A synthesis of plant phenology in the Fynbos Biome

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PREFACE

The southern and south-western Cape is occupied by an exceptionally rich flora occurring as sclerophyllous shrublands and heathlands known locally as fynbos. The various fynbos ecosystems, their plants and animals, are of considerable scientific and aesthetic interest, while the mountain catchment areas of the fynbos biome are of particular economic importance both as sources of water and as recreational areas.

Much research has been conducted in the biome in the past and in order to coordinate current activities, to stimulate new research and to synthesize available scientific information within the region, the Fynbos Biome Project was initiated in 1977.

The project is one of several national scientific programmes within the National Programme for Environmental Sciences administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up as a focus of international non-governmental scientific effort in the environmental field.

The first phase (1977 to 1980) of the Fynbos Biome Project centred on baseline studies, including the review and synthesis of current knowledge, and on broad surveys of climate, soils, vegetation, fauna and land use patterns. Phase II, comparative studies of ecosystem structure and functioning, have been running simultaneously with Phase I studies. This document is a synthesis of existing phenological information which has emerged from work done in fynbos ecosystems to date. It is representative of review and synthesis activities being carried out by study groups and individuals within the Fynbos Biome Project.

ABSTRACT

This synthesis provides an inventory of plant phenology in the fynbos biome up to February 1983, and an evaluation of the methods used. Phenology of species, genera and families, and also of communities in terms of growth forms, individuals and species is compared and discussed in terms of current theory. This includes speculation about phenological implications of tropical origins and biogeography. The ecophysiological model of Specht et al (1983) which explains the summer growth of certain species in Australian and Cape mediterranean-type ecosystems is refuted for the Cape. Instead, in order to understand plant-function, investigations into root architecture, water budgets, plant-animal interactions and the influence of radiation accumulation are suggested. Synthesis of the data shows that attempts at characterizing seasonality in different growth form types are weak. Also, categorization of species into groups showing particular seasonal patterns is limited. The role of phenology in management of fynbos biome vegetation is discussed and its importance in understanding plant dynamics is stressed. Although the summer growth of proteoids is well-known, similar behaviour by certain ericoids and restioids is also observed. However, there is no evidence that "fynbos" grows in summer and statements concerning the phenology of fynbos biome vegetation types should be more explicit.

SAMEVATTING

Hierdie sintese voorsien 'n lys van plantfenologie in die fynbosbioom tot en met Februarie 1983, asook 'n evaluasie van die metodes wat gebruik is. Fenologie van spesies, genera en families, en ook van gemeenskappe met betrekking tot groeivorme, individue en spesies word vergelyk en bespreek met betrekking tot huidige teorie. Dit sluit in bespiegeling oor fenologiese implikasies van tropiese oorsprong en biogeografie. Specht et al (1983) se ekofisiologiese model wat die somergroei van sekere spesies in Australiese en Suid-Afrikaanse mediterreense-tipe ekosisteme verduidelik, word vir die Kaap weerlê. In plaas daarvan, om plantfunksie te verstaan, word ondersoeke na wortelargitektuur, watergebruik, plant-dier interaksies en die uitwerking van uitstralingopeenhoping voorgestel. Sintese van die data dui daarop dat pogings om seisoenaliteit in verskillende tipes groeivorme te klassifiseer, swak is. Verder is kategorisasie van spesies in groepe wat bepaalde seisoenale patrone aandui, beperk. Die rol van fenologie in die bestuur van fynbosbioomplantegroei word bespreek en die belangrikheid daarvan om plantdinamika te verstaan, word beklemtoon. Alhoewel die somergroei van proteoïde goed bekend is, word soortgelyke gedrag by sekere erikoïde en restioïede ook opgemerk. Daar is egter geen bewys dat "fynbos" in die somer groei nie en stelings aangaande die fenologie van fynbosbioomplantegroei behoort duideliker gestel te word.

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INTRODUCTION

DESCRIPTION, DEFINITIONS AND APPROACH

This synthesis forms part of Phase II in the Fynbos Biome Project, the phase which includes comparative studies of ecosystem structure and functioning. Theories pertaining to phenology and particularly those concerning mediterranean-type ecosystems and their relevance to the fynbos biome are discussed. Mediterranean-type ecosystems of the world display spring growth peaks (Kummerow 1983). However, in the Cape and southern Australia, dominant species show distinctive summer/autumn growth peaks and this "anomalous" behaviour has been the subject of much speculation.

