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RESEARCH LETTER

Rainfall and topo-edaphic influences on woody community phenology in South African savannas

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ABSTRACT

Woody community phenology was studied in the central lowveld, South Africa, over a twelve month period at three sites along a rainfall gradient, with both toplands and bottomlands sampled at each site. Each month, individual plants, in replicated samples, were scored into a number of categories describing their phenological state. Position on the rainfall gradient influenced: (1) onset and magnitude of leaf emergence, (2) onset and duration of mature leaves, and (3) the proportion of leafless trees. Generally, the moist site demonstrated earlier leaf growth than the intermediate or arid sites. Emergent and mature leaves were recorded earlier, and in the case of mature leaves, retained longer. Overall, there was a lower proportion of leafless trees during the dry season at the moist site, followed by the semi-arid site, followed by the arid site. Differences with respect to catenal position were evident for the proportion of trees in winter with mature leaves, and the proportion of trees with senescent leaves. Bottomlands had a greater proportion of trees with leaves during winter, but a lower proportion of trees recorded with senescent leaves. Both of these findings were a result of the greater proportion of evergreen species in bottomlands, as well as increased leaf retention by the deciduous species. Phenological activity of leaves was related to plant stem size. In particular, there was greater leaf retention during the dry period by small stems, relative to large stems.

Key words. Bottomlands, community phenology, lowveld, rainfall gradient, savanna, soil moisture, South Africa, toplands.

INTRODUCTION

Analysis of community phenology provides information regarding the abiotic and biotic variables that determine the seasonal development and senescence of plant tissues and organs. Since the initiation and termination of growth phases represent the boundaries of periods of growth and productivity, an understanding of the triggers and controlling variables can contribute to an understanding of plant productivity, and hence resource availability. As with many aspects of savanna dynamics, most past phenological research has focussed on the herbaceous layer (Scholes & Walker, 1993), because of the clear correlation with rainfall patterns in tropical and semi-arid systems (Prins, 1988).

It has been argued that low and variable precipitation is the primary determinant of savanna dynamics (Noy-Meir, 1973; Tinley, 1982). This has been questioned by Scholes & Walker (1993), who suggest that the influence of precipitation is through its effect on nitrogen mineralization, rather than directly on plant growth through photosynthesis and transpiration. Whilst nitrogen mineralization may be the proximate determinant, its effect is controlled through the presence or absence of plant available moisture. This is mirrored in the role of water stress on plant nutrient concentrations (Prins, 1988). Plant available moisture is a function of the amount and timing of precipitation in combination with the effect of temperature on evaporative demand (Bate, Furniss & Pendle, 1982). At a gross scale, annual rainfall is a coarse index of seasonal plant available moisture, and can therefore

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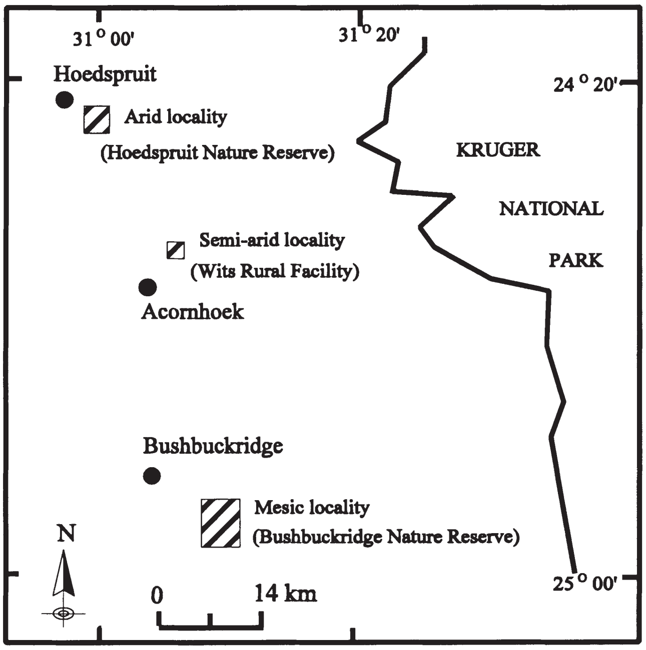


Fig. 1. Location of the three study localities.

be regarded as the proximate determinant of savanna dynamics.

Following this reasoning, it can be hypothesized that community phenology and productivity would vary along a gradient of soil moisture availability. This has been clearly demonstrated with respect to herbaceous communities (e.g. Sarmiento, 1983; Prins, 1988), but less so with respect to savanna woody communities. Such soil moisture gradients can be manifest as a direct gradient in rainfall in an area of homogenous soil type, or as a gradient in soil type from sands to clays under a uniform rainfall regime (Scholes & Walker, 1993). This study sought to investigate woody community phenology across both such gradients.

