Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape

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Qualitative and quantitative phenological observations were made on 173 species in eight communities in climatically similar sites. Results indicated that in species growing on different substrates. soil type had a minimal effect on phenophases. Phenophase patterns were analyzed by grouping species into growth form classes. Geophytes and annuals grew from autumn to spring. The majority of restioids and C3 grasses grew most in the cool wet seasons. C4 grass species showed either a summer growth season or an additional cooler growth season; the former species do not occur westwards in the winter rainfall region while the latter do. Most succulents grew in autumn and spring while two species also grew in summer. Small leaved sclerophyll shrubs grew throughout the year and/or showed a summer growth peak. The former pattern is consistent with a 'generalist strategy' but the latter is not readily explained because of summer drought conditions. Subtropical large leaved sclerophyll shrubs showed irregular growth and reproduction whereas large leaved proteoid shrubs grew in summer and autumn. In all shrub growth forms maximum leaf loss occurred in summer. Phenophase patterns were explained in terms of ecophysiological factors but biological and historical factors were also considered.

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Kwalitatiewe en kwantitatiewe fenologiese waarnemings is op 173 plantspesies in agt gemeenskappe uit klimatologies-ooreenstemmende gebiede gemaak. Die resultate dui daarop dat in die geval van spesies wat op verskillende substrate groei, die grondsoort 'n minimale invloed op fenofases het. Fenofasepatrone is ontleed deur spesies in groeivormklasse te groepeer. Geofiete en eenjarige plante het vanaf die herfs tot die lente gegroei. Die meerderheid restio-agtige en C3 grasse het meestal in die koel nat seisoene gegroei. C4 grasspesies het òf 'n somergroeiseisoen òf 'n addisionele koeler groeiseisoen getoon. Eersgenoemde spesies kom nie weswaarts tot in die winterreënvalstreek voor nie terwyl laasgenoemde wel daar voorkom. Die meeste sukkulente groei in die herfs en lente terwyl twee spesies ook in die somer groei. Die sklerofiliese struike met klein blare groei dwarsdeur die jaar en/of toon 'n groeipiek in die somer. Eersgenoemde patroon is in ooreenstemming met 'n 'algemene strategie' maar vanweë die droë somertoestande, is laasgenoemde patroon nie maklik verklaarbaar nie. Die subtropiese struike met groot blare se groei en voortplanting was onreëlmatig terwyl die protea-agtige struike met groot blare in die somer en herfs groei. By alle struikagtige groeivorme het maksimum blaarval in die somer voorgekom. Die fenofasepatrone is in terme van ekofisiologiese faktore verklaar maar biologiese en historiese faktore is ook in aanmerking geneem. S.-Afr. Tydskr. Plantk. 1984, 3: 1-16

Keywords: Fynbos, phenology, renosterveld, south eastern Cape, subtropical thicket

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Introduction

Phenology is the study of the timing of recurring biological events. The phenology of plant growth and reproduction is a major focus of the Fynbos Biome Project (Kruger 1978) and is the subject of two reviews (Kruger 1981; Pierce 1983). The phenology of plants from the south western region of the biome has been reviewed by Kruger (1981) while Bond (1980) presents data from the southern region. Earlier studies have been carried out in Namaqualand (van Rooyen *et al.* 1979) and the eastern Cape (Palmer 1982). This study reports on the phenology in the south eastern Cape of three shrubland types (fynbos, renosterveld, subtropical thicket) in the biome.

The south eastern Cape forms the eastern limit of the Fynbos Biome and comprises the meeting place of four African phytochoria, namely the Cape, Karoo-Namib, Tongaland-Pondoland and Afromontane Regions (Goldblatt 1978; Werger 1978; Gibbs Russell & Robinson 1981; White 1983). The area is rich in vegetation types (cf. Acocks 1953; Gibbs Russell & Robinson 1981) most of which are chorologically complex (Werger 1978; Cowling 1983a). We studied the phenology of eight plant communities, representing three vegetation classes (sensu Cowling 1983a), in a climatically homogeneous area within a 10 km radius. Species were grouped into growth forms, and phenophases within each group were discussed in terms of ecophysiological, biological and historical factors. The data have been used for periodicity comparisons across the Fynbos Biome (Pierce 1983) to test the overstorey/understorey phenological model for mediterranean shrublands (Pierce & Cowling 1983) and as a basis for improving the grazing quality of renosterveld (Cowling et al. 1983).

Study Area

Site descriptions

The study area is located near Humansdorp, south eastern Cape (Figure 1) on a level coastal plain which cuts across two geological formations: sandstone of the Table Mountain Group (TMG) and shales of the Bokkeveld Group. Along the coast there are deposits of recent calcareous sands. A detailed description of the environment of the study area is given in Cowling (1983a). Since the principle vegetation types correspond closely to geological substrate, it was possible to study eight communities which all experience similar mesoclimatic conditions. Some details of the sites, including dominant species, structure and soil data are given in Table 1. The following vegetation concepts are defined and described in detail by Cowling (1983a). Grassy Fynbos communities are endemic to the south eastern Cape and occur on infertile, sandy soils.

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South Coast Dune Fynbos is distributed along the southern Cape coast and is confined to calcareous coastal dune sands.

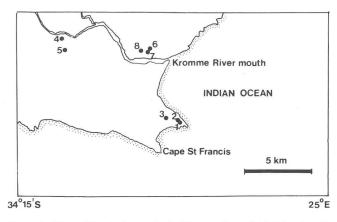
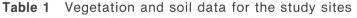


Figure 1 Map of the study area in the Humansdorp district showing the numbered study sites in each community (see Table 1).

South Coast Renosterveld is a shrubland confined to the south coastal foreland of the Cape Region (*sensu* Goldblatt 1978), and in contrast to Cape Fynbos, occurs on loamy, moderately fertile soils (Taylor 1978; Boucher & Moll 1980) which, in the study area, are derived from Bokkeveld shale. Kaffrarian Thicket is a subtropical thicket type which penetrates the Cape Region on deepish, well drained fertile soils in the lowlands. In the study area, thicket occurs on deep, well drained soils derived from Bokkeveld shales as well as on dune sands.

Land use

The dune grassland, shale grassland, renosterveld and restioid grassland sites (Table 1) are moderately grazed and mowed or burnt on a 4-5 year rotation. The last mentioned site was inadvertently burnt in February 1981, at the start of the sampling. Grazing animals were excluded from the grassland sites during the sampling period. The dune fynbos and grassy fynbos sites (Table 1) were ungrazed and unburnt for seven and