The definition of phenology accepted here is "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces and the interrelation among phases of the same or different species" (Lieth 1974). A phenophase is an "observed stage of plant development clearly circumscribed in time which is accomplished by an individual in a given site and ecosystem during a precise period of observation" (Monasterio and Sarmiento 1976). This synthesis has been severely limited by the nature and paucity of available information. Readily observable phenophases only are dealt with, and microscopic phases such as cambial growth, bud initiation and also underground root seasonality are absent from our literature. Published studies on causes of phenophases are non-existent.

This synthesis includes comparisons at the specific, generic and familial level and also within and amongst communities. Vegetation concepts and terminology are according to Cowling (1984a). Categorization of species' distributions into winter, non-seasonal and summer rainfall regions is according to Weimarck's (1941) biogeographic centres: the north-western and south-western centres form the winter rainfall region; the Langeberg, Karoo Mountain, Knysna Region and the south-eastern centre west of Port Elizabeth form the non-seasonal rainfall region; and east of Port Elizabeth forms the summer rainfall region. Those species which occur in both winter and non-seasonal rainfall regions are treated as members of the latter region, and are too few in number to bias trends. Seasons are defined as follows: November, December, January is summer; February, March, April is autumn; May, June, July is winter and August, September, October is spring.

AIMS OF THE SYNTHESIS

:   to provide an inventory of plant phenology within the fynbos biome

:   to evaluate phenological methods

:   to synthesize fynbos biome phenology and apply present theory to explain aspects of plant structure and functioning

:   to explain biogeographic patterns

:   to determine east-west gradient patterns in phenology

:   to discuss and evaluate the role of phenology in management

:   to indicate gaps in the knowledge and provide guidelines for future research.

INVENTORY

The following six pages comprise Table 1 which includes details of completed and current phenology in the fynbos biome. There is a conspicuous lack of studies on causal relationships, an essential part of phenology as defined earlier. The only study determining causal relationships is Sommerville's work at Pella on phenophases in relation to water relations and also to plant and soil nutrients (Brown, Coley, Jongens-Roberts, Stock). Also poorly represented are seasonality studies on plant-animal interactions such as pollination, dispersal and predation. Studies of this nature already completed include: Slingsby and Bond (1982) on myrmecochory; Siegfried (1982) on bird-plant communities and seasonality. Studies only recently initiated and reported on in poster form at the 4th Annual Research Meeting of the Fynbos Biome Project, June 1982, include: A Rebelo on bird pollination; J H Coetzee and J H Giliomee on Protea-associated insects; P Novellie and P Norton on ungulate feeding; D Donnelly and J H Giliomee on epigaeic invertebrate fauna in fynbos; M A Loos on soil microbial biomass in the fynbos biome.

Table 1. Inventory of phenology in the fynbos biome.

Researcher	Vegetation Type	Study site	No. of species/Community	Duration of study	Visual assess-ment of phenophases	Growth measure-ment	Litter-fall	Data	Form of final report	Publication date/Estimated time of completion
F J Kruger	Mountain Fynbos	S W Cape	unstated	-	+	-	+	Synopsis of phenology prior to 1978	Seasonal growth and flowering rhythms: South African heathlands. In: R L Specht (ed). Ecosystems of the World Vol 9B Heathlands and Related Shrublands. Analytical Studies. Elsevier, Amsterdam. pp 1-3.	1978
M W van Rooyen, G K Theron & N Grobbelaar	Namaqualand Broken Veld	Springbok - Hester Malan Nature Reserve	116	8 months	+	-	-	Published	Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. 1. General observations. Jl.S.Afr.Bot 45: 279-293.	1979
W J Bond	Mountain Fynbos	1. Outeniqua mtns 2. Swartberg Pass	3 3	12 months	+	+	-	Published	Periodicity in fynbos in the non-seasonal rainfall belt. Jl.S.Afr.Bot 46: 343-354.	1980
S M Pierce & R M Cowling	1. Dune Fynbos & Thicket 2. Dune Grassland 3. Grassy Fynbos 4. Restioid Grassland 5. Kromme River Thicket 6. South Coast Renosterveld 7. Shale Grassland	Humansdorp/ Cape St Francis	1. 26 2. 28 3. 17 4. 30 5. 18 6. 35 7. 25	± 15 months	+	+	+	Written up / Published / Published / Submitted	CSP Final Reports; Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. S. Afr. J. Bot. 3(1):1-16; Seasonal growth of the over-storey and understorey in shrublands in the S E Cape; Utilization and conservation of South Coast Renosterveld. S. Afr. J. Bot. 3(1):17-21	1982 1984 1984 1984