STUDY AREA

Three conserved areas were identified along a rainfall gradient in the central lowveld straddling the boundary between Mpumalanga and Northern Province, South Africa (Fig. 1). The north–south distance between the localities is approximately 62 km. The east–west displacement is 16 km. The altitude at all these localities is approximately 550 m a.s.l. For convenience the three localities are termed the arid, semi-arid and mesic sites.

All three sites are situated on weathered granites with doleritic intrusions reaching the surface in isolated places. Typical soil catenal sequences are evident throughout the region (Gertenbach, 1983; Scholes, 1987; Witkowski & O'Connor, 1996). Thus, upland soils (on the slope crests) are shallow, coarse-textured and dystrophic, whilst bottomland soils (at the base of the slope) are deeper, finer-textured and more eutrophic. Unpublished management records at each site indicate that mean annual rainfall (MAR) is the primary variable differentiating the three localities, being 484 mm ± 32 (1971–1997) at the arid site, 651 mm ± 123 (1970–1997) at the semi-arid site, and >870 mm at the mesic site; MAR at Injaka (2 km west of mesic site, 780 m a.s.l.) is 1161 mm ± 225 (1992–1997). At all localities, rainfall is concentrated into the summer season from October to May. Rain is received largely in the form of convectional thundershowers, although periods of prolonged cyclonic showers do occur. Frost is rare, and when it does occur, is generally confined to the bottomlands.

The three localities fall into Acocks' (1988) broad vegetation type of Tropical Bush and Savanna. More specifically, the arid locality is in Veldtype 11, Arid

Table 1. The species contributing 3% or more to either the density, biomass or basal area at each locality (from random transects, 95 at the arid, 30 at the semi-arid and 54 at the moist sites (Shackleton, 1997)).

Locality	Species	Density		Basal area		Biomass	
		(stems/ha)	%	(m^2/ha)	%	(t/ha)	%
Arid	*Acacia nigrescens*	133.1	2.6	1.211	12.2	5.41	23.5
	Albizia harveyii	130.5	2.5	0.889	9.0	1.96	8.5
	Combretum apiculatum	557.9	10.8	2.058	20.8	3.68	16.0
	Commiphera schimperii	172.6	3.3	0.048	0.5	0.01	0.1
	Dichrostachys cinerea	932.6	18.0	0.580	5.9	0.50	2.2
	Grewia bicolor	700.6	13.5	0.467	4.7	0.37	1.6
	Grewia flava	452.6	8.7	0.248	2.5	0.18	0.8
	Grewia flavescens	212.2	4.1	0.044	0.5	0.03	0.1
	Lannea stuhlmanniana	13.1	0.3	0.307	3.1	0.99	4.3
	Ormocarpum trichocarpum	409.3	7.9	0.253	2.6	0.19	0.8
	Sclerocarya birrea	16.8	0.3	1.271	12.8	4.67	20.3
	Total	3731.3	72.0	7.3733	74.6	17.98	78.2
Semi-arid	*Acacia swazica*	304.3	5.5	0.2270	2.6	0.15	0.8
	Albizia harveyii	144.3	2.6	0.2976	3.5	0.49	2.4
	Combretum collinum	292.5	5.3	1.0365	12.0	3.18	15.7
	Dichrostachys cinerea	1227.5	22.0	0.9111	10.6	0.86	4.3
	Diospyros mespiliformis	32.5	0.6	0.4469	5.2	1.67	8.3
	Euclea natalensis	192.5	3.5	0.1100	1.3	0.08	0.4
	Lonchocarpus capassa	41.8	0.7	0.5185	6.0	2.14	10.6
	Maytenus senegalensis	215.0	3.9	0.0981	1.1	0.06	0.3
	Sclerocarya birrea	107.5	1.9	1.3481	15.6	6.22	30.7
	Strychnos madagascariensis	321.8	5.8	0.6669	7.7	1.40	6.9
	Terminalia sericea	1116.8	20.1	1.4615	16.9	2.14	10.6
	Total	3996.5	71.9	7.1222	82.5	18.41	91.0
Mesic	*Antidesma venosum*	113.1	5.2	0.4410	3.1	0.71	1.7
	Combretum collinum	793.1	3.7	1.0533	7.5	3.01	7.2
	Dichrostachys cinerea	2896.1	13.6	0.6890	4.9	0.52	1.3
	Dombeya rotundifolia	1059.2	5.0	0.0726	0.5	0.07	0.2
	Faurea saligna	820.0	13.3	2.1931	15.6	8.91	21.5
	Ochna sp	659.2	3.1	0.0104	—	0.01	—
	Parinari curatellifolia	1936.9	9.1	0.7747	5.5	1.43	3.5
	Pavetta schumanianna	1131.5	5.3	0.0927	0.7	0.06	0.2
	Pterocarpus angolensis	326.9	1.5	2.5744	18.3	9.29	22.4
	Sclerocarya birrea	37.7	0.2	1.2223	8.7	5.23	12.6
	Strychnos madagascariensis	1793.1	8.4	0.5131	3.7	0.99	2.4
	Terminalia sericea	1999.2	9.4	1.7832	12.7	5.66	13.6
	Total	13566.0	77.8	11.4198	81.2	35.89	86.6

