Correlation between evolutionary history, flowering phenology, growth form and seral status for important veld grasses

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Thirty species of veld grasses were analysed for their evolutionary history, flowering phenology, growth form and range of veld types. These characteristics were correlated with successional classes as reported in the literature, and the classes were defined on the basis of the parameters considered. The lowest and highest seral states were clearly distinguished from each other, but there was some overlap between the intermediate class and the highest and lowest classes. Six of the species differed from other representatives of their class. They were either in vegetation types atypical of other species in their group, were known to comprise a number of ecotypes, or were members of hybrid complexes.
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Dertig veldgrasspesies is ten opsigte van blomfenologie, groeivorm, evolusionêre geskiedenis en verskeidenheid veldtipes geanaliseer. Hierdie kenmerke is met die suksessieklasse, soos in die literatuur vervat, gekorreleer en die klasse is op grond van die parameters onder bespreking, gedefinieer. Die laagste en hoogste seerklasse word duidelik van mekaar onderskei maar daar was 'n mate van oorvleueling tussen die intermediêre klas en die hoogste en laagste klasse. Ses van die spesies het van die ander verteenwoordigers in hulle klas verskil. Hulle was of in ongewone veldtipes, of bekend vir hulle ekotipes, of was lede van hibriedkomplekse.
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Introduction

In developing a method to assess veld condition for pastures, Foran *et al.* (1978) and Tainton *et al.* (1980) have listed grass species in Natal which occur in veld that has been subjected to different intensities of defoliation over an extended period. They divide the grasses into three major categories. 'Decreasers' are the most valuable pasture species and are of intermediate seral status. Under conditions of under-utilization, the Decreaser species are replaced by 'Increaser I' species which are of higher seral status. Under conditions of over-utilization, the Decreasers are replaced by 'Increaser II' species which are of lower seral status. In this paper, the three successional states are described and defined by their evolutionary history, flowering phenology, growth form and range of veld types. The species in each group are listed in Tables 1, 2 and 3.

Methods

The evolutionary history of each species is reflected in its classification at subfamily and tribal level because each of the five grass subfamilies, Bambusoideae, Arundinoideae, Panicoideae, Chloridoideae and Pooideae, represents different evolutionary lines (Renvoize 1981) which developed under different environmental conditions (Hartley 1963). The subfamily placing of the genera follows Clayton (1970, 1982) and Clayton *et al.* (1974).

The flowering phenology of each species was extracted from PRECIS (Pretoria National Herbarium Computerized Information System) (Morris & Manders 1981; Magill *et al.* in press). Flowering specimens in the Herbarium were selected and sorted by month of flowering and locality as indicated by quarter degree square latitude and longitude grid. Only information for Natal specimens has been used. Flowering in each month is expressed as a percentage of the total number of flowering specimens reported for each species, so that comparisons between species can be made. Five species are represented by fewer than 20 specimens from Natal and could not show a clear flowering pattern, so were eliminated from the study.

The growth form of the species is expressed according to an unpublished system of vegetative character states developed by the author. Measurements for each species were made using herbarium specimens from Natal at the National Herbarium (PRE), and were checked against the descriptions given by Tainton *et al.* (1976).

The range of veld types in Natal for each species was taken from the original lists of Tainton *et al.* (1980), checked against Acocks (1975).

Results and Discussion

Subfamilies

The species in this study represent only three of the five grass subfamilies, namely Panicoideae (18 species), Chloridoideae (11 species) and Arundinoideae (1 species). All three of these subfamilies are most abundant in the tropics, and the C_4 photosynthetic pathway, which is advantageous in warm climates, occurs only in these three subfamilies and not in the other two (Renvoize 1981). The Panicoideae, composed of the major tribes Paniceae, Andropogoneae and Arundinelleae, evolved in high rainfall areas with a high annual or midwinter temperature (Hartley 1958a, 1958b). The Chloridoideae, composed of the major tribes Eragrostideae, Sporoboleae and Chlorideae, evolved in arid or semi-arid areas, again with a high annual or midwinter temperature (Hartley & Slater 1960). The Arundinoideae is a primitive subfamily with a number of diverse tribes that are not closely related and according to Renvoize (1981) the tribe Aristideae is best included in this subfamily. Although a climatic history for the whole tribe has not been determined, De Winter (1965) has shown that most of the southern African species of *Aristida* occur in areas of low rainfall and that species which occur in higher rainfall areas often grow at sites where available moisture is limited.