	Site number ^a								
	1	2	3	4	5	6	7	8	
Vegetation order ^b	South Coast Dune Fynbos	Kaffrarian Thicket	South Coast Dune Fynbos	Grassy Fynbos	Grassy Fynbos	Kaffrarian Thicket	South Coast Renosterveld	South Coast Renosterveld	
Community ^b	Restio eleocharis- Agathosma steno- petala Dune fynbos	Cassine aethiopica- Cussonia thyrsiflora Dune thicket	Themeda triandra- Stenotaphrum secundatum Dune grassland	Thamnochortus glaber-Erica diaphana Grassy fynbos	Thamnochortus fruticosus-Tristachya leucothrix Restioid grassland	Pterocelastrus tricuspidatus-Euclea undulata Kromme River thicket	Elytropappus rhino- cerotis-Metalasia muricata Renosterveld	Themeda triandro Cliffortia lineari folia Shale grassland	
Dominant species	Agathosma steno- petala, A. apiculata, Restio eleocharis, R. leptoclados, Passerina vulgaris	Sideroxylon inerme, Pterocelastrus tri- cuspidatus, Cassine aethiopica, Olea exasperata	Themeda triandra, Stenotaphrum secun- datum, Passerina vulgaris, Rhus laevigata	Erica diaphana, E. pectinifolia, Leuca- dendron salignum, Thamnochortus glaber, Restio triticeus	Themeda triandra, Tristachya leu- cothrix, Thamno- chortus fruticosus, Elegia vaginellata	Euclea undulata, Maytenus acumi- natus, Olea africana, Sideroxylon inerme	Themeda triandra, Elytropappus rhi- nocerotis, Ruschia tenella, Metalasia muricata	Themeda triandra Sporobolus african Cynodon dactylor Pentaschistis angustifolia	
Vegetation structure ^c	Low closed ericoid shrubland with open restioid under- storey	Mid-high closed large leaved shrubland	Closed grassland with low sparse ericoid shrub over- storey	Mid-high closed ericoid and proteoid shrubland with open restioid overstorey	-	Tall closed large leaved shrubland	Low open grassy small leaved shrubland	Closed grassland with sparse dwar small-leaved shru overstorey	
Soil properties									
Soil description and depth (m)	Excessively drained, moderately fertile, fine calcareous dune sand >3	Excessively drained, moderately fertile, medium, calcareous dune sand >3	Seasonally water- logged, moderately fertile, fine, cal- careous dune sand 1,5	Excessively drained, infertile, acid, coarse sand 1,1	Seasonally water- logged, infertile, acid, medium sand 1,5	Well drained, fertile loam 0,3 - 1,0	Poorly drained, (duplex) moderately fertile, loam 0,4	Seasonally water- logged, (duplex) moderately fertile loam 0,5	
Soil form & series ^d	Fernwood Motopi	Fernwood Motopi	Fernwood Brinley	Constantia Strombolis	Longlands Orkney	Clovelly	Glenrosa Williamson	Swartland Bridbach	
Geology	Recent sand	Recent sand	Recent sand	Table Mountain Group sandstone	Table Mountain Group sandstone	Bokkeveld shale	Bokkeveld shale	Bokkeveld shale	
H ₂ O holding capacity ^e (g)	27,6	?	48,6	29,8	40,2	69,3	42,1	40,9	
pH	7,7	7,6	7,6	4,2	4,3	5,1	5,3	5,3	
Na (ppm)	44	193	130	34	119	196	182	379	
K (ppm)	40	63	98	31	34	414	240	129	
Ca (ppm)	1918	2031	3039	186	209	2168	756	712	
Mg (ppm)	57	246	309	58	172	773	264	427	
S values (m-equiv.) ^f	10,3	13,3	18,6	1,65	3,09	19,16	7,38	9,10	
Oxidizable C ^g (%)	2,4	4,5	7,4	3,2	3,5	18,6	5,1	5,0	
Total N ^h (%)	0,075	0,102	0,305	0,046	0,089	0,443	0,124	0,195	
Available P ⁱ (ppm)	35,7	15,1	15,6	1,5	3,9	25,7	2,0	3,3	

^aReference to site marked on map (Figure 1)

^bVegetation orders and communities sensu Cowling (1983a); names below binomial in column 3 are those used in the text

^cStructural characterization sensu Campbell et al. (1981)

^dSoil classification sensu MacVicar et al. (1977)

Weight absorbed at saturation by 100 g soil (Piper 1950)

fsum of exchangeable cations (1 mol dm⁻³ NH₄ acetate leachate)

^gWalkley-Black method ^hKieldahl method

ⁱModified Olsen (alkali extraction, pH 8) for 1-3 Bray No. 2 (acid extraction, pH 3) for 4-8.

fourteen years respectively, according to records kept by the landowners. The thickets on shale and dune sand were probably unburnt for fifty years or longer.

Climate

The climate is warm temperate and transitional between Koppen Csa and Csb climates (Specht & Moll 1983). Most rain is cyclonic and associated with fronts from the circumpolar westerly belt. The study area is usually included in the nonseasonal rainfall region although the three summer months (December – February) are always the driest (Figure 2b). Bond (1980) has shown that semi-arid and subhumid climates in the Cape constant rainfall region have an effective moisture regime that is unequivocally mediterranean as typified by moisture surpluses in winter and deficits in summer (Figure 2b). The warmest month at Cape St. Francis is February (mean monthly temperature of 19,9 °C) and the coolest is July (14,2 °C). Highest and lowest mean temperatures are 29,7 °C (in April) and 5,0 °C (in August) respectively (Anon 1942). Frost is uncommon. The area is subject to strong winds and occasional gales at any time of the year. Evaporation and radiation are clearly highest in the summer months (Nov – Feb) (Figure 2a). As all sites are on level ground, the radiation regime was assumed to be similar for all vegetation types. During the study (1981), exceptionally heavy precipitation resulted in doubling the average annual total and rainfall was unequivocally bimodal (Figure 2c).

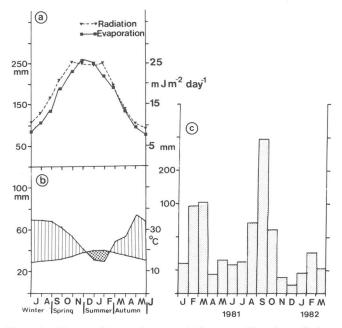


Figure 2 Climate of the study area. (a) Mean monthly solar radiation (earth's surface) for 1957 – 1958 and mean monthly evaporation (American Class 'A' Evaporation Pans) for 1957 – 1961 at Port Elizabeth (McCallum 1972). (b) Walter-Lieth climate diagram for Cape St. Francis (Heydorn & Tinley 1980). (c) Rainfall at Cape St. Francis during the sampling period (Weather Bureau, unpublished).

Methods

At each of the eight sites (see Table 1) the most common species were selected for study. The 173 species selected were identified by one of us (RMC) and voucher specimens are located in the Albany Museum Herbarium.

The results were analysed for phenological patterns. The most meaningful patterns emerged when species were grouped into growth forms, equivalent to guilds or groups of directly competing individuals (Peet 1978). We grouped species into growth forms (Table 2) defined in terms of height of perennating bud (Raunkiaer 1934), photosynthetic mode and leaf size.

The 'classical' descriptive method involving the qualitative assessment of phenophase by simple observation has been widely used in phenology (Williams 1971; Dickinson & Dodd 1976; Heinrich 1976). We have similarly used a descriptive method in which elements of time and site are preselected and the phenophase then determined.

Table 2 Growth form classes

Herbaceous growth forms	
Annuals	
Geophytes	
Non-geophytic forbs	
Graminoids	
Grasses (Poaceae) – C ₃	
- C ₄	
Restioids (Restionaceae) (Campbell et al. 1983)	
Cyperoids (Cyperaceae) (Campbell et al. 1983)	
Succulents	
CAM species (Mooney, Troughton & Berry 1977)	
Woody growth forms	
Small leaved shrubs ^a (Campbell et al. 1983)	
Large leaved shrubs ^a (Campbell et al. 1983)	
Proteoids ^b	
Thicket species ^c	

^aMost species have sclerophyllous leaves

^bIsobilateral sclerophyll leaves (all species are Proteaceae)

^cDorsiventral sclerophyll leaves (components of Subtropical Transitional Thicket (Cowling 1983a)).

In phenology, measures of different plant processes can give different growth peaks (Groves 1965). Because detailed measures of processes such as translocation of metabolites and cambial growth were beyond the scope of this study, we recorded the most obvious manifestations of growth which included shoot elongation, leaf initiation and development. Other conspicuous phenophases noted were: preflowering (bud) and full flowering (open flower); and unripe and ripe fruiting/ seeding. Leaf yellowing, prior to and including abscission, was noted.