Lowveld, dominated by members of the Mimosaceae (especially *Acacia nigrescens*, *A. gerrardii*, *Albizia harveyii*, *Dichrostachys cinerea*), along with *Combretum apiculatum*, *Sclerocarya birrea*, *Ormocarpum trichocarpum* and *Grewia* spp. (Table 1). Nomenclature follows Gibbs Russel *et al.* (1985). Mean height of the canopy is 5–6 m, and basal area is 10 m^2/ha (Table 2). The semi-arid locality is situated on the boundary between the Arid Lowveld and Lowveld Veldtypes. The woody stratum is dominated by Combretaceae species (including *Terminalia sericea*, *Combretum collinum*, *C. hereroense*), with *S. birrea* and *D. cinerea* also being significant contributors to the biomass (Table 1). Mean canopy height is 6–7 m and the basal area is 8.6 m^2/ha (Table 2). The mesic locality is situated on the boundary between the Lowveld Veldtype and Lowveld Sour Bushveld Veldtype, dominated by taller (8–9 m), more broadleaved species than the other two sites, namely *Pterocarpus angolensis*, *Faurea saligna*, *T. sericea*, *C. collinum*, *Parinari curatellifolia* and

Table 2. Attributes of woody community structure at the three study localities (mean ± SE in brackets). See Table 1 for sample size per locality. Unlike superscripts between localities indicate significant differences at at least the 99% significance level, determined via one-way ANOVA and subsequent pairwise comparison using LSD (from random transects (Shackleton, 1997)).

Variable	Locality		
	Arid	Semi-arid	Mesic
Density (stems/ha)	5208^a (235.1)	5583^a (328.0)	21374^b (1410.6)
Basal area (m^2/ha)	10.1^a (0.61)	8.6^a (0.90)	14.1^b (0.93)
Biomass (t/ha)	23.1^a (2.28)	18.9^a (3.67)	41.3^b (4.53)
Height of tallest stem/transect (cm)	661.1^a (27.9)	669.0^a (52.5)	890.8^b (35.4)

Dombeya rotundifolia, along with *S. birrea* and *D. cinerea* (Table 1). More details of the vegetation at each site are provided in Shackleton (1997).

Biomass of indigenous fauna at the semi-arid and mesic localities is low. The arid locality supports several species of indigenous ungulates, with a mean biomass of 34 kg/ha, dominated by giraffe (30%), Burchell's zebra (12.5%), blue wildebeest (10.5%), impala (9.5%) and waterbuck (8.9%) (Shackleton, 1997).

METHODS

Within the first week of each month (from Sept. 1993 to Sept. 1994), phenology transects were recorded at each of the three study localities along the rainfall gradient. Ten transects were randomly located in each reserve, five in toplands and five in bottomlands (on the same slope, therefore they were paired). Transects were in the same position each month, but the starting point was not permanently marked, and hence the same trees were not necessarily inspected every month. Each transect consisted of fifteen points, 15 m apart. At each point the nearest tree (>1 m tall) within four 90° quadrants was inspected with respect to its phenological state, resulting in sixty trees per transect. However, to promote inclusion of the less abundant species, no more than two of the trees at each point could be of the same species. Therefore, if the species in the third quadrant was the same as that in the previous two, then the second nearest tree in that quadrant was considered. If that was also of the same species, then the third nearest was inspected, and so on. Each tree recorded was classified into one of three height classes; <2 m, 2–4 m, and >4 m. Thereafter, its phenological state was rated according to one or more of the following categories: 1, leaf initials/buds present; 2, leaves emerging from buds; 3, mature leaves present; 4, leaves senescing; 5, leafless; 6, reproductive buds/flowers present; 7, immature fruits present; 8, mature/dehiscing fruits present; 9, fruits from previous season present; 10, shoot elongation evident.

Data were expressed as the mean proportion (%) of plants per transect displaying any of the above phenological conditions. An individual plant could be classed in more than one phenophase simultaneously. The value for each of the five transects in a given rainfall zone and slope position were averaged and summarized graphically. Although there were five replicates per rainfall zone and slope position interaction, standard errors were not plotted on the graphs to allow ease of observation of central trends. The magnitude of the coefficients of variation during the peak periods for each phenophase are provided in the text. Arcsine transformations were applied to percentage values prior to statistical analyses. The influence of plant height on phenological state was tested via a paired *t*-test between the proportion of small stems (<2 m tall) and large stems (mean of the two tallest height classes) with leaves during the 3 months of peak leaflessness.