The subfamily of each of the species studied is shown in Tables 1, 2 and 3. The species of lowest seral status (Increaser II), are nearly all chloridoid or arundinoid, and by their evolutionary history may be expected to be better adapted to the drier conditions brought about by overgrazing. The species of highest seral status (Increaser I) are all panicoid and by their evolutionary history may be expected to be better adapted to the more mesic conditions of unused veld. The species of intermediate seral status (Decreasers) are a mixture of panicoid and chloridoid species.

When moving upward in succession, panicoid grasses replace the panicoid, chloridoid or arundinoid grasses of lower seral state. When moving downward in succession, chloridoid or arundinoid grasses replace the panicoid or chloridoid grasses of higher seral state.

Table 1 Species of lowest seral status (Increaser II) which increase with over-utilization, replacing the species of intermediate seral status

	Sub-family[a]	Flowering time[b]	Leaf width[c]	No. of veld types
Aristida congesta subsp. *barbicollis* (Trin. & Rupr.) De Wint.	A	L	1	1
Sporobolus pyramidalis Beauv.	C	L	2–3	1
Eragrostis plana Nees	C	L	1	1
Sporobolus africanus (Poir.) Robyns & Tournay	C	L	2–3	1
Hyparrhenia hirta (L.) Stapf.	P	L(p)	2	4
Eragrostis curvula (Schrad.) Nees	C	EL	1–2	2
Eragrostis chloromelas Steud.	C	EL	1–2	1
Bothriochloa insculpta (Hochst.) A. Camus	P	EL(p)	2	1
Eragrostis superba Peyr.	C	E	2–3	2
Microchloa caffra Nees	C	E	1	2
Sporobolus stapfianus Gand.	C	E	1	1
Eragrostis capensis (Thunb.) Trin.	C	E	1–2	1
Eragrostis racemosa (Thunb.) Steud.	C	E	1–2	1

[a] Subfamily symbols: A = Arundinoideae; C = Chloridoideae; P = Panicoideae
[b] Flowering time symbols: L = late-flowering; EL = early-and-late-flowering; E = early-flowering; p = prolonged
[c] Leaf width: width ranges taken from Table 4.

Table 2 Species of intermediate seral status (Decreaser) which decrease with either over-utilization or under-utilization (Symbols as in Table 1)

	Sub-family	Flowering time	Leaf width	No. of veld types
Themeda triandra Forssk.	P	EL	2	4
Heteropogon contortus (L.) Beauv. ex Roem. & Schult.	P	EL	2	4
Brachiaria serrata (Thunb.) Stapf	P	EL	3	3
Panicum maximum Jacq.	P	EL	2–4	1
Panicum deustum Thunb.	P	EL	3–4	1
Rhynchelytrum setifolium (Stapf) Chiov.	P	EL	1–2	3
Cenchrus ciliaris L.	P	EL	2–3	1
Diheteropogon amplectens (Nees) Clayton	P	L	3–4	3
Monocymbium ceresiiforme (Nees) Stapf	P	L	2	3
Digitaria eriantha Steud.	P	L	3	1
Eustachys paspaloides (Vahl) Lanza & Mattei	C	E	2	1
Eragrostis capensis (Thunb.) Trin.	C	E	1–2	2
Eragrostis racemosa (Thunb.) Steud.	C	E	1–2	3

Table 3 Species of highest seral status (Increaser I) which increase with under-utilization, replacing the species of intermediate seral status (Symbols as in Table 1)

	Sub-family	Flowering time	Leaf width	No. of veld types
Tristachya leucothrix Nees	P	E	2	2
Alloteropsis semialata (R. Br.) Hitchc.	P	E	3	1
Setaria nigrirostris (Nees) Dur. & Schinz.	P	E	2–3	1
Eulalia villosa (Thunb.) Nees	P	E	2–3	1
Cymbopogon excavatus (Hochst.) Stapf ex Burtt Davy	P	L	2–3	2
Trachypogon spicatus (L.f.) Stapf	P	L	2	1