In this way we made qualitative observations at monthly intervals on a total of 173 species in the eight communities shown in Table 1 during the period January 1981 – April 1982. Observations were made on 3-5 individuals of each species. In addition, successive monthly measures of shoot length increments on 20 of the selected species were made to show peak growth periods. To do this we tagged two shoots and measured their lengths on each of six specimens of each shrub species. Shoot elongation on two shoots per ten tufts of each restioid species was monitored. Twelve shoots of different grass tufts were tagged and the number of tillers and/or leaves per shoot were counted, depending on the species' growth habit. To measure growth of the arborescent rosette succulent, Aloe africana, we recorded the length of the three newest leaves on six tagged specimens. Leaf fall of selected species was measured by placing traps (200 mm diameter) beneath each of two specimens. Leaves trapped during each sampling interval were air-dried to a constant mass and weighed. At each sampling we also recorded all geophytes within a set area of 95 m² in each community.

Increments were used in growth analysis of shoots and aloe leaves, but actual counts of tillers and/or leaves each month were used for grasses. The data were not normally distributed and therefore would be poorly represented by means and standard errors. Instead the growth data are presented in the form of five-number summaries (*sensu* Underhill 1981).

The method of measuring shoot length increment is compared with an alternative, widely used method of growth determination. This latter method involves the use of bar graphs of relative abundance (percentage) of tagged specimens of a species showing the same phenophases at the time of sampling (Frankie *et al.* 1974; Guy *et al.* 1979).

Results and Discussion

Phenodiagrams of the common species in each community are shown in Appendices 1-7. The classification of species into growth forms is shown in Appendix 8. Five-number summaries depicting the detailed growth measurements of selected species and including information on other phenophases are shown in Figures 3-11.

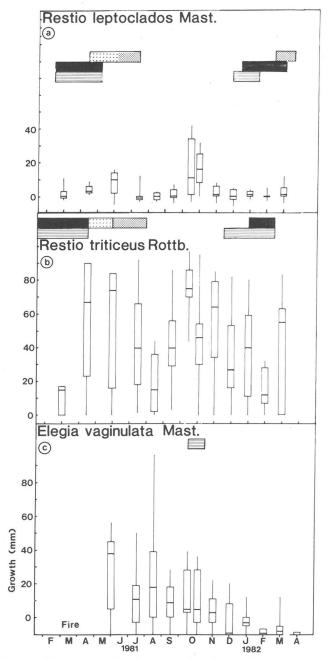


Figure 3 Phenophases of restioids in (a) dune fynbos, (b) grassy fynbos and (c) restioid grassland. Key: growth depicted in five-number summaries — see text; pre-flowering – stripes; full flowering – shaded; unripe seeds – open stipples; mature seeds – dense stipples.

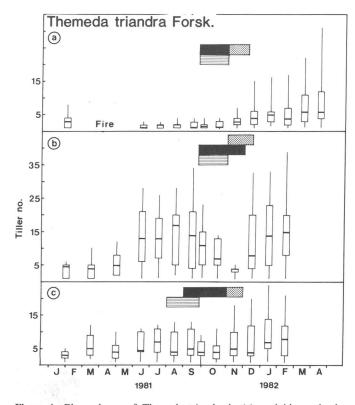


Figure 4 Phenophases of *Themeda triandra* in (a) restioid grassland, (b) dune grassland and (c) shale grassland. Key: see Figure 3.

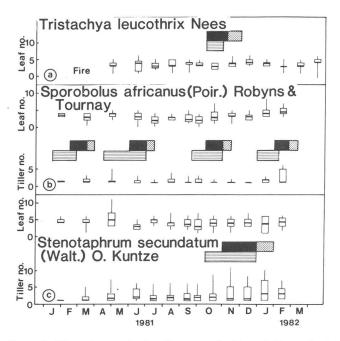


Figure 5 Phenophases of other C_4 grasses in (a) restioid grassland, (b) shale grassland and (c) dune grassland. Key: see Figure 3.

Evaluation of methods

In Figure 11 the two methods of determining growth are given: bar graphs denote the percentage of observed individuals growing at any one sampling time while detailed increments are expressed as five-number summaries. The bar graphs simply indicate that most of the growth of both species occurs from autumn, through winter to spring. The five-number summaries, however, reveal the bimodal nature of this cooler season growth on the loam soil. Low shoot increment in *Pterocelastrus tricuspidatus* in September (Figure 11a) and in *Sideroxylon inerme* in October (Figure 11d) coincided with a high percentage of shrubs showing growth (Figures 11b and e). This ex-

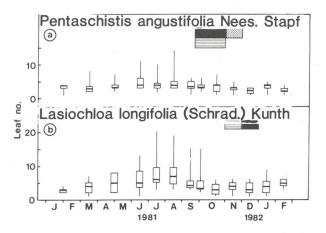


Figure 6 Phenophases of C_3 grasses in (a) shale grassland and (b) dune grassland. Key: see Figure 3.

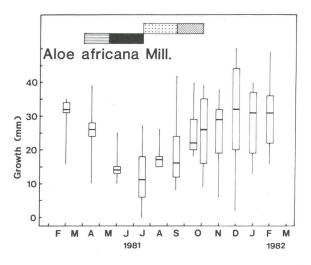


Figure 7 Phenophases of *Aloe africana* in Kromme River thicket. Key: see Figure 3.

emplifies the point raised earlier that different measures give different peaks. In this case, however, the results of the two methods are not contradictory; a high proportion of shoots could be growing but their growth, expressed as shoot increment, could be minimal.

Effects of substrate on phenophase

Species which occurred on more than one substrate type are listed in Table 3 where their phenodiagrams are referred to by figure number. In general, the phenophases of these species were synchronous, suggesting that substrate type does not have a marked effect on phenophases. Heyward (1931) analysed the flowering of 554 indigenous genera occurring in Victoria, Australia and found that most species' anthesis differed by less than a few weeks in spite of substantial environmental variation. In our study, loam soil tended to initiate growth (e.g. *Pterocelastrus tricuspidatus* and *Sideroxylon inerme*, Figure 11) and flowering (*Helichrysum teretifolium*, Appendices 3 and 6) in certain species earlier than the dune sand but showed no other marked difference.

Metalasia muricata showed no growth from autumn to late winter in the dune sand (Figure 8) and acid sand (Appendix 3) though some growh was apparent at the loam site (Figure 10) for the same period. However, maximal growth occurred in November on all three substrate types. Highest leaf fall in the loam was recorded in February following maximal growth (Figure 10). Inclusion of old flowers in the litter sample from

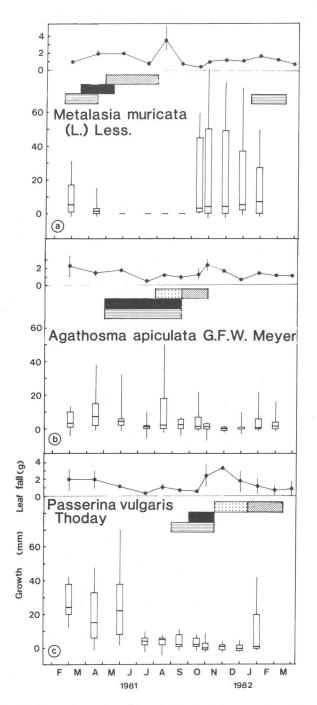


Figure 8 Phenophases of small leaved sclerophyll shrubs in dune fynbos. Leaf fall is expressed as the mean of two values (bars). Key: see Figure 3.

the dune sand site (Figure 8) resulted in a 'false peak' in August.

The tendency for earlier initiation of phenophases in the loam soils might be explained by the higher water-holding capacity of the loam (42,1 g per 100 g H_2O) relative to the dune sand and acid sand (27,6 and 29,8 g per 100 g H_2O respectively) (Table 1). After a light rainfall, more moisture would be held in the loam than in the excessively drained sand.