With only one locality per climatic zone, this study may be regarded as pseudoreplicated (Hurlbert, 1984). However, this notion has been challenged by Webster (1992), who argues that pseudoreplication is a matter of scale. The large size of each study locality, and the original selection of transect sites in a random manner within these large areas, mitigate against the pseudoreplication perspective. Nevertheless, application of the findings to other localities should be done with caution.

Rainfall data were obtained from the officer in charge at each locality.

RESULTS

Rainfall during the study period

The annual rainfall during the study period (1 July 1993–30 June 1994) was below the long-term mean at all three localities (421.5 mm at the arid; 494 mm at the semi-arid, and 767.5 mm at the moist locality). The highest rainfall was in December at each locality (Fig. 2). However, the proportion of the total rainfall received in December decreased with increasing mean annual rainfall, being 52%, 39.2% and 23.1% at the arid, semi-arid and mesic localities, respectively. The rainfall at the mesic locality was spread more evenly throughout the growing season, relative to the greater concentration at the arid site. For example, at the moist locality, ⩾20 mm rain was received in each of 8 months of the year, but for only 4 months of the year at the arid locality. At the semi-arid locality, there were 7 months with ⩾20 mm rainfall. The end of the growing season was relatively abrupt with no rain in May 1994 at the arid or mesic localities, and only 1.5 mm at the semi-arid locality.

Community phenology

A clear seasonal phenological pattern was evident at each site, with differences between sites and catenal position evident for some phenophases (Fig. 3).

Leaf buds/initials were evident for a 2-month period from mid-September to mid-November at all sites. The peak was in the second month of this period (except for toplands at the moist site), with a rapid decline by the first week of December. Leaf buds/initials were not recorded from December through to August. The peak was greatest at the semi-arid site, followed by the moist site and lastly the arid site. The low value of the peak, and high variability (coefficient of variation was 50–220% across all the sites), suggests that most of the initials are short-lived, and a monthly monitoring interval was too long to record a full flush of initials on most of the trees, i.e. the peak was between two data collection periods.

Emergent leaves were concentrated into spring and early summer. Leaf emergence in the moist site, and in the topland samples from the semi-arid site, peaked in November. Values for emergence in the arid site, and in the bottomlands from the semi-arid site, peaked a month later in December. The coefficient of variation was approximately 30% in the peak months. The magnitude of the peak was greatest at the moist site, followed by the arid site, and least at the semi-arid site. Relatively few leaves had emerged prior to the onset of summer rains in October. Generally, there were no, or very few, trees with emergent leaves from January through to August.

Mature leaves were present on a small proportion of trees at all sites throughout the year. This probably reflects the presence of evergreen species, although some leaves, in significantly reduced numbers, were observed on some individual plants of deciduous species (albeit relatively rare). During winter, the proportion of trees with leaves was lower in the topland samples than in the bottomlands. The same also generally applied during summer. The peak in mature leaves was from January through to May, except for the moist site, where the peak was a month earlier and the leaves were retained a month longer. Except for the peak months, when most sites approached 100% of trees with mature leaves, the moist sites had a greater proportion of trees with mature leaves than the semi-arid site, which in turn had more than the arid site. There were anomalous drops in the proportion of trees with mature leaves, from 100% to approximately 60%, in toplands at the arid site (February) and semi-arid site (March). At the arid site, the decrease was associated with a mid-season ‘drought’ (Fig. 2). This did not apply at the semi-arid site. The coefficient of variation was less than 5% for most of the peak months.

Shoot elongation was largely confined to the summer months, with a very concentrated peak in January. At the arid and moist sites, topland sites had a greater proportion of trees where shoot elongation was evident than the bottomland sites. However, at the semi-arid site, the opposite trend was evident, with values for bottomlands being greater than toplands. The coefficient of variation in the peak month ranged between 8% and 56% across the different sites.

The presence of buds and flowers peaked in December and January with a rapid decline thereafter. There was no visible trend according to rainfall zones or catenal position. The coefficient of variation was approximately 30% for the peak months at all sites, except for the bottomland transects at the moist site, where it was 60%. It was approximately double this during non-peak months.

Immature fruits were evident approximately two months after the appearance of buds and flowers, peaking in March. Generally, some fruits were evident throughout the year, but with lowest levels from July to October. At the moist site, toplands had a lower proportion of trees with immature fruits during the peak months than did bottomlands. The reverse applied at the arid and semi-arid sites. The coefficient of variation during March was between 50% and 100% across all the sites.