Flowering phenology

Three flowering patterns were found: species with flowering peaks both early and late in the season (Figure 1); species with flowering peaks only early in the season (Figure 2); and species with flowering peaks only late in the season (Figure 3). 'Peaks' are taken to be months in which flowering is more than 10%. Each of the basic flowering patterns has a variant in which the flowering is more prolonged and the slope of the curve more gradual (Figure 4). The flowering pattern for each of the species is given in Tables 1, 2 and 3.

Each of the seral states has species that flower early in the season and late in the season. Each of the seral states also has a group of species with a unique combination of subfamily and flowering time. All early-flowering panicoids are in the highest seral state; all early-and-late-flowering panicoids are in the intermediate seral state; all late and early-and-late-flowering chloridoids are in the lowest seral state. On the other hand, the intermediate seral state shares certain combinations of subfamily and flowering time with the higher and lower seral states. Late-flowering panicoids occur in both high and intermediate seral states, and early-flowering chloridoids occur in both intermediate and low seral states.

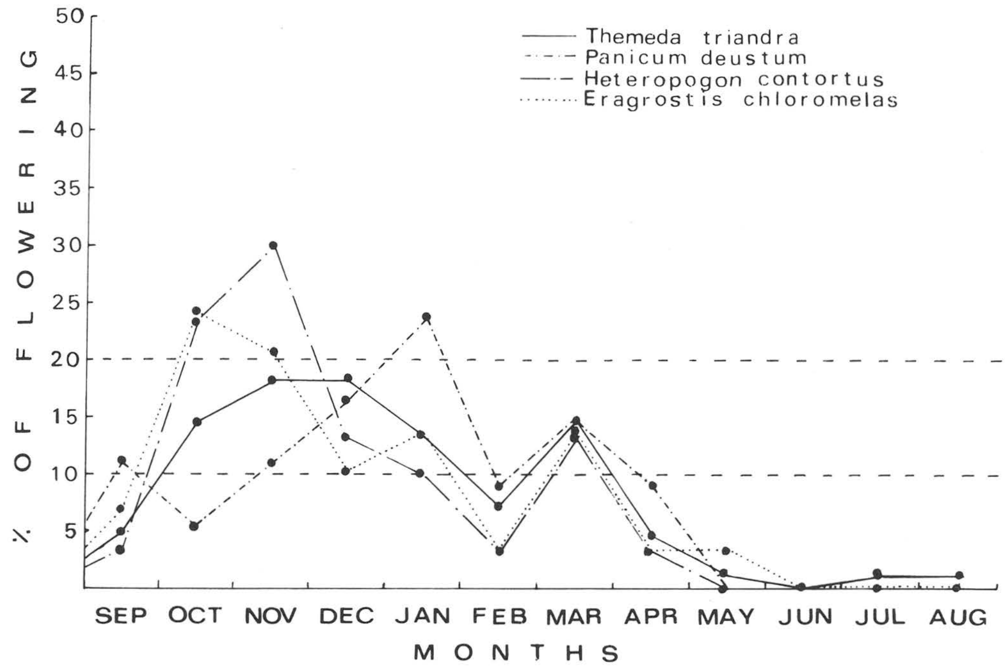

Figure 1 Early-and-late-flowering pattern. There are two peaks, the first from October to Janaury with a trough in February and a lower peak in March. At least 5 months have flowering greater than 10%. Seven panicoid and two chloridoid species have this pattern.