Author	Vegetation type	Site	Number	Duration				Processing	Publication	Year
E J Moll & J E M Sommerville	1. Mountain Fynbos	Bains Kloof	± 12	12 months	+	+	+	Oral paper	SAAB Congress.	1981
J E M Sommerville	1. Mountain Fynbos	1. Sir Lowry's Pass & Swartboschkloof	1. 58 & 48	14 months	+	-	-	Oral paper semi-processed	SAAB Congress. Intended: Publication.	1980
	2. West Coast Lowland Fynbos	2. Darling	2. 14						Presented by W R Siegfried - Trophic structure of some communities of fynbos birds. Proc. Symp. Coastal Lowlands of W. Cape Univ. Western Cape, pp 31-51.	1984
	3. Dune Thicket	3. Melkboschstrand & Geelbek (Langebaan)	3. 45 & 43							1982
	4. West Coast Renosterveld	4. Tygerberg	4. 36							
	West Coast Lowland	Pella	11	22 months	+	+	+	Semi-processed	Intended: FRD Final Report M Sc thesis	1983
A le Roux & G Orshan	Namaqualand Broken Veld	Springbok-Hester Malan Nature	± 60	12 months	+	-	-	Semi-processed	Intended: semi-processed in Bontebok SAAB paper publication	Dec 1982 Jan 1983 May 1983
X Kyriacou & G Orshan	1. Mountain Fynbos	1. Kirstenbosch	58	18 months	+	-	-	Semi-processed	Intended: semi-processed in Bontebok Publication in Proceedings of symposium at Montpellier	1983/1984
	2. West Coast Renosterveld	2. Signal Hill	20							
	3. West Coast Lowland Fynbos	3. Pella	30							
P Perry & G Orshan	Karoo Broken Veld	Worcester	37	12 months	+	-	+	Raw	?	?
M C Olivier	Karoo Broken Veld	Worcester	community	12 months	+	-	-	Semi-processed	D Sc thesis - A plant survey of the Worcester Veld Reserve. Univ. Stell.	1966
B J Durand	Mountain Fynbos	Kogelberg	6 plus	12 months	+	-	-	Processed	M Sc thesis - A study of the short term responses of fynbos to fire in the Kogelberg State Forest, S A. UCT.	1981

Table 1. cont.

Author	Vegetation type	Location	No. species	Duration				Status		Intended / Publication	Date
B Low	Dune Fynbos and Thicket	Cape Flats Nature Reserve	23 - 30	24 months	+	-	+	Raw/semi-processed		Intended: Publication	1983?
J Glyphis	Dune Thicket	Rondeberg (near Darling)	community	6 months	+	-	-	Semi-processed		CSP Final Report	1980
C Boucher	West Coast Lowland Fynbos	Pella	± 186 spp	12 months	+	-	-	Not available		? BRI Report SANPR No	? 1984 / 1984
A Lamb	Mountain Fynbos	Swartboschkloof	3 / 43	12 months / +24 months	+	+	+	Raw semi-processed		Intended: Forestry Centre Report	? 1984
G Slabbert	Mountain Fynbos	Jakkalsrivier	4	12 months	+	+	-	Raw		Intended: Forestry Centre Report	? 1984
		Swartboschkloof	3	13 months	+	+	+	Raw/semi-processed			1984
D Le Maitre	Mountain Fynbos	Cedarberg	2		+	+	+	Semi-processed		Intended: ? Forestry Centre Report	? 1984
			15		+	-				Publication	
Dept Environment Affairs	Mountain Fynbos	Jakkalsrivier	?	?	+	?	?	Raw/semi-processed		?	?
S Milton & E J Moll	Dune Fynbos Mountain Fynbos	Rondevlei Table Mountain	4	14 months	+	+	+	Published		Phenology of Australian acacias in the S W Cape, South Africa and its implications for management. Bot. J.Linn.Soc. 84: 295-327	1982

Author	Vegetation	Location	No.	Duration				Status	Reference	Year
J E M Sommerville	West Coast Lowland Fynbos / Mountain Fynbos	Swartklip / Silvermine	4 / 8	12 months +	−	−		Published	A comparison of the seasonal growth of indigenous and non-indigenous species in the South-Western Cape. J.S.Afr.Bot 47: 797-805.	1981
E J Moll & A A Gubb	Mountain Fynbos	Cape of Good Hope Nature Reserve	5	<12mths +	+	+		Published	Aspects of the ecology of _Staavia dodii_ in the South Western Cape of South Africa. H Synge (ed). The Biological Aspects of Rare Plant Conservation. John Wiley, pp 331-342.	1981
J Winter	Fynbos	Kirstenbosch	many	? +	+	+		Raw	Intended: Horticultural pamphlet. Data available for processing by Fynbos Biome Project/Forestry, subject to collaboration and co-authorship.	?
F Coley	West Coast Lowland Fynbos	Pella	3	<12 mths −	−	+		Processed	Intended: Publication − Litter production