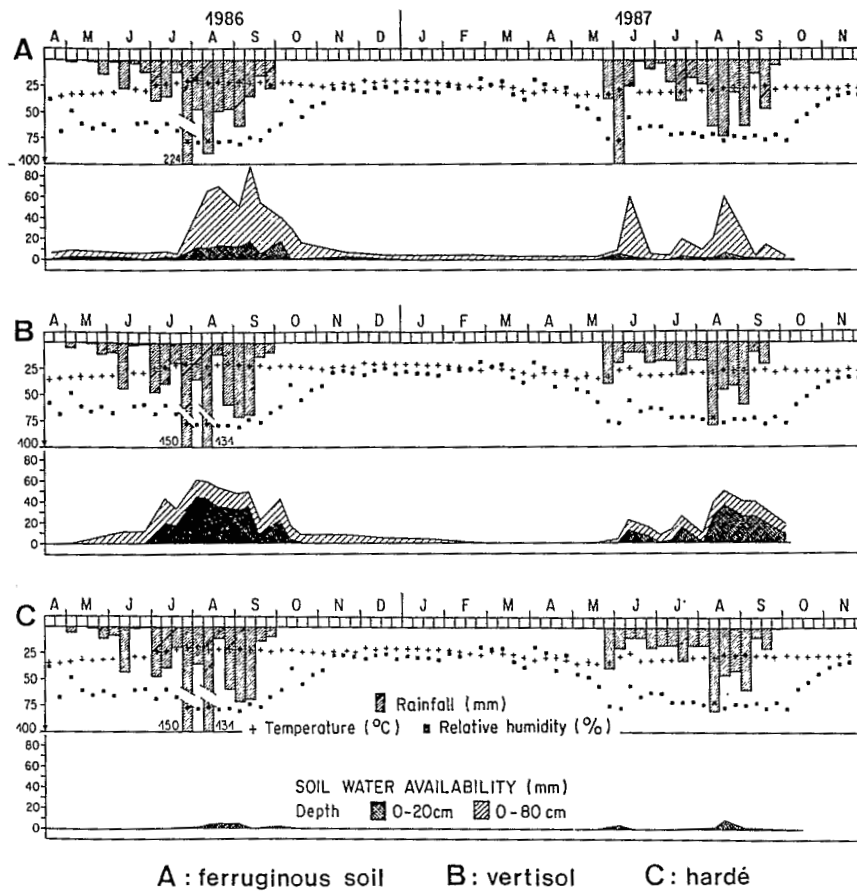


Figure 1. Climate and soil water availability during 1986 and 1987, A in ferruginous soil, B in vertisol and C in 'hardé'.

region was 700 mm, which was well distributed over the wet season. In contrast, 1987 was a drier year with 580 mm and with a more irregular distribution of rain events. The principal results for herbaceous species are presented in Figures 2 and 3, and for woody species in Figure 4. The two years for which observations were conducted were dissimilar in their rainfall patterns. On the 'hardé' soil, few phenological differences occurred between the two years, probably due to poor water infiltration (Figure 1). For the other two soil types, however, less water was available to plants in 1987 than in 1986, and periods suitable for establishment of annuals were interrupted by periods of edaphic drought in the top 20 cm of soil (Figure 1). Accordingly, magnitude of the flowering was lower in 1987 than in 1986 for woody plants (Figure 4).

The species have been separated in several groups based primarily on the onset, duration and variability of flowering during the two years on the three soil types (Table 2).