The presence of mature fruits peaked two months after the peak in immature fruits. Likewise, there were

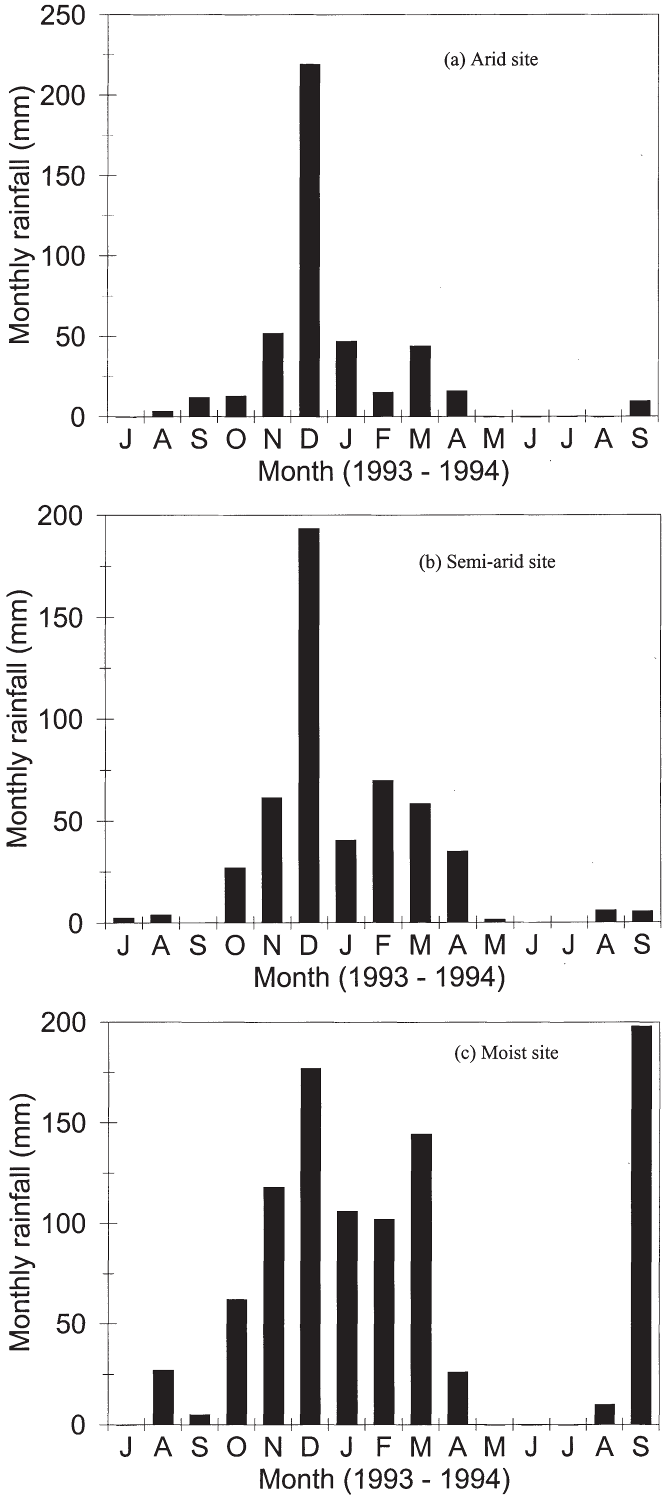
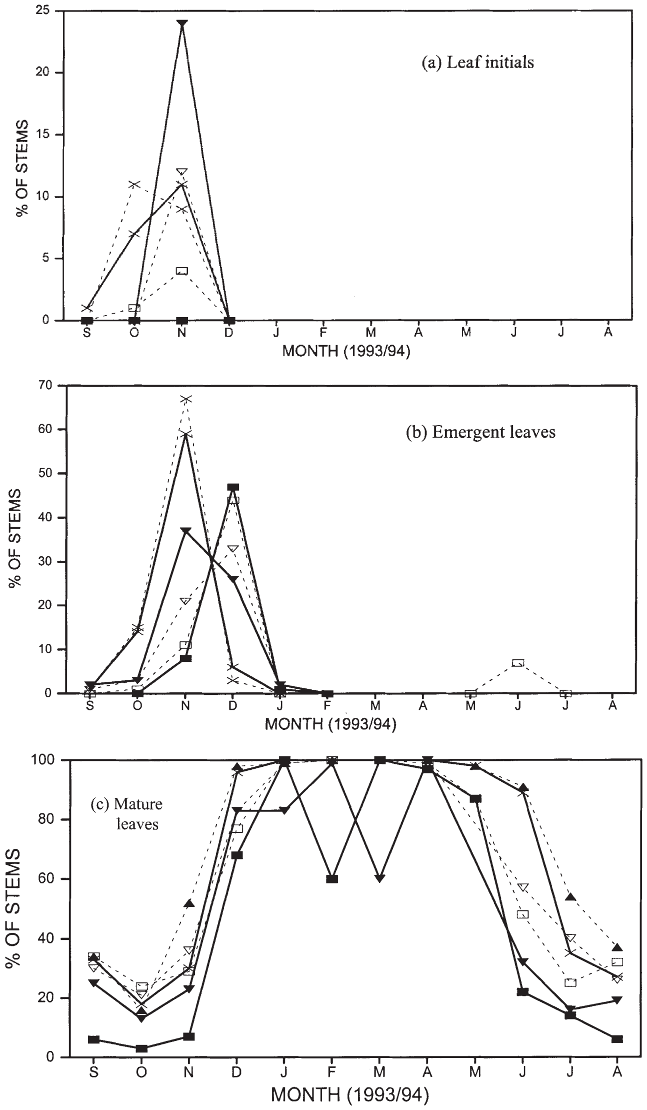