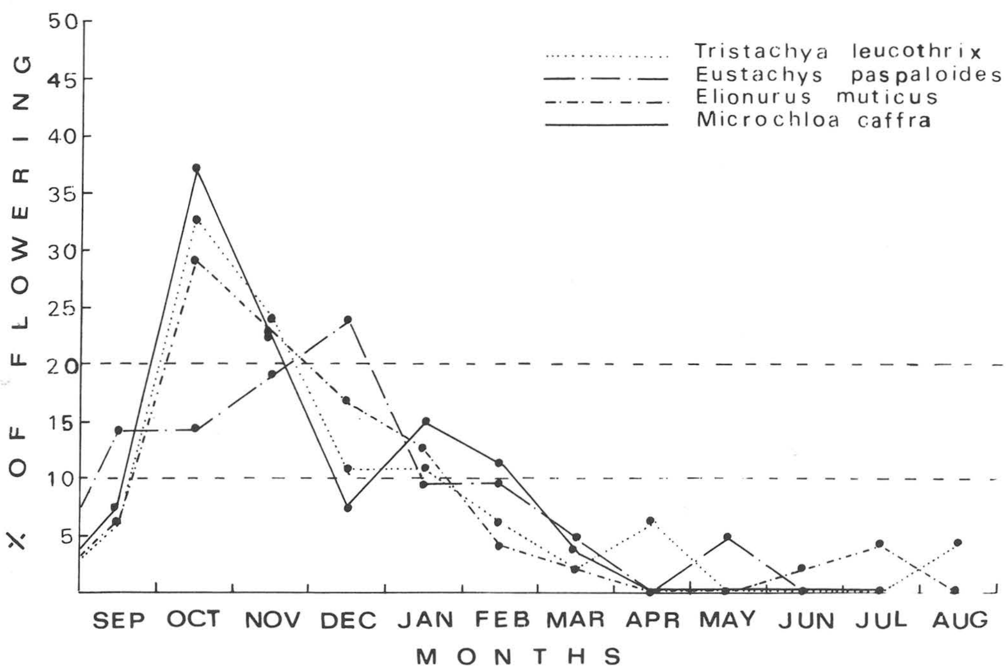

Figure 2 Early-flowering pattern. There is a single peak with flowering reaching 10% as early as September and extending to January. Only 3 or 4 months have flowering above 10%. Three panicoid and six chloridoid species have this pattern.

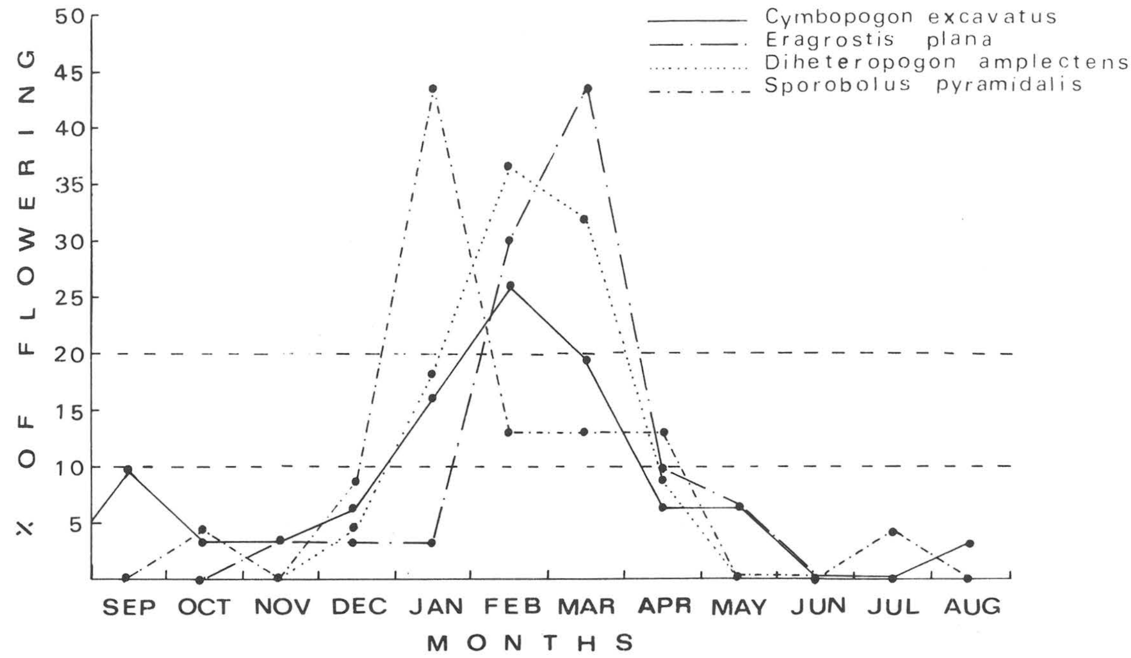

Figure 3 Late-flowering pattern. There is a single peak with flowering reaching 10% only in January or February and continuing to March or April. Only 3 or 4 months have flowering above 10%. Five panicoid and four chloridoid species have this pattern.