Themeda triandra showed similar growth rhythms in dune sand and loam, though early summer growth on the loam preceded that on the sand by about a month (Figure 4). The contrasting pattern of ever increasing growth of *Themeda triandra* on the acid sand of the restioid grassland is seen as a consequence of post-fire recovery.

Differences in fruiting behaviour associated with different substrate type were apparent in *Sideroxylon inerme* (Figure 11). No fruits were produced at the loam site while unripe fruits were recorded continuously in the dune sand. Flowering was

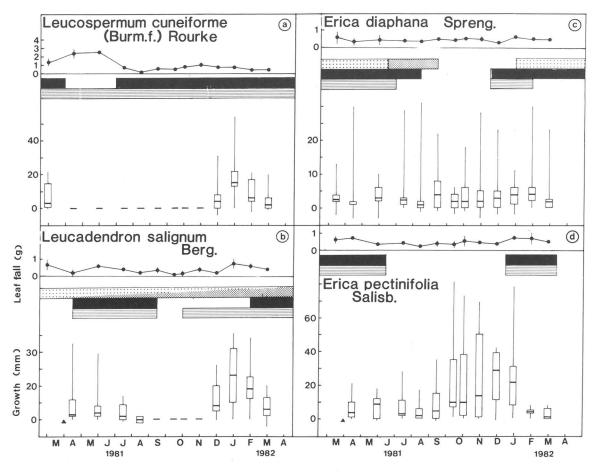


Figure 9 Phenophases of proteoids (a) and (b) and small leaved shrubs (c) and (d) in grassy fynbos. Leaf fall is expressed as the mean of two values (bars). Key: see Figure 3.

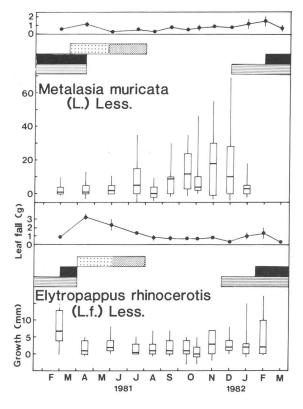


Figure 10 Phenophases of small leaved shrubs in renosterveld. Leaf fall is expressed as the mean of two values (bars). Key: see Figure 3.

noted at both sites, though to a lesser extent on the loam. However, irregular flowering and fruiting of individuals of subtropical thicket shrubs is common in mesic, coastal environments (Liversidge 1972; K.L. Tinley pers. comm.).

Phenophases of growth forms

Geophytes

Numbers of geophyte species recorded at each site within a 95 m² plot were: five in dune grassland; fifteen in renosterveld; none in grassy fynbos; two in dune fynbos and dune thicket; thirteen in restioid grassland and eight in shale grassland (Appendices 1, 2, 3, 4, 6 and 7). These results support the evidence for a tendency towards a greater diversity of geophytes with increasing soil fertility (Kruger 1979). Geophytes tended to initiate leaf growth from autumn (April/May) through to spring (September/October). Flowering in all communities was mainly in spring with occasional flowering in summer (Monadenia bracteata, Micranthus plantagineus, Appendix 4) and autumn/winter (Oxalis polyphylla, Appendix 6). Our data indicate that flowering behaviour may be a response to rainfall coinciding with higher temperatures. Maximum growth of geophytes in spring was also noted in Dark Island heath, Australia (Specht & Rayson 1957). In the S.W. Cape, Kruger (1981) reported geophyte leaf initiation in autumn/early winter but anthesis and leaf death varied considerably. Observations on leaf initiation in our study indicated similar timing to that in the S.W. Cape.

Annuals

Almost all annuals observed grew and flowered in early autumn, later winter and spring (Appendices 2, 4, 6 and 7). Thus growth of annuals in the study area coincided with an essentially winter growing season for agricultural crops.

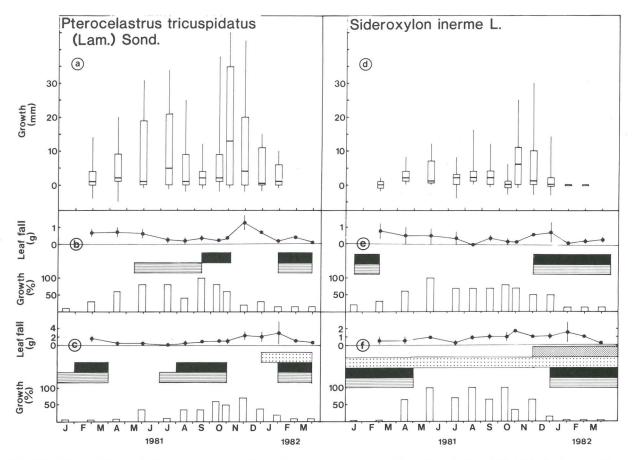


Figure 11 Phenophases and growth (five-number summaries and bar graphs — see text) of large leaved sclerophyll shrubs in Kromme River thicket (a), (b), (d) and (e); and dune thicket (c) and (f). Leaf fall is expressed as the mean of two values (bars). Key: see Figure 3.

Table 3	List of species occurring on more than one sub-	strate type. Their phenodiagrams are shown in
correspo	onding figures (Fig.) and appendices (App.)	

	Site numbers ^a							
Species occurring on more than one substrate type	1 Dune sand	2 Dune sand	3 Dune sand	4 Acid sand	5 Acid sand	6 Loam	7 Loam	8 Loam
Pterocelastrus tricuspidatus		(Fig. 11)				(Fig. 11)		
Sideroxylon inerme		(Fig. 11)				(Fig. 11)		
Themeda triandra			(Fig. 4)		(Fig. 4)			
Metalasia muricata	(Fig. 8)			(App. 3)			(Fig. 10)	
Helichrysum teretifolium				(App. 3)			(App. 6)	
Ixia orientalis			(App. 2)					(App. 7)
Briza maxima				(App. 4)			(App. 6)	
Babiana patersoniae					(App. 4)			(App. 7)
Sporobolus africanus			(App. 2)		(App. 4)			(App. 7)
Tephrosia capensis			(App. 2)					(App. 7)
Oxalis polyphylla					(App. 4)		(App. 6)	

^aSee Table 1 for detailed soil descriptions

Restioids

Restio leptoclados in dune fynbos and *R. triticeus* in grassy fynbos, both on well drained sand, showed most growth in spring and autumn (Figure 3) when most rain fell (Figure 2). However, *Elegia vaginulata* behaved differently with growth peaking in May (Figure 3), coinciding with the onset of winter waterlogging at that site.

This winter shoot increment was very high, possibly as a result of post-fire regrowth in response to higher soil nutrients following a burn (Rundel 1983).

Qualitative observations on Thamnochortus fruticosus in

the restioid grassland showed growth through autumn and winter while the soil was waterlogged (Appendix 4). *Restio sieberi* in the shale grassland grew most from April to June but also grew in the hot months of February/March 1982 (Appendix 7) when above average rainfall was noted.

Bond (1980) found a similar growth pattern for restioids in the southern Cape, with maximal growth correlating with moisture availability, though he also noted some summer growth. Further westwards, in the south western Cape, restioids start growth in spring/early summer (Kruger 1981) while some species grow only in summer (J. Sommerville pers. comm.). These data suggest that there is a trend for growth of restioids to occur earlier in the year the further east they occur in the Cape Region. Apart from rainfall differences, south eastern Cape regions have higher mean winter temperatures and 1-2 h more bright sunshine per day relative to the south western Cape (Fuggle 1981). It is possible that restioid growth is temperature controlled (Cowling 1983b).