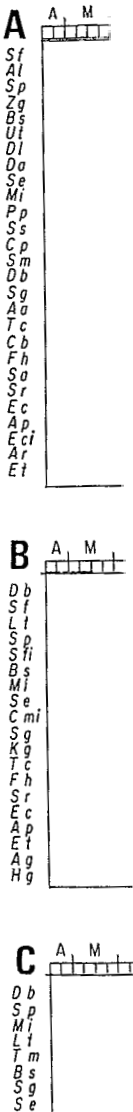
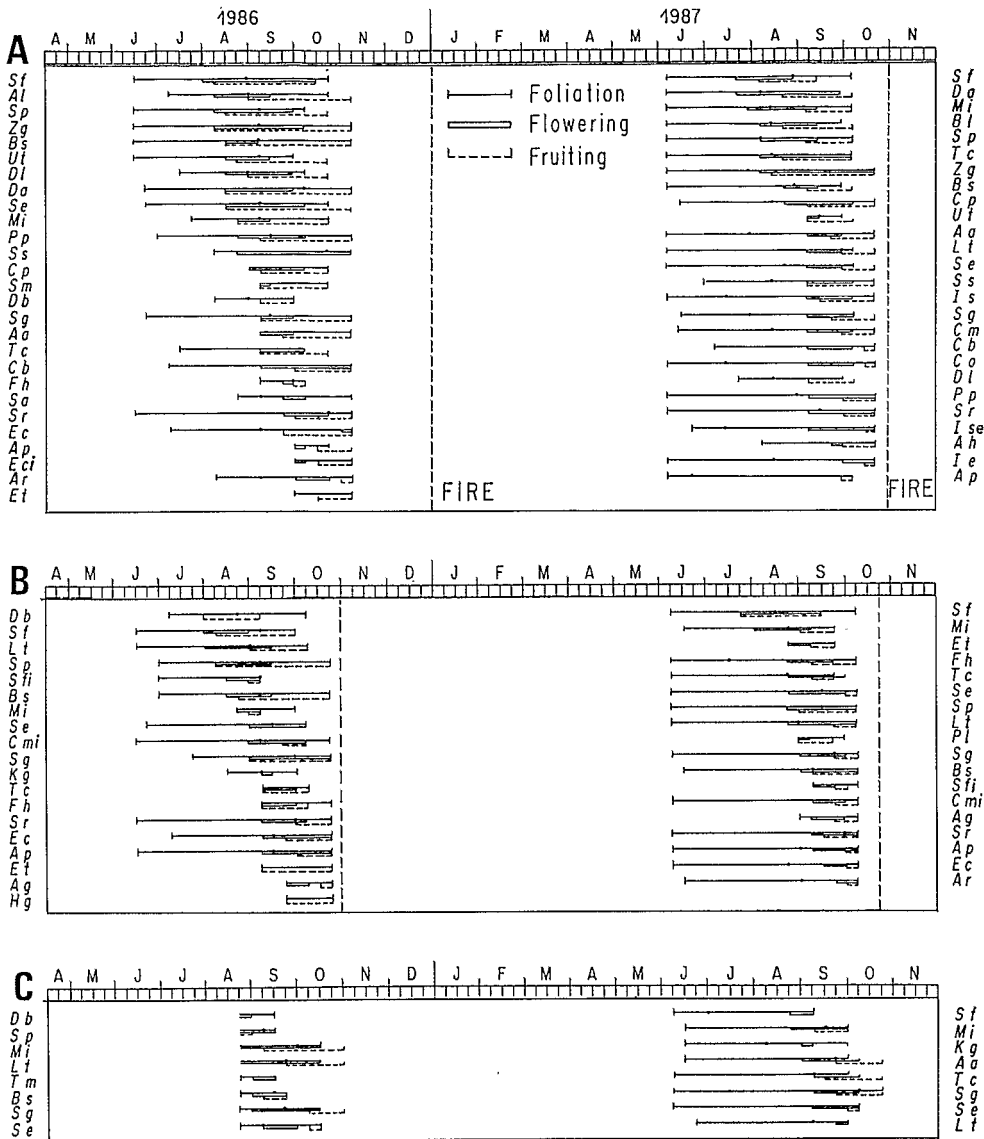


Figure 2. Phenology of herbaceous species in ferruginous soil. Aa: *Aristida adscandens*; Ar: *Crotalaria microcarpa*; Db: *Drimiopsis bursiflora*; Sg: *Schoenefeldia stachydeia*; Tc: *Tillandsia usneoides*; Ch: *Chenopodium album*; Sa: *Sida acuta*; Sr: *Sida sp.*; Ec: *Echinochloa crusgalli*; Ect: *Echinochloa crusgalli*; Ar: *Aristida adscandens*; Et: *Echinochloa crusgalli*.



A : ferruginous soil B : vertisol C : hardé

Figure 2. Phenology of some herbaceous species on each type of soil and during 1986 and 1987, A on ferruginous soil, B on vertisol and C on 'hardé'. Species are arranged in order of flowering precociousness.

Aa: *Aristida adscensionis*; Ag: *Andropogon gayanus*; Ah: *Aristida hordeacea*; Al: *Aneilema lanceolatum*; Ap: *Andropogon pseudapricus*; Ar: *Alysicarpus rugosus*; Bl: *Brachiaria lata*; Bs: *Brachiaria stigmatiasata*; Cb: *Crotalaria barkae*; Cm: *Crotalaria microcarpa*; Cmi: *Cassia mimosoïdes*; Co: *Cassia obtusifolia*; Cp: *Chloris pilosa*; Da: *Dactyloctenium aegyptium*; Db: *Drimiopsis barteri*; Dl: *Digitaria leucardii*; Ec: *Euphorbia convolvuloides*; Eci: *Eragrostis ciliaris*; Et: *Eragrostis turgida*; Fh: *Fimbristylis hispida*; Hg: *Hachelochloa granularis*; Ie: *Ipomea eriocarpa*; Is: *Indigofera stenophila*; Ise: *Indigofera secundiflora*; Kg: *Kohautia grandiflora*; Lt: *Loudetia togoensis*; Mi: *Microchloa indica*; Pl: *Panicum laetum*; Pp: *Pennisetum pedicellatum*; Sa: *Striga asiatica*; Se: *Schizachyrium exile*; Sf: *Sporobolus festivus*; Sfi: *Spermacoce filifolia*; Sg: *Schoenefeldia gracilis*; Sm: *Sporobolus microprotus*; Sp: *Setaria pallide-fusca*; Sr: *Spermacoce ruelliae*; Ss: *Spermacoce stachydea*; Tc: *Tetrapogon cenchriformis*; Tm: *Tripogon minimus*; Ut: *Urochloa trichopus*; Zg: *Zornia glochidiata*.