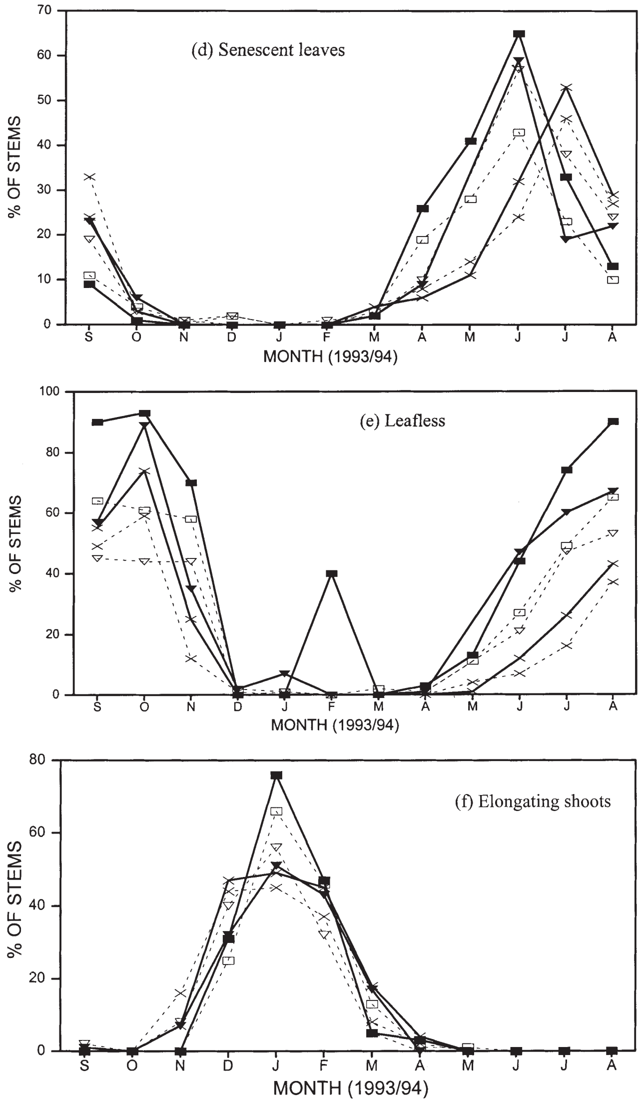
Fig. 2. Monthly rainfall at each locality during the study period.



low levels of fruit throughout most of the year, as individual species came into season. For example, the various species of *Acacia* commonly fruited during mid- to late-summer, whereas *Euclea* species fruited from April to September. Overall, levels of fruiting were lowest from September through to December. There were no trends with respect to catenal position or rainfall zone.

A few trees with senescent leaves were recorded throughout the year, but these were fewest from October through to March. Senescence increased rapidly with the cessation of rains in April. At the arid and semi-arid sites, the peak was in June, whereas at the moist site the peak was one month later. The peak in senescent leaves was lower at bottomland sites than at toplands. The coefficient of variation was less than 20% during the peak months.

Contrasting with the presence of leaves throughout the year on a small proportion of trees, there was a small proportion of trees that were largely leafless even during the rainy season. However, the lowest proportions of leaflessness were evident from December



through to April/May. The peak was in September and October, during which time the coefficient of variation was between 6% and 42% depending on site. The toplands always had a greater proportion of leafless trees than the bottomlands. Generally, the arid site had a greater proportion of trees without leaves than the semi-arid site, which had a greater proportion than the moist site. Toplands had a greater proportion of leafless trees during winter than bottomlands, and a higher proportion of trees recorded with senescent leaves. Both of these were a consequence of the greater proportion of evergreen species, such as *Euclea* spp. and *Cassine aethiopica*, in bottomlands ($t = 3.14$; d.f. $= 4$; $P < 0.03$), as well as of increased leaf retention by the deciduous species in bottomlands ($t = 2.79$; d.f. $= 4$; $P < 0.05$) (Table 3). The differences between rainfall zones could not be attributed to differing proportions of evergreen species between sites, as the values were comparable, with 3.0%, 4.8% and 3.2% of stems at the arid, semi-arid and moist sites, respectively, being of evergreen species.