Bond (1980) predicted that winter drought in the summer rainfall region would limit the eastward distribution of restioids and reduce their competitive advantage. He inferred that a combination of high soil moisture, low temperatures and low light conditions are a prerequisite for growth. However, the fact that some restioids grow only in summer during periods of high temperature, high light intensity and low moisture, contradicts this theory. Restioid roots appear to be shallow and able to exploit any chance summer rainfall. The limited distribution of restioids eastwards of the Cape Region may be related to factors such as limitations to seed dispersers (*cf.* Bond & Slingsby 1983) or the lack of highly infertile soils (*cf.* Campbell 1983).

Grasses

Counts of tillers and/or leaves per shoot of the C_4 grasses *Themeda triandra* (Figure 4), *Tristachya leucothrix, Stenotaphrum secundatum* and *Sporobolus africanus* (Figure 5) showed more than one peak of maximum growth. Other C_4 grasses which showed growth interrupted by a period of inactivity were *Cynodon dactylon* and *Eragrostis capensis* (Appendix 4). In contrast, *Elionurus muticus* (Appendix 4) and *Diheteropogon filifolius* (Appendix 3) had only one growth season, occurring in summer.

Growth measures of the C_3 grass species, *Pentaschistis* angustifolia and Lasiochloa longifolia indicated mostly autumn/early winter growth (Figure 6) while *Helictotrichon* hirtulum grew in autumn and spring (Appendix 7). These findings support the generalized notion of cool season growth of C_3 species and warm season growth of C_4 species (e.g. Teeri & Stowe 1976; Ehleringer 1978; Boutton *et al.* 1980).

From our study and from analysis of Palmer's (1982) work we were able to classify C4 grass species according to growth patterns of either one growth season or more than one growth season per year. We then compared the distributions (Meredith 1955) of these grass species in the Cape Region and found a correlation between growth pattern type and distribution. Almost all species which had a continuous, summer growth season do not occur much west of Humansdorp, (e.g. Eragrostis lehmanniana, Elionurus muticus, Diheteropogon filifolius), while Panicum deustum does not penetrate the truly winter rainfall area of less than 30% summer rain. These singlegrowth season species are apparently limited to summer and non-seasonal rainfall areas which receive a critical level of summer rain. In contrast, those grass species with more than one growth season all appear to penetrate into the winter rainfall area of the south western Cape.

The ability of both growth pattern types of C_4 grasses to grow during the summer enables them to dominate in the eastern, summer rainfall area of southern Africa (*cf.* Vogel *et al.* 1978). However, the capacity for growth during more than one season, the second season usually in early/midwinter, clearly gives these species a competitive advantage in the winter rainfall region. C_3 species are well adapted to the winter rainfall area, shown by their predominance in the south western Cape (Vogel *et al.* 1978), because they require lower temperatures associated with periods of low water stress (Boutton *et al.* 1980); Ellis *et al.* 1980). Our study confirms a cool, wet growth season for C_3 species in our area.

The study area in the south eastern Cape has equal numbers of species of C_3 and C_4 grasses (Cowling 1983b) which suggests that this region of non-seasonal rainfall, lying between the winter rainfall area to the west and the summer rainfall region to the east, is the overlap area for the C_3 and C_4 photosynthetic modes (see also Vogel *et al.* 1978). However, in terms of cover abundance, C_4 species (particularly *T. triandra* and other species capable of cool season growth) predominate over C_3 species in the study area (Cowling 1983b). We suggest that this high cover abundance is largely the result of the competitive advantage of the C_4 grass species with more than one growth season per year, in a region of mild temperatures and nonseasonal rainfall.

The C₄ grasses with more than one growth season, the C₃ grasses, the sedges and the restioids, all show some or all growth in the autumn to spring period. All are shallow rooted and able to exploit any summer rainfall but most of the growth occurs in the moderately warm, wetter months. These data refute the hypothesis that greater grass cover in eastern fynbos communities is due to a distinct temporal separation of growth activities within grasses and restioids in a given community (Cowling 1983a).

Succulents

The succulents observed were: *Aloe africana* (Figure 7), *Crassula cultrata* and *Sarcostemma viminale* (Appendix 5) in the Kromme River thicket; *Ruschia tenella* (Appendix 6) in the renosterveld and *Crassula expansa* (Appendix 1) in the dune fynbos. All these succulents grew in spring and autumn while *A. africana* and *S. viminale* also grew in summer. The phenophases of *A. africana* (Figure 7) are similar to those of *A. ferox*, another arborescent, rosette succulent (Holland *et al.* 1977).

Most, if not all the succulents we studied probably have crassulacean acid metabolism (CAM) (see Mooney et al. 1977) and possibly facultative CAM, whereby the mode of carbon fixation changes to C₃ (Hartstock & Nobel 1976) and less commonly to C4 (Bartakke & Joshi 1976) under changing conditions of temperature and soil moisture. The autumn and spring growth of succulents in our area may be explained by C₃ fixation during these moist, mild periods with small diurnal fluctuations in temperature. C3 fixation ensures much greater carbon fixation than CAM fixation which has low productivity (Ting & Szarek 1975; Kluge & Ting 1978). The additional summer growth of two succulent species may be the result of C₄ fixation. The strategy of CAM, and in particular facultative CAM, is especially suited to a non-seasonal rainfall regime. CAM enables plants to tolerate dry periods in a vigorous, nondormant state so that response to any available moisture is rapid (Sutton & Osmond 1972). The shallow roots characteristic of most CAM succulents (Kluge & Ting 1978) would also enable an almost immediate response to very light precipitation.

In the Fish River Valley of the eastern Cape, Palmer (1982) found similar spring and autumn growth patterns in some succulents (e.g. *Crassula expansa, Crassula muscosa (* = *lycopodioides)*) while other succulents tended to grow at all times except in spring and autumn (e.g. *Euphorbia bothae*). Optimum growth of *Kalanchoe daigremontiniana* requires low night and high day temperatures (Osmond *et al.* 1976) which may explain the winter growth of *K. rotundifolia* and other succulents in the Fish River Valley.

Small leaved shrubs

Growth patterns showed mainly either summer peaks or variable growth throughout the year. In some species, summer growth was preceded by a spring increment (e.g. Erica pectinifolia, Figure 9; Phylica litoralis, Appendix 1) or continued into autumn (e.g. Passerina vulgaris, Figure 8; Stoebe plumosa, Appendix 3). Peak growth in summer was shown by Disparago ericoides (Appendix 1) and Carpacoce vaginellata (Appendix 3), both in very well drained sand, and by Helichrysum teretifolium in loam (Appendix 6). These are all small, shallow rooted species. Other small leaved shrubs which showed most growth in summer were the deep rooted shrubs, Elytropappus rhinocerotis (Figure 10) and Metalasia muricata (Figures 8 & 10; Appendix 3), though slight, variable growth was apparent in some individuals throughout the rest of the year. Intermittent growth throughout the year was apparent in *Erica diaphana* (Figure 9); *Agathosma apiculata* (Figure 8); A. stenopetala, Sutera microphylla and Muraltia squarrosa (Appendix 1). In the southern Cape Mountain Fynbos, Erica seriphiifolia showed variable growth throughout the year while Phylica paniculata had a summer growth peak (Bond 1980).

Bond (1980) inferred from the aseasonal growth of an ericoid (sensu Campbell et al. 1981) small leaved shrub in the southern Cape that it had adopted a 'generalist' strategy (cf. Morrow & Mooney 1974) of growing whenever soil moisture and temperature are suitable. In our study, the phenology of ericoids showing similarly variable, aseasonal growth could also be explained by this strategy. Bond (1980) predicted that this year-round growth of ericoids and small leaved sclerophyll shrubs might be flexible enough to allow subtle seasonal division of resources between species which could allow for high species diversity within this growth form. His theory would help to explain the coexistence in a small stand of numerous species of Erica, Agathosma, Phylica and other ericoids. Temporal partitioning of resources between the two closely related Agathosma species, A. apiculata (Figure 8) and A. stenopetala (Appendix 1) may be inferred from their staggered flowering and fruiting phases. Both have similar sized flowers (Pillans 1950) and may reduce competition for pollinators and dispersers (ants) by staggered reproductive phenophases.