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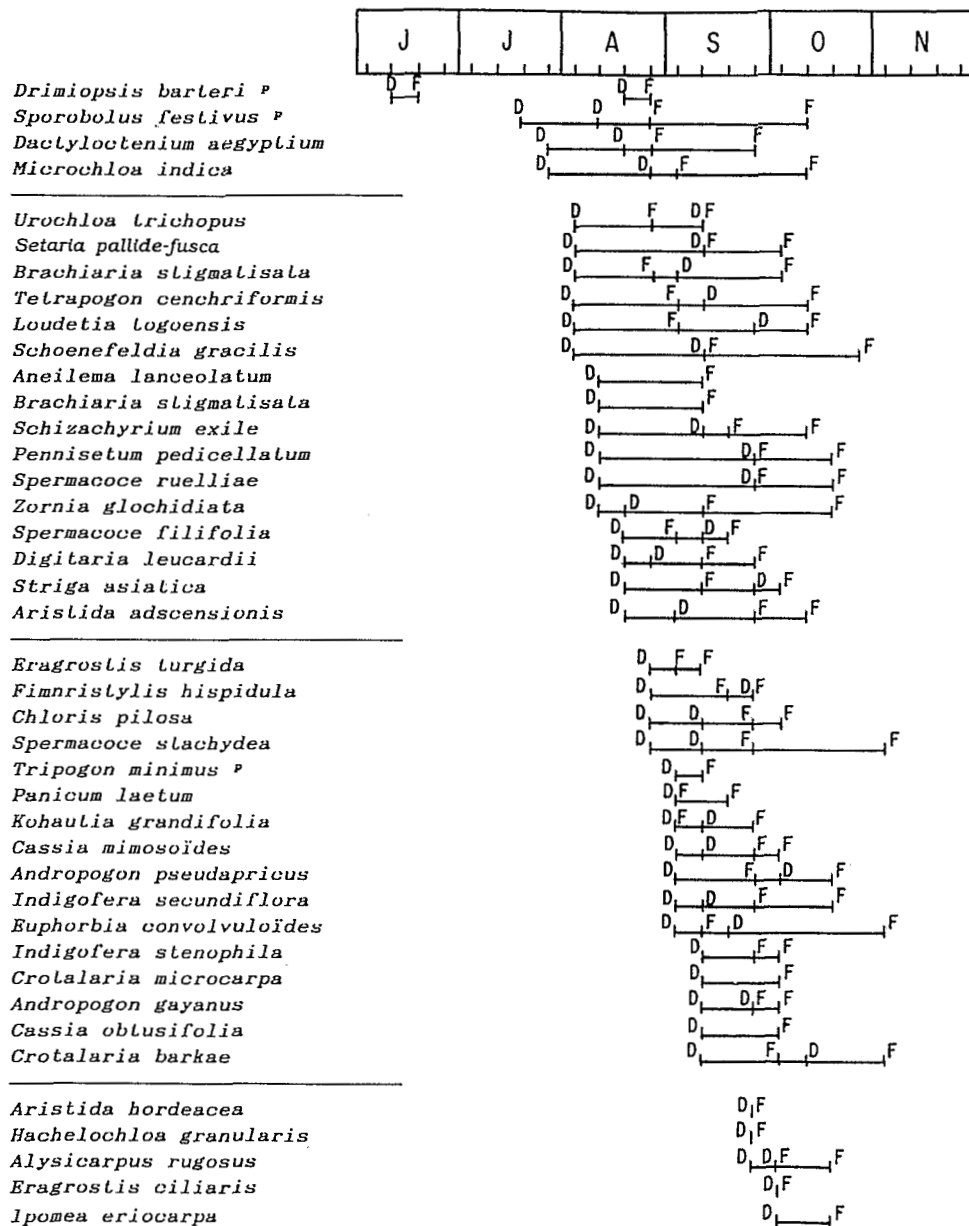


Figure 3. Timing of flowering of selected herbaceous species at Mouda, northern Cameroon, on the three sites, ferruginous soil, vertisol and 'hardé', during 1986 and 1987. p=perennial species.