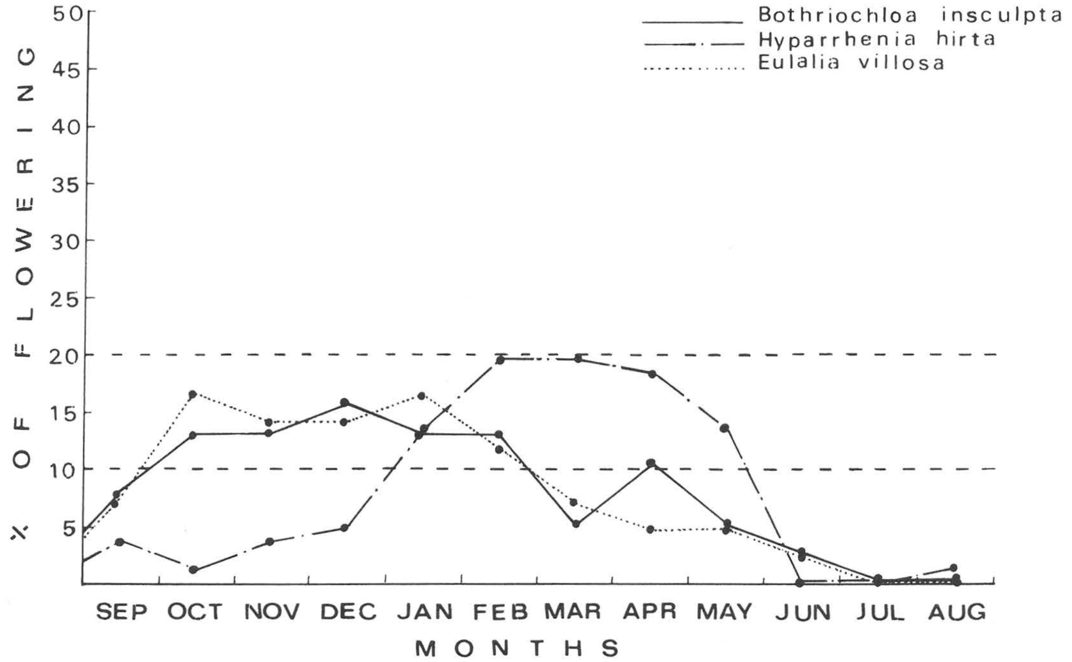

Figure 4 Prolonged-flowering variants of the three basic patterns. Flowering spans the months of January and February when other patterns are declining or increasing, but flowering never reaches 20%. All three species with this variant are panicoid.

Vegetative characteristics

Vegetative characters were determined for all species, and are shown in Table 4. The 30 species have similar character states for most of their organs, showing strong convergence from diverse evolutionary backgrounds. Slight differences between the species occur in foliage height and greater differences occur between them in leaf blade width, as shown by the numbers of species occurring in each of the character state categories for these two characters. The leaf blade width for each species is given in Tables 1, 2 and 3.

Leaf blade width is generally correlated with seral state and subfamily in that chloridoid and arundinoid grasses with an evolutionary history of adaptation to dry environments are in the lowest seral state and have the narrowest leaf blades, whereas panicoid grasses with an evolutionary history of adaptation to wetter environments are higher in the succession and have broader leaf blades.