No simple explanation, such as the 'generalist' strategy, exists for species which had growth peaks during the hottest, driest summer months when moisture is presumably limiting. In contrast, growth rhythms of mediterranean-type shrublands (*sensu* Di Castri 1980) are clearly related to soil moisture availability, with most of the growth in spring (Rundel 1977; Mooney 1983). Productivity gradually decreases as summer drought progresses (Mooney & Dunn 1970; Mooney 1983). In the southern Cape, Bond (1980) recorded maximal growth of the ericoid *Phylica paniculata* during the summer water deficit period. This ability of small leaved, fynbos shrubs, possibly all shallow rooted, to grow during hot periods of high water stress is difficult to explain and needs detailed studies on water budgets, rooting depths and water stress tolerances (*cf.* Kruger 1981; Mooney 1983).

Summer growth by the ericoid shrubs, *Metalasia muricata* and *Elytropappus rhinocerotis* is more easily explained by their extensive root systems. The depth of the tap root alone of *E. rhinocerotis* has been measured as 6,06 m and the laterals spread to a diameter of 4-5 m (Scott & van Breda 1937); the latter are probably effective exploiters of chance summer rains. In the renosterveld community, the roots of these species easily reached the pedocutanic horizon, 0,65 m deep, which was moist

even in midsummer when the upper layers (0, 3 - 0, 6 m deep) lacked moisture.

Levyns (1956) noted that the summer growth of the two shrubs, *E. rhinocerotis* and *M. muricata*, was 'not at harmony with present climatic conditions'. Also, although seed is set in time for favourable germination conditions, germination is delayed for a year. These two factors suggested to her a summer rainfall origin for these species. We suggest that their ability to tap underground water reserves does not limit their growth during summer drought and an historical hypothesis need not be invoked.

Large leaved (sclerophyll) shrubs

Thicket Species. No obvious pattern of growth emerged from phenology of the large leaved sclerophyll shrubs in both the dune and Kromme River thickets, though there was a strong tendency for growth to cease for a short period in midsummer and all leaf fall occurred in summer (Appendices 1 and 5). In the dune thicket, new leaves and shoots were produced in spring (e.g. Cussonia thyrsiflora); winter, spring and autumn (e.g. Rapanea gilliana) and throughout most of the year (e.g. Olea exasperata) (Appendix 1). In the Kromme River thicket, spring and summer growth was most common although Rhus incisa and R. longispina grew in autumn and R. glauca grew mostly from spring through the autumn but ceased growth in December (Appendix 5). The 'generalist' strategy of continuous carbon fixation and growth whenever conditions are suitable is shown by deep rooted, large leaved sclerophyllous shrubs of Californian chaparral (Morrow & Mooney 1974; Mooney et al. 1975; Mooney et al. 1974; Mooney 1983). This description may fit the behaviour in our area of some deep rooted thicket species with relatively long lived leaves (more than $1^{1}/_{2}$ years, pers. obs.).

Certain thicket species were observed growing at any time of the year but when all thicket species were considered, spring and autumn growth predominated (Pierce 1983). Many species can grow throughout the winter (e.g. *Sideroxylon inerme, Pteroclastrus tricuspidatus, Rapanea gilliana*) which indicates that winter temperatures are not an important limiting factor for the growth of thicket species in the mild coastal climate of the south eastern Cape. Leaf loss for all species was highest in summer. The predominance of midsummer leaf loss if usually associated with low soil moisture (Frankie *et al.* 1974; Kummerow 1983).

Cowling (1983c) has argued that subtropical thicket species would have migrated into the Cape Region from the north east with the onset of warmer, wetter Holocene conditions after \pm 12 000 B.P. Only those species with wide phenological flexibility would have been able to penetrate the non-seasonal rainfall area as insufficient summer rainfall would severely restrict summer growing and winter deciduous thicket species (e.g. Acacia caffra and A. schweinfurthii). We suggest that flexibility in the growth phenophases of deep rooted, 'high costlow profit' (Orians & Solbrig 1977) sclerophyll shrubs would pre-adapt them for penetration of the non-seasonal and winter rainfall regions of the Cape. The ability to exploit bimodal and winter rains has led to the successful penetration of the southern and south western Cape by two thicket species in particular. Sideroxylon inerme gains importance as a dune thicket element further westwards of our area as far as the Cape Peninsula and Pterocelastrus tricuspidatus penetrates the dry (150mm y^{-1}) mediterranean climate area of the Cape west coast as far as Elands Bay, where summer rain is less than 20% of the total.

Flowering and fruiting patterns of thicket species were ir-

regular. However, when all species were considered, there were reproductive peaks in spring and autumn (Appendices 1 and 5; Liversidge 1972; Siegfried 1982; Pierce 1983; K.L. Tinley pers. comm.). Individuals within a species flower and fruit at different times of the year and also show variability in the quantity of their reproductive output (this study; Liversidge 1972; Frost 1976; K.L. Tinley pers. comm.). Of the nine species monitored both in this study and in Liversidge's (1972) study of dune thicket near Port Elizabeth, seven species showed marked differences in flowering and fruiting phenophases between the two study areas.

There are major differences between Frost's (1976) data from a south western Cape dune thicket and ours on reproductive phenophases of Euclea racemosa and Pterocelastrus *tricuspidatus*, though strict comparison was limited by the short duration of her study (April – August). In the south western Cape, P. tricuspidatus has peaks of ripe fruit in May and August and a high proportion of unripe fruits throughout the study period. Frost (1976) suggests that this staggering fruiting pattern, even on individual shrubs, is a strategy to reduce competition for dispersers. In the south western Cape E. racemosa set fruit in a short well-defined period (April – June). However, in our area, E. racemosa produced unripe fruit over a long period culminating in a short period of mature fruit (October -December) (Appendix 1). Irregular timing of reproductive behaviour has been noted in tropical trees and has been variously explained as strategies for pollination (Stiles 1977) and possible escape from seed predation (Janzen 1969, 1970).

Asynchrony in fruit production and dispersal within a species may be a way of limiting competition (McKey 1975; Grubb 1977) and thus account for the relatively high alpha diversity and lack of single species dominance in thickets in the south eastern Cape (Cowling 1983d). The proportion of viable seed of different species available to recolonize the small disturbance patches characteristic of thicket will show appreciable temporal and spatial variability. In contrast, south western Cape dune thickets are often dominated by a few species of thicket shrubs (viz. Sideroxylon inerme, Euclea racemosa, Pterocelastrus tricuspidatus, Olea exasperata). We argue that this is an historical consequence of the westward depauperization in the temperate Cape Region of subtropical thicket (cf. Cowling 1983a).

Proteoid species. The proteoid Cape endemics, *Leucadendron* salignum and *Leucospermum cuneiforme* (Figure 9) show summer growth maxima with *L. salignum* continuing growth into autumn. Bond (1980) found similar growth patterns for two proteoids in the southern Cape. *Leucadendron uliginosum* and *Protea repens*, which grew mostly in the dry summer period. Our findings of a summer/autumn peak in *L. salignum* agrees with the generalized phenology for the genus in the south western Cape (Kruger 1981). *L. cuneiforme*, however, ceased growth earlier than the time generalized for *Leucospermum* in the south western Cape (Kruger 1981).

L. salignum flowered in autumn/winter (Figure 9) and retained its seeds for about a year, releasing them only when new seed was present in the next season's cones (Williams 1972). Maximum leaf fall followed peak growth of L. cuneiforme, but L. salignum showed variable leaf loss (Figure 9). Both proteoids studied are widespread in the Cape Region and resprout from persistent woody rootstocks after fire (Rourke 1972; Williams 1972).