Some fruits were retained from the previous season through to January of the following year, with very

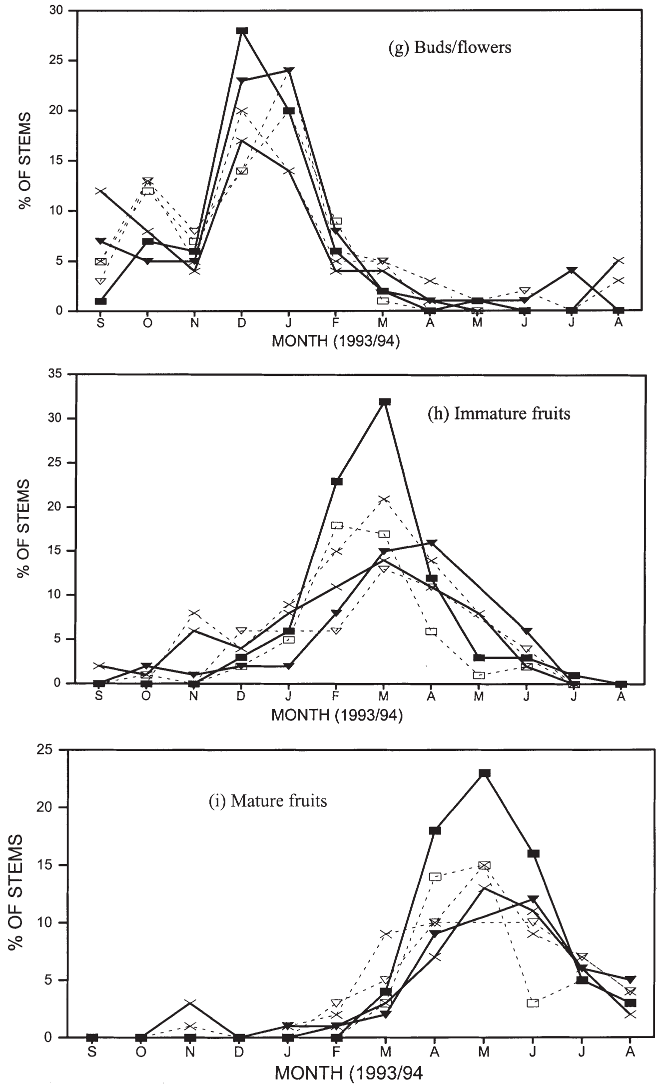


Fig. 3. (a–i) Phenophases at the arid (squares), semi-arid (triangles) and mesic localities (crosses) on toplands (—) and bottomlands (----). $n=5$ transects in both toplands and bottomlands for each locality, with sixty trees per transect. Note the unequal scales on the *y*-axis.

Table 3. The proportion of evergreen and deciduous stems with mature leaves during late winter (August 1994) at the arid site (%±SE; $n=5$ transects for toplands and for bottomlands; sixty trees per transect).

Position	Evergreen species		Deciduous species	
	Occurrence	% with mature leaves	Occurrence	% with mature leaves
Toplands	1.0±0.7	100.0±0	99.0±0.7	4.7±1.4
Bottomlands	19.3±6.3	100.0±0	80.7±6.3	16.6±4.0

Table 4. The proportion of stems (%±SE) in different height classes with mature leaves or leafless during the late dry period at the arid site (bottomland and topland transects pooled, therefore $n=10$; sixty trees per transect).

Month	% with mature leaves			% leafless		
	<2 m	2–4 m	>4 m	<2 m	2–4 m	>4 m
Aug. 1994	22.1 (5.24)	14.8 (6.53)	21.3 (6.58)	67.9 (4.82)	77.0 (5.93)	68.8 (7.50)
Sept. 1993	21.9 (5.13)	14.6 (3.76)	13.5 (3.74)	69.8 (5.45)	77.4 (4.83)	72.7 (5.89)
Oct. 1993	14.4 (4.45)	11.8 (5.53)	7.4 (4.89)	83.2 (5.06)	86.5 (5.26)	88.8 (4.88)

little remaining thereafter. No trends were discernable between sites or according to slope position.

The influence of stem size

Phenological activity of leaves was a function of stem size. In particular, there was greater leaf retention during late winter by small stems than by large stems ($t=4.8$; $P<0.05$; d.f. 3) (Table 4). Similarly, at the same time, a greater proportion of large stems were leafless relative to small stems ($t=20.7$; $P<0.005$; d.f. $=2$). This was particularly evident when comparing the smallest height class with either of the two taller height classes, but comparison between the two tallest height classes did not always conform to this pattern.

DISCUSSION

As to be expected from previous literature, a clear seasonal pattern was detected at all sites with respect to the different phenophases. However, the primary concern of this study was whether or not the onset, duration and magnitude of individual phenophases was related to soil moisture as determined by rainfall zone, or catenal position.