The first D is the first date at which we observed a beginning of flowering; the second D is the last date at which we observed a beginning of flowering; between the two D's, there is the length of the beginning of flowering for one species on the three sites; when there is only one, that means beginning of flowering was observed only one time (i.e. its length is inferior to one week). It is the same principle for F, the end of flowering.

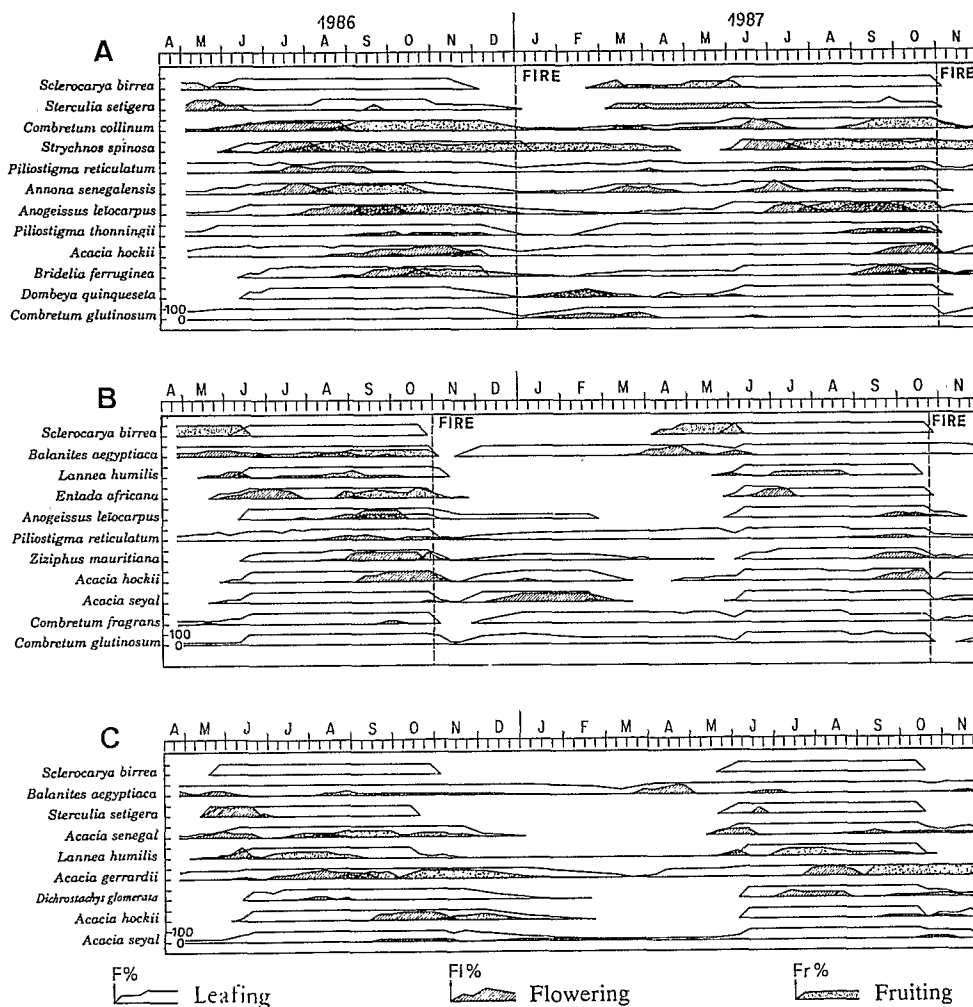
- A**
- Sclerocarya birra*
 - Sterculia setiger*
 - Combretum collini*
 - Strychnos spine*
 - Piliostigma reticulat*
 - Annona senegalens*
 - Anogeissus leiocarp*
 - Piliostigma thonning*
 - Acacia hooi*
 - Bridelia ferrugin*
 - Dombeya quinque*
 - Combretum glutinosu*

- B**
- Sclerocarya birra*
 - Balanites aegyptia*
 - Lannea humi*
 - Entada africa*
 - Anogeissus leiocarp*
 - Piliostigma reticulatu*
 - Ziziphus mauritia*
 - Acacia hooi*
 - Acacia sey*
 - Combretum fragra*
 - Combretum glutinosu*

- C**
- Sclerocarya birra*
 - Balanites aegyptiac*
 - Sterculia setiger*
 - Acacia senega*
 - Lannea humilli*
 - Acacia gerrardi*
 - Dichrostachys glomerat*
 - Acacia hooi*
 - Acacia seyo*

Figure 4. Phenology of species A and C on 'hardé'.

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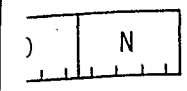


A : ferruginous soil B : vertisol C : hardé

Figure 4. Phenology of selected woody species during 1986 and 1987, A on a ferruginous soil, B on vertisol and C on 'hardé'.