The two proteoid shrubs showed maximum growth in midsummer when soil water deficits were highest. Even the large leaved, evergreen 'generalists' of Californian chaparral grow in the moister springtime and not in midsummer (Morrow & Mooney 1974; Rundel 1977; Mooney 1983). We suggest that deep roots reaching underground water supples explain the summer growth of proteoids. Thus for example, Fernandez & Caldwell (1975) found that continued root growth to greater depths allowed a semi-desert shrub to transpire and fix carbon during the driest time of the year.

Other large leaved proteoid shrubs which grow during summer in a mediterranean-type climate are the dominant overstorey shrubs (e.g. *Banksia* in Australian heath (Specht & Rayson 1957)). This 'out of phase' growth is explained as the heritage of a tropically evolved flora, which now, by geographic circumstance and changing world climates, occupies a mediterranean climate area (Groves 1965). Bond (1980) considers the summer growth of proteoids to be better suited to a summer rainfall (or even non-seasonal) area, which further supports the theory of a tropical or subtropical origin for the family Proteaceae (Johnson & Briggs 1975) and the genus *Leucospermum* (Rourke 1972). Even the genus *Leucadendron*, for which Williams (1972) has argued a mediterranean climate origin, exhibits summer growth.

Within the constraints of limiting factors (e.g. light, nutrients, temperature) growth of proteoids may be determined by other phenophases such as periodicity of pollinators e.g. insects (Williams 1972), birds (Rourke 1972) and mice (Rourke & Wiens 1977), dispersers e.g. ants (Bond & Slingsby 1983), and predators e.g. rodents (Bond 1983) may be the ultimate determinants (*cf.* Mooney 1983).

Concluding Remarks

This study is essentially a descriptive account of phenophases of a wide range of species and growth form in four major vegetation types. It was not possible to explain adequately the phenophases of all species. However, many hypotheses emerged from this study and detailed autecological studies are required to test these. For example, reciprocal transplant and controlled environment studies should test hypotheses regarding the competitive interplay between grasses and restioids. Experimental evidence is necessary to determine the relative roles of soil moisture and temperature in determining the growth of thicket species. Ecophysiological and root behaviour studies should explain the summer growth of certain fynbos species. Much more work is required on the periodicity of pollinators and dispersers before we can evaluate their effects in governing phenophases. An experimental approach is likely to yield a fuller understanding of phenophases in a shorter time than more detailed long term observations (cf. Rutherford & Panagos 1982).

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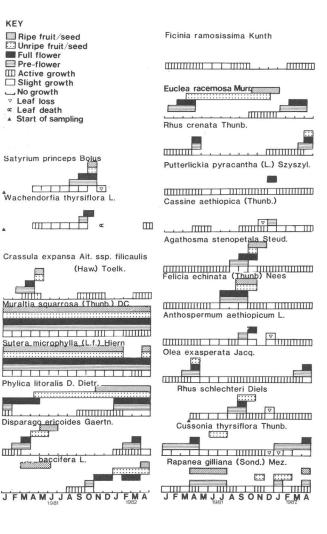
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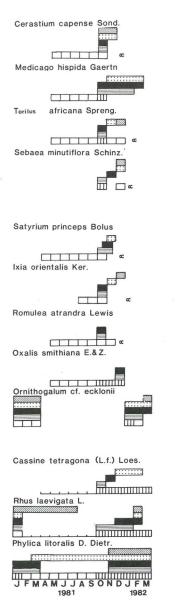
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Appendix 1 Phenodiagrams of species in dune fynbos and thicket

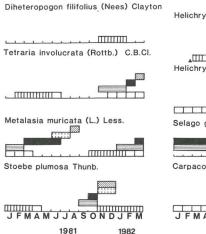


Appendix 2 Phenodiagrams of species in dune grassland. Key: see Appendix 1



Centella coriacea Nannfd. TTT Sporobolus africanus (Poir) Robyns & Tournay Rhynchosia caribaea (Jacq.) DC TITIT Tephrosia capensis (Thunb.) Pers _ _____ Psoralea decumbens Ait. Sutera campanulata (Benth.) O.Kze. Senecio burchellii DC. Cullumia decurrens Less <u>....</u> Indigofera stricta L.f. Indigofera incana Thunb. Manulea obovata Benth. Cotula sericea L.f. Vigna unguicullata (L.) Walp MAMJJASONDJ 1981 JFM

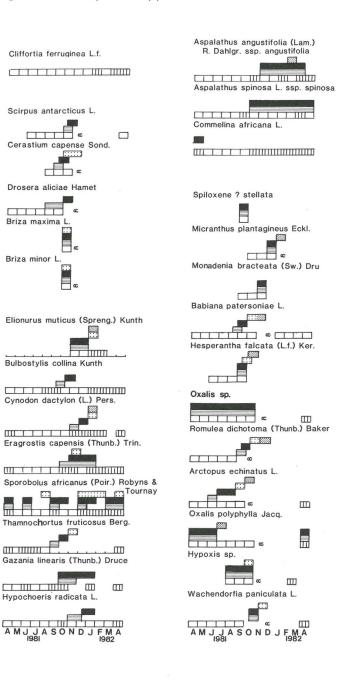
Appendix 3 Phenodiagrams of species in grassy fynbos. Key: see Appendix 1



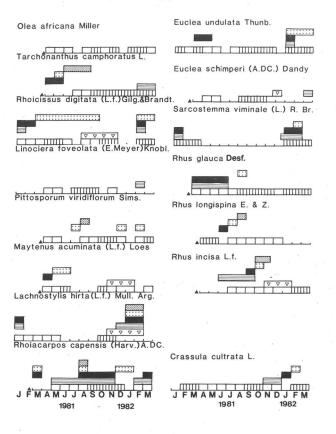
Helichrysum cymosum (L.) Less. Helichrysum teretifolium (L.) Less. Selago glomerata Thunb Carpacoce vaginellata Salter SONDJEM JFMAMJJA



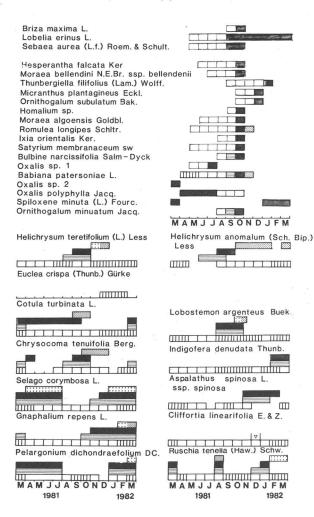
Appendix 4 Phenodiagrams of species in restioid grassland. Key: see Appendix 1



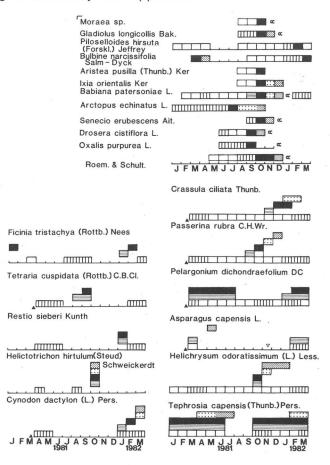
Appendix 5 Phenodiagrams of species in Kromme River thicket. Key: see Appendix 1



Appendix 6 Phenodiagram of species in renosterveld. Key: see Appendix 1



Appendix 7 Phenodiagrams of species in shale grassland. Key: see Appendix 1



Appendix 8 Classification of species into growth form classes (see Table 2). Phenophases are given in appendices and figures where indicated

Dune fynbos and thicket (see Appendix 1) Geophytes Satyrium princeps Bolus Wachendorfia thyrsiflora L. Restioids Restio leptoclados Mast. (Figure 3) Cyperoids Ficinia ramosissima Kunth Succulents Crassula expansa Ait. ssp filicaulis (Haw.) Toelk. Small leaved shrubs Muraltia squarrosa (Thunb.) DC Sutera microphylla (L.F.) Hiern Phylica litoralis D. Dietr. Disparago ericodes Gaertn. Chironia baccifera L. Agathosma stenopetala Steud. Felicia echinata (Thunb.) Nees Anthospermum aethiopicum L. Metalasia muricata (L.) Less. (Figure 8) Agathosma apiculata G.F.W. Meyer (Figure 8) Passerina vulgaris Thoday (Figure 8) Large leaved shrubs Thicket Species Euclea racemosa Murr.