Range of veld types

The number of veld types from which each species has been recorded is given in Tables 1, 2 and 3. The majority of species in the intermediate seral state are important in several veld types, but the species in the highest and lowest seral states are usually important in only one or two veld types. Thus, the species of intermediate seral status are of widespread occurrence, but different species characterize the

Table 4 Vegetative characters of all species in the study. Some species may exhibit more than one state for a single character

	No. of spp. showing character state
Growth form	
Annual, fibrous root	1
Perennial, mat-forming, stoloniferous	3
Perennial, mat-forming, rhizomatous	0
Perennial, tussock-forming, rhizomes compact	33
Perennial, rhizome solitary	0
Culm position	
Erect	32
Decumbent	5
Prostrate	0
Culm branching	
Unbranched	28
Branched only at base	0
Branched above base	8
Leaf position	
Cauline only	1
Basal only	2
Basal and cauline	32
Maximum foliage height	
30 – 200 mm	5
200 – 500 mm	27
500 – 1000 mm	19
1 – 1,5 m	9
1,5 – 2 m	1
Greater than 2 m	0
Leaf blade width	
1 – 2 mm	12
2 – 5 mm	22
5 – 10 mm	13
Greater than 10 mm	3

highest and lowest seral states in different veld types.

Definition of successional classes

The characteristics of the species in each of the successional classes are summarized in Table 5. The highest and the lowest seral states are distinguished from each other on the basis of subfamily, flowering phenology and leaf blade width. The intermediate seral state has some species that show characteristics of the highest seral state and other species that show characteristics of the lowest seral state. This summary disregards a few problem species that do not appear to fit in with the rest of their class. Their aberrant behaviour may be the result of several different factors which are discussed below.

Problem species

Each of the successional classes has at least one species that differs from the pattern established by the others. These six problem species exhibit biological traits that set them apart from the other species in the study.

Table 5 Species characteristics typical of the three successional states

Highest seral state (Increaser I)	
Each spp. in 1 – 2 veld types only	Panicoid early-flowering
Medium to broad leaf blade width	↑
– – – – – – – – – – – – – – – –	Panicoid late-flowering
Intermediate seral state (Decreaser)	↓
Each spp. in 1 – 4 veld types	Panicoid early-&-late-flowering
Medium to broad leaf blades	↑
– – – – – – – – – – – – – – – –	Chloridoid early-flowering
Lowest seral state (Increaser II)	↓
Each spp. in 1 – 2 veld types only	Chloridoid early-&-late-flowering
Filiform to medium leaf blade width	Chloridoid late-flowering

Variation in vegetation types

Two of the problem species, *Eustachys paspaloides* and *Bothriochloa insculpta,* are given only for the lowveld. This vegetation type includes the Valley Bushveld which Acocks (1975) classifies as a karroid vegetation type. Its affinity is, therefore, with the arid west of the country rather than with the tall grasslands that extend far into tropical Africa. It is in the lowveld that a chloridoid species may be higher in the succession and that a panicoid species may be lower. Another species, *Eulalia villosa,* is reported only from the highland sourveld and has in addition an atypical prolonged flowering pattern, as does *Bothriochloa insculpta.*

Ecotypes

Eragrostis racemosa and *E. capensis* both occur in the lowest and in the intermediate seral states. Both the species have wide ranges in Africa and it may be that their differing behaviour is due to ecotypic differences commonly encountered in grasses of widespread distribution. Alternatively, they may be at different stages of succession in different communities because their seral state may depend on the species with which they are associated.

Hybridization

Hyparrhenia hirta is the only species in the lowest seral state that is panicoid, has a prolonged flowering pattern and is reported from all four veld types of Tainton *et al.* (1980). *Hyparrhenia* is a large and difficult tropical genus renowned for the hybridization between its species, and *H. hirta* is a member of a complex that includes *H. anamesa, H. filipendula* and *H. dregeana* (Clayton 1969). It is widely recognized that hybrid populations often inhabit disturbed sites and it may be for this reason that specimens named *H. hirta* are often found in overgrazed areas. The broad flowering curve (Figure 4) may further illustrate its hybrid state since the flowering peaks of the component species may tend to run together in a complex hybrid.

Conclusions

The present study shows that evolutionary history, flowering phenology and certain morphological features are correlated with the ecological behaviour of species. Furthermore, information on herbarium specimens, collected from many localities over a long time, shows patterns that are not easily discernible from the examination of a few individuals and which in the field may be obscured by local or annual variations.

The results reported here are based on species lists for Natal. The patterns derived from them will be tested by comparing them with similar data from other regions.

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