Phenological strategies of herbaceous species

Consisting mostly of annual species, the herbaceous stratum of northern Cameroonian savannas shows a peak period of leafing corresponding closely to the rainy season (Figures 1, 2 and 3). For most species, the onset of flowering coincides with the end of vegetative growth (maximum cover), and continues approximately for four months (end of July to the beginning of November). Flowering times overlap both within and between species. However, a gradient of species behaviour emerges when flowering is analysed for all the stations over two years combined (Figures 2 and 3). Thus, on the basis of timing of onset, the duration and the variability of flowering during the two years on the three



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Table 2. Classification of phenological groups of species studied in northern Cameroonian savannas as a function of the timing of their flowering period during two years 1986 and 1987 (rainy season spreads from May to September).

HERBACEOUS SPECIES	
Group 1	Onset of flowering prior to the first week of August
Group 2	Onset of flowering between the first and third weeks of August
Group 3	Onset of flowering between the second week of August and the second week of September
Group 4	Onset of flowering after the third week of September
WOODY SPECIES	
Evergreen species	
Group 5	Flowering entirely in the dry season
Group 6	Onset of flowering at the end of the rainy season
Group 7	Onset of flowering in the dry season; end of flowering in the rainy season
Group 8	Several flowering periods during the year; only one surviving crop of fruit
Deciduous species	
Group 9	Onset of flowering at beginning of the rainy season
Group 10	Onset of flowering in the middle of the rainy season
Group 11	Onset of flowering at the end of the rainy season
Group 12	Flowering entirely in the dry season
Group 13	Onset of flowering in the dry season; end of flowering in the rainy season

soil types, four groups can be identified among the herbaceous species (Table 2).

The precocity of the species in group 1 is the result of a very short vegetative growth phase, and can be interpreted as an adaptation to harsh growing conditions (Aronson *et al.* 1992, Granier & Cabanis 1975). Those species entering the reproductive phase early in the season gain a competitive advantage for space colonization next season by establishing large seed banks in the soil (Seghier 1990). It is noteworthy that neither of the herbaceous perennials studied (*Sporobolus festivus* Hochst. ex A. Rich. and *Drimiopsis barberi* Bak.) showed important differences from the annual species in their phenological rhythms. No doubt the absence or very low levels of ground water reserves at 0–20 cm of depth prevented an early start or a prolonged growth period on the part of these herbaceous perennials, especially on 'hardé' (Figure 2C). Regular early fires set by humans may be another limiting factor of a longer life cycle (Figure 2A,B).

Species in group 2 (Table 2) begin flowering when soil water reserves have been amply recharged, i.e. in August (Figure 1). In this way, they reduce the likelihood of abortive flowers due to periods of drought following the onset of flowering. In this group is *Setaria pallide-fusca* (Schumach.) Stapf & C. E. Hubbard, the most common and abundant species on ferruginous soils, as well as *Loudetia togoensis* (Pilger) C. E. Hubbard, the species that dominates on vertisol, and *Schoenefeldia gracilis* Kunth, the dominant species on 'hardé'. The reproductive strategy of these three species together with a strong annual contribution to the soil seed stock ensures a high capacity for colonization and rapid growth rates immediately after establishment (Seghier 1990).

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For members of group 3 (Table 2), flowering is relatively late in the rainy season, and the reproductive period is thus considerably shortened as compared with that of the first two groups. In addition, there is an increased risk of drought or, on vertisol, of an early fire set by farmers planning to plant sorghum in the dry season. Often such fires spread to ferruginous soils, as they did in 1987. Generally, fire occurs later on this type of soil, as in 1986, to prepare it for rainy season cultivation (Figure 2A). Both these factors can prevent the full maturation of seeds. Some species in the group (e.g. *Eragrostis turgida* (Schumach.) De Wild. and *Panicum laetum* Kunth.), compensate by reducing the plasticity expressed in the timing of flowering onset (all individuals start flowering in a very short time, Figure 3).

Group 4 (Table 2) contains a few, rather rare species (e.g. *Aristida hordeacea* Kunth, *Eragrostis ciliaris* (L.) R. Br., *Hackelochloa granularis* (L.) O. Ktze.) that have a markedly later onset of flowering, and a much condensed reproductive phase (Figure 3). It is not clear whether the small number of individuals of these species sampled limited the range of flowering times observed, or whether they have indeed a genetically fixed, late and short flowering period.

At Mouda, the rather tightly grouped occurrence of life cycles in the herbaceous stratum, on all three soil types, may be the result of the growth form (therophytes) to which they mostly belong. In general, therophytes grow and reproduce rapidly in periods of abundant moisture, regardless of the season of the year (Fournier 1990, Kemp 1983, Menaut 1983, Sarmiento & Monasterio 1983). In particular, the duration of their life cycle often appears unrelated to the duration of the period during which soil water reserves are abundant (Breman 1991, Jackson & Roy 1986). For this reason, when their growth periods end, soil water reserves remain for use by woody plants (Figure 1, A and B horizon 0–80 cm) which have 80% of their root system in the first 40 cm of depth (Seghieri 1990).