Rainfall zone appeared to influence: (1) the onset and magnitude of leaf emergence, (2) the onset and duration of mature leaves, and (3) the proportion of leafless trees. Generally, leaf growth was initiated earlier at the moist locality than at the semi-arid or arid localities. Emergent and mature leaves were recorded earlier, and in the case of mature leaves, retained longer. Overall, there was a lower proportion of leafless trees at the moist site, followed by the semi-arid site, followed by the arid site. The finding with respect to the earlier onset and longer duration of mature leaves at the moist site is particularly pertinent, in that it suggests that the often greater productivity of sites in higher rainfall areas (Shackleton, 1997) may relate to a longer growing season, rather than the greater rainfall *per se*, as commented by Murphy & Lugo (1986), although the two are generally correlated. However, evergreen forest species, although retaining leaves throughout most of the year, are generally less productive than deciduous species in the same environment (Geldenhuys, 1993; Geldenhuys & Rathogwa, 1997).

Previous work suggests that leaf initiation at the start of the growing season appears to be related more to changes in temperature than to rainfall (Monasterio & Sarmiento, 1976; Rutherford & Panagos, 1982; Milton, 1987; Steinke, 1988), although day length has also been identified as a possible factor (van Rooyen, Theron & Grobbelaar, 1986a; Milton, 1987). The common phenomenon of savanna trees flushing prior to the start of the rainy season (Rutherford, 1984; Fatubarin, 1985; Milton, 1987; Zietsman, van Wyk & Botha, 1989; Chidumayo, 1993) suggests that rainfall is not the proximate trigger. Prins (1988) suggests otherwise, classifying woody shrubs into categories depending upon their phenological response to accumulated rainfall at the start of the rainy season in Lake Manyara National Park, Tanzania. The incidence of flowering and fruiting of arid zone *Acacias* is also largely a function of soil moisture (Freidel *et al.*, 1994).

This study parallels the findings of Hoffman (1989), who investigated community phenology in subtropical thicket and karroid shrublands along a rainfall gradient in the south-eastern Cape (South Africa). In his study, increasing aridity resulted in a concentration of phenological activity into a shorter period. This is possibly a response to a greater carry-over of soil-moisture in higher rainfall regions than occurs at more arid sites (Scholes & Walker, 1993). Teague (1987) recorded that *Acacia karroo* would initiate shoot growth whenever there was sufficient subsoil moisture, irrespective of climatological season. However, if the soil-moisture carry-over was of sufficient quantity from the previous season, why then would leaf senescence occur at all, and why are there not frequent mid-winter growth events resulting from use of this carry-over soil moisture? This reasoning again leads to the inclusion of some other variable, possibly temperature, acting in conjunction with soil-moisture. For instance, a given temperature may act as a trigger. Whether or not leaf emergence occurs at this critical temperature depends upon the availability of sufficient carry-over, or current season soil moisture, both of which are greater at sites of higher mean annual precipitation.

Differences with respect to catenal position were evident for (1) the proportion of trees in winter with mature leaves, and (2) the proportion of trees with senescent leaves. Bottomlands had a greater proportion of trees with leaves during winter, but a lower proportion of trees recorded with senescent leaves. In a synthesis of work in tropical dry forests, Murphy & Lugo (1986) concluded that soil type was an important determinant of the degree of evergreenness of a community. Pierce & Cowling (1984) concluded that soil type had no influence on species phenology for species occurring across several soil types in the Cape fynbos. However, the contrast of catenal position in this study does not relate solely to contrasting soil types but also to soil water dynamics. Bottomlands have a greater soil moisture status but reduced availability due to their higher clay content. It has been argued that the timing of leaf fall is related to reduction in soil-moisture indicating the onset of the dry season (Rutherford & Panagos, 1982; van Rooyen, Theron & Grobbelaar, 1986b), and that this may vary from year to year (Murphy & Lugo, 1986). Menaut & Cesar (1979) suggested the same, noting that leaf fall is generally synchronous between different species in a given year, but the exact timing differs between years. At low rainfall regimes, available soil-moisture is greater in sands than in clays during the limiting periods, i.e. at the start and cessation of the rainy season. This was not reflected in the data presented here with respect to the onset and magnitude of leaf emergence or senescence.

The influence of tree height on individual plant phenology has a bearing on community phenological patterns. This study demonstrated that a greater proportion of small stems retain some leaves in the dry season than do larger stems. Similar results were found by Milton (1987) and Novellie (1989), who suggested that the differences relate more to tree age than size. Rutherford & Panagos (1982) found the opposite for *Ochna pulchra* in a broadleaf savanna on the South African highveld. If this is a relatively common feature of many savanna species, then the height class distribution within a given stand will have considerable bearing on the overall community phenology and the consequent availability of browse material in the critical dry season. The greater availability of leaf browse would counter the lower availability of fruits and seeds, as the reproductive output of small individuals is less than that of mature trees (Shackleton, 1997). The role of competition in affecting tree size and height, and hence phenology, requires investigation.

In conclusion, this work has demonstrated that soil moisture, as determined by rainfall and soil texture, has a marked effect on woody community phenology in savannas. In particular, increasing aridity resulted in the concentration of growth related phenophases into a shorter period of time, and a greater proportion of stems losing leaves in the dry period.

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