Rhus crenata Thunb. Putterlickia pyracantha (L.) Szyszyl. Cassine aethiopica Thunb. Olea exasperata Jacq. Rhus schlechteri Diels Cussonia thyrsiflora Thunb. Rapanea gilliana (Sond.) Mez. Sideroxylon inerme L. (Figure 11) Pterocelastrus tricuspidatus (Lam.) Sond. (Figure 11)

Dune grassland (see Appendix 2)

Annuals Cerastium capense Sond. Medicago hispida Gaertn Torilus africana Spreng Sebaea minutiflora Schinz. Geophytes Satyrium princeps Bolus Ixia orientalis Ker. Romulea attandra Lewis Oxalis smithiana E. & Z. Ornithogalum cf. ecklonii Non-geophytic forbs Centella coriacea Nannfd. Rhynchosia caribaea (Jacq.) DC Tephrosia capensis (Thunb.) Pers Psoralea decumbens Ait. Sutera campanulata (Benth.) O. Kze. Senecio burchellii DC Indigofera stricta L.f. Indigofera incana Thunb. Manulea obovata Benth. Cotula sericea L.f. Vigna unguiculata (L.) Walp Grasses C4 Sporobolus africanus (Poir) Robyns & Tournay Themeda triandra Forsk. (Figure 4) Stenotaphrum secundatum (Walt.) O. Kuntze (Figure 5) C3 Lasiochloa longifolia (Schrad.) Kunth (Figure 6) Small leaved shrubs Phylica litoralis D. Dietr. Cullumia decurrens Less Large leaved shrubs Thicket species Cassine tetragona (L.f.) Loes Rhus laevigata L. Grassy fynbos (see Appendix 3) Grasses C4 Diheteropogon filifolius (Nees) Clayton Restioids Restio triticeus Rottb. (Figure 3). Cyperoids Tetraria involucrata (Rottb.) C.B.Cl. Small leaved shrubs Metalasia muricata (L.) Less. Stoebe plumosa Thunb. Helichrysum cymosum (L.) Less. Helichrysum teretifolium (L.) Less. Selago glomerata Thunb. Carpacoce vaginellata Salter Erica diaphana Spreng. (Figure 9) Erica pectinifolia Salisb. (Figure 9) Large leaved shrubs Proteoids

Leucospermum cuneiforme (Burm. f.) Rourke (Figure 9) Leucadendron salignum Berg. (Figure 9).

Annuals Scirpus antarcticus L. Cerastium capense Sond. Drosera aliciae Hamet Briza maxima L. Briza minor L. Geophytes Monadenia bracteata (Sw.) Dru. Spiloxene? stellata Micranthus plantagineus Eckl. Babiana patersoniae L. Hesperantha falcata (L.f.) Ker. Oxalis sp. Romulea dichotoma (Thunb.) Baker Arctopus echinatus L. Oxalis polyphylla Jacq. Hypoxis sp. Wachendorfia paniculata L. Non-geophytic forbs Gazania linearis (Thunb.) Druce Hypochoeris radicata L. Commelina africana L. Grasses C4 Elionurus muticus (Spreng.) Kunth Cynodon dactylon (L.) Pers. Eragrostis capensis (Thunb.) Trin. Sporobolus africanus (Poir.) Robyns & Tournay Themeda triandra Forsk. (Figure 4) Tristachya leucothrix Nees (Figure 5) Restioids Thamnochortus fruticosus Berg. Elegia vaginulata Mast. (Figure 3) Cyperoids Bulbostylis collina Kunth Small leaved shrubs Cliffortia ferruginea L.f. Aspalathus angustifolia (Lam.) R.Dahlgr. ssp. angustifolia

Restioid grassland (see Appendix 4)

Kromme River thicket (see Appendix 5)

Aspalathus spinosa L.

Succulents Sarcostemma viminale (L.) R.Br. Crassula cultrata L. Large leaved shrubs Thicket species Olea africana Miller Tarchonanthus camphoratus L. Rhoicissus digitata (L.f.) Gilg. & Brandt. Linociera foveolata (E. Meyer) Knobl. Pittosporum viridiflorum Sims. Maytenus acuminata (L.f.) Loes Lachnostylis hirta (L.f.) Mull. Arg. Rhoiacarpos capensis (Harv.) A.DC. Euclea undulata Thunb. Euclea schimperi (A.DC.) Dandy Rhus glauca Desf. Rhus longispina E. & Z. Rhus incisa L.f. Pterocelastrus tricuspidatus (Lam.) Sond. (Figure 11) Sideroxylon inerme L. (Figure 11).

Renosterveld (see Appendix 6)

Annuals Briza maxima L.

Lobelia erinus L. Sebaea aurea (L.f.) Roem. & Schult. Geophytes Hesperantha falcata Ker. Moraea bellendinii N.E.Br. Thunbergiella filifolius (Lam.) Wolff. Mircranthus plantagineus Eckl. Ornithogalum subulatum Bak. Homalium sp. Moraea algoensis Goldbl. Romulea longipes Schltr. Ixia orientalis Ker. Satyrium membranaceum Sw. Bulbine narcissifolia Salm-Dyck Oxalis sp. 1 Babiana patersoniae L. Oxalis sp. 2. Oxalis polyphylla Jacq. Spiloxene minuta (L.) Fourc. Ornithogalum minuatum Jacq. Non-geophytic forbs Pelargonium dichondraefolium DC Cotula turbinata L. Succulents Ruschia tenella (Haw.) Schw. Small leaved shrubs Aspalathus spinosa L. Cliffortia linearifolia E. & Z. Metalasia muricata (L.) Less (Figure 10) Elytropappus rhinocerotis (L.f.) Less (Figure 10) Helichrysum teretifolium (L.) Less Helichrysum anomalum (Sch. Bip.) Less Chrysocoma tenuifolia Berg. Selago corymbosa L. Gnaphalium repens L. Lobostemon argenteus Buek. Indigofera denudata Thunb.

Large leaved shrubs Thicket species *Euclea crispa* (Thunb.) Gürke

Shale grassland (see Appendix 7)

Annuals Senecio erubescens Ait. Drosera cistiflora L. Sebaea aurea (L.f.) Roem. & Schult. Geophytes Moraea sp. Oxalis purpurea L. Galdiolus longicollis Bak. Piloselloides hirsuta (Forsk.) Jeffrey Bulbine narcissifolia Salm-Dyck Aristea pusilla (Thunb.) Ker Ixia orientalis Ker Babiana patersoniae L. Arctopus echinatus L. Non-geophytic forbs Pelargonium dichondraefolium DC Tephrosia capensis (Thunb.) Pers. Grasses C3 Helictotrichon hirtulum (Steud) Schweickerdt C4 Cynodon dactylon (L.) Pers. Restioids Restio sieberi Kunth. Cyperoids Ficinia tristachya (Rottb.) Nees Tetraria cuspidata (Rottb.) C.B.Cl. Succulent Crassula ciliata Thunb. Small leaved shrubs Passerina rubra C.H.Wr. Asparagus capensis L. Helichrysum odoratissimum (L.) Less