Moreover, phenological plasticity in tropical African savanna therophytes allows increased concentration of species' life cycles as environmental constraints upon them increase (Fournier 1990). At Mouda, there are two principal constraints: fire and drought. Fires, set just after the end of the rainy season (October), prevent the reproduction of perennial species or late-season annuals and reduce the expression of phenological heterogeneity of well-established populations. Despite the possibility of late cohorts of germinants, no extension of life cycles was apparent, as is observed for Mediterranean annuals grown under simulated drought conditions by Aronson *et al.* (1992a), even on ferruginous soil where fire occurs most often late in the dry season.

On degraded 'hardé' soils, the length of the period during which water is available is very brief (Figure 1C). Plants begin reproduction early in this period, or else have a resource allocation strategy which maximizes reproduction before their threshold of resistance to drought is passed (Jackson & Bliss 1984). Those species that succeed in establishing themselves on these soils make little vegetative growth, yet they reproduce regularly. They exhibit a dwarfing syndrome typical of many Sahelian annuals (Bille 1975, Burgess & Shmida

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1989). Short life cycles and a precocious reproductive phase may represent an adaptive strategy of species growing in environments where the risk of mortality is high during all the life of the plants (Schaffer & Gadgil 1975).

Soil aridity may accentuate climatic aridity (Floret & Pontanier 1984) and may limit the attainment of full maturity in late-germinating individuals, and/or retard the establishment of the most precocious ones. Thus, seasonal drought can act as a strong selective force on the period of flowering, yet the actual stimulation of flowering by drought should be viewed cautiously (Fox 1990). Cissé (1986) has shown that redistribution of rainwater by a given topography leads to the same difference in soil water content (and to similar effects on annual vegetation) as that which exists between a degraded and non-degraded soil: the length of the life cycle decreases upslope and increases downslope. For this reason, on all three soil types studied, a correlation appears between the lateness of flowering, the shortness of flowering duration and the timing of the onset of flowering (Figure 3), i.e. the later the onset of flowering is in a species, the shorter will be its flowering season and the more compressed will be its period of anthesis. Thus, water availability in the horizon 0–20 cm (the depth of most annual species' roots) and fire are generally the main limiting factors of the duration of the life cycles.

Regeneration of a population of annual species consequently depends upon the possibilities for establishment and the species' ability to capture resources after germinating (i.e. the timing of germination, early growth rate and seedlings' resistance to unpredictable periods of drought (Seghieri 1990). The number and quality of seeds produced for the following rainy season is in part determined by the species' relative importance in a community at the time of its seed production. Intra-specific heterogeneity in the timing of seed maturation and dispersal is common in most of the species included in this study; presumably this leads to different parts of each population being adapted to different hydrological conditions. Thus, for annual species, timing of the reproductive period must be first a result of selection exercised during the seedling stage. The length of the season favourable to plants' development acts on the possibilities for seedlings to reach maturity. However, seasonal drought can directly affect the evolution of flowering time by acting as a selective agent, and can have indirect effects on the evolution of flowering time, because water stress during reproduction can affect seed characteristics (Fox 1990). Annual and perennial herbaceous species are both 'arido-passive' (*sensu* Evenari 1985, Evenari & Guterman 1976). 'The term "arido-passive" refers to plants whose drought-surviving parts are metabolically inactive (quiescent, dormant) during the dry season' (Evenari 1985).

Phenological strategies of woody species

Nine different groups of woody species were identified, and these in turn can be put into two larger groups based on the length of their periods of leafing in the course of the year, i.e. evergreen and deciduous species (Table 2). The evergreen

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species (groups 5–8) limit their leafing in the dry season specially on 'hardé' (Figure 4C), and their foliage cover is highest during the rainy season. They maximize carbon gain during the wet season and reproduce in the less favourable period (December–April) when their leafing is in any case limited by low soil water availability (Monasterio & Sarmiento 1976, Sarmiento & Monasterio 1983). At the two other sites (Figure 4A,B), fire is a more likely cause of deleafing. It leads to a strong foliage increase in the dry season after trees had been burnt. The deciduous species (groups 9–13) drop their leaves in the dry season.

For species in group 5, the first of the evergreen woody species groups, the most favourable period of the year, in terms of water availability, is used exclusively for leafing. Flowering and reproduction take place after October or after December i.e. after the risk of fire is over (Figure 4A,B). In this way, reproductive organs in these species are rarely burnt. Furthermore, as they are produced during the dry season, their fruits are seldom parasitized or lost to frugivores. The permanent leafing may further enable reproductive periods in the dry season, as long as water resource contributions are sufficient.

On non-degraded soils, the flowering of group 6 species benefits greatly from the amount of water available at the end of the rainy season (Figure 4A,B). However, there is the risk of not completing the reproductive phase before the post-fallow fires begin in October. For example, group 7 species start their reproduction during a period of low water availability since flowering ends and seed maturation is achieved during the rainy season. Again, 'permanent' leafing may allow the beginning of the reproductive period during the least favourable water conditions. They also avoid flower and seed loss to fire, but can lose considerable numbers of seeds to the numerous parasites and frugivores active in the rainy season.

The species in group 8 show an opportunistic, and apparently costly, strategy by flowering whenever rainfall allows, often doing so several times a year. Fruit and seed maturation, however, only occur during the rainy season, at the time of year when soil water reserves are abundant. Flowers produced at other times are mostly aborted.

Members of group 9, the first of deciduous woody species groups, begin flowering soon after, or occasionally just before, the first rains. Flowering closely follows, or just precedes, the appearance of leaves. At this time, only the ferruginous soil contains available water (0–80 cm, Figure 1), though in very low quantities. Atmospheric relative humidity improves rapidly in this period, a change which may well be the environmental signal triggering flowering in these species. Group 9 species thus have the entire rainy season to grow vegetatively and to reproduce. The passage of fire poses no threat to their reproduction, even in the case of *Strychnos spinosa* Lam., which shows a very long fruiting period, extending well into the dry season (Figure 4A). Partial protection of this species' seeds is provided by a large fleshy drupe.

Group 10 contains species that reproduce under the most optimal conditions from the hydrological point of view. As long as they limit their reproductive

phase, and thereby avoid damage by fire, the life cycle of these species appears to be the group least at risk from a lack of water resources during reproduction.

Among the deciduous woody species flowering in the dry season, the members of group 11 have a phenological pattern most closely resembling that of the majority of the herbaceous species in the study area. They use the more favourable part of the rainy season for their greatest leafing; reproduction is initiated just prior to soil water reserves beginning to diminish and growth conditions becoming more unfavourable.

Although deciduous, the members of groups 12 and 13 are 'arido-active' (*sensu* Evenari 1985, Evenari & Gutterman 1976). 'The term "arido-active" refers to plants which even during the dry season remain at least in part metabolically active' (Evenari 1985). Species in group 12 have a similar reproduction time to those of group 5, despite their leafing being limited to the rainy season. Similarly, those species in group 13 share life history features with those of group 7. This behaviour is possible if there is an accumulation of carbon and nutrient reserve in the trees during the photosynthetic phase and this can be translocated to reproductive organs in the dry season (Kemp 1983).

In contrast to co-occurring herbaceous species, the woody species studied generally show leafing over most of the year, which demonstrates their higher degree of independence from current rainfall (immediate rain supplied) and suggests a superior exploitation of soil water resources during the year (Crawley 1986). Their perennial growth habit and their stronger resistance to fire allow them to take advantage of the water supplies (0–20 cm) in non-degraded soils that are not exploited by herbaceous plants at the end of the rainy season. Additionally, their vaster, deeper root systems allow them to reach water reserves out of reach of the herbaceous stratum, i.e. below 20 cm (Seghieri 1990).

Despite the small number of species studied, the limited number of individuals per species (3–11) and the limitations of sampling to one site on each soil type, our observations of phenological rhythms of the selected woody species corroborate those previously published for the same taxa in other West African savannas (Fournier 1990, Menaut & César 1979, Nouvellet 1987, Piot *et al.* 1980). The onset and duration of phenological phases of these woody species appear to be independent of soil type and of a specific year's rainfall regime. The only exceptions in our study were *Acacia hockii* De Wild. and *Sterculia setigera* Del. for leafing; *Acacia hockii*, *Acacia seyal* Del. and *Piliostigma reticulatum* (DC.) Hochst. for onset of flowering.

Other factors, such as relative humidity, photoperiodism and temperature also contribute to such variations. However, decreasing soil water reserves strongly affect the intensity of flowering and the outcome of the reproductive phase, even when flowering has begun normally. For example, an exceptionally dry year, such as 1987, tends to cause a reduction of the proportion of individuals that flower in a population compared to a normal year (e.g. 1986). Examples include *Sterculia setigera* Del., on ferruginous soils and 'hardé',

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Piliostigma reticulatum on ferruginous soils and vertisols, *Lannea humilis* (Oliv.) Engl., on vertisol and 'hardé', *Anogeissus leiocarpus* (DC.) Guill. & Perr., on vertisol, *Ziziphus mauritiana* Mill., on vertisol, *Acacia hockii* on 'hardé', and others.

Even under identical rainfall regimes, the edaphic aridity of the 'hardé' soil can cause a reduction in the proportion of flowering individuals (*Acacia hockii* or *A. seyal*), or totally inhibit flowering (e.g. in *Sclerocarya birrea* (A. Rich.) Hochst.) (Figure 4). Similarly, from February to May, these vertisols have little or no water reserves (0–80 cm), despite their moisture content remaining high (Figure 1). By contrast, the ferruginous soils contain much less water at the permanent wilting point of most plants, yet retain some water reserves throughout the year that most of the woody species can use (Figures 1 and 4). Consequently, those species found on vertisols that are not plastic with regard to timing of their reproductive cycle in the dry season (e.g. *Combretum glutinosum* Perr. ex DC.) can run short of water necessary for flower and seed production. Reduction in the intensity of flowering is also sometimes expressed by a shortening of the period during which the percentage of individuals flowering within a population is at its maximum, e.g. *Combretum Loeffl. collinum* (of ed.1), on ferruginous soil (Figure 4A), *Acacia senegal* (L.) Willd. on 'hardé' (Figure 4C) and *Anogeissus leiocarpus* on ferruginous soils (Figure 4A), for which flowering shows two peaks corresponding closely to peaks in soil water availability (Figure 1).

The possibility of no fruiting occurring after flowering has taken place (as a result of water stress) has been described by Poupon (1979). This effect is illustrated in our study by the total absence of fruit for several members of group 8 in 1987 (*Balanites aegyptiaca* (L.) Del., *Piliostigma reticulatum* and *Entada africana* Guill. & Perr.). Retaining the capacity to flower several times in a single year is not unique to these group 8 species. In a different study site (Laf, near Mouda), Nouvellet (1987) observed the brief appearance of flowers on *Combretum glutinosum* in April (not observed by us), and noted that flowering periods followed by fruiting have been reported for this species in April in Niger. Poupon (1979) reported a second flowering in January–February for *Acacia senegal* in the Sahelian zone of Senegal. Such plasticity in flowering time and frequency suggests that plants in this group are able to adapt their reproduction to different rhythms of water availability. This feature should enhance and facilitate their phytogeographical expansion.

Even if environmental parameters other than water availability play a role in triggering onset and duration of various phenological phases in the woody species under study, water, nevertheless, remains the key limiting factor. Despite the fact that the watershed was too small to allow more replicate sample sites for each soil type, it seems clear that water resource levels, in time and in space, determine both the intensity and the maintenance of dominant reproductive rhythms in the woody communities considered here. A more extensive sample could have confirmed these results.

CONCLUSION

Few perennial species have vegetative growth in the dry season, and there is no reproduction out of the rainy season for all herbaceous species. Consequently, it is essential, for annuals and perennials alike, to carry out flowering within the rainy season. Among other things, reproduction assures the renewed occupation of niches. Catastrophic inhibition of regeneration mechanisms (seed production dispersal, and germination) can result from a series of dry years, severe edaphic aridity in extremely degraded soils (e.g. 'hardé') or from permanent human interventions such as fire, clearing and overgrazing. Such interventions typically prevent completion of the life cycle of many annual species. These interrelated factors are, to a large degree, responsible for the recent decline in species richness of the northern Cameroonian savannas (Letouzey 1985). In the woody stratum, this trend is aggravated by the invasion of woody, spiny Sahelian species, e.g. *Acacia* spp., *Balanites aegyptiaca*, *Dichrostachys glomerata* (Forsk.) Chiov. On the least degraded soils, there is also a growing abundance of typical fallow field colonizers (groups 5-7), characterized by preponderantly vegetative reproduction and quasi-permanent leafing. Anthropic pressures appear to be more responsible for the dominance of annual or ephemeral species than the short duration of the rainy season. On the least degraded soils, like vertisol and ferruginous soil, herbaceous species achieve their life cycle before water resources disappear.

Annual plant development depends on the available water resources during a precise, rather brief period (Seghieri 1990). In contrast, the great majority of herbaceous perennials require a considerably longer period of favourable water conditions to reach maturity (Jackson & Roy 1986). As we have seen, environmental degradation leads to a considerable reduction of the period during which soil water is available to plants, and thereby limits reproduction in many species and life forms. Even for annual plants, there exists a threshold of soil water availability, and of duration of favourable water conditions, beneath which the majority of species fail to reproduce. This explains why so few species survive on 'hardé' soils (Figures 2 and 4). It also suggests that as soils become degraded in the Cameroonian savannas, there is growing competition among woody and annual plants seeking adequate water supplies for their reproductive needs. Finally, the wide variety of phenological rhythms encountered among the woody species occurring on the three soil types typical of the northern Cameroon savannas indicates the great number of solutions available to tropical plants, at the present time, in the pursuit of survival and reproduction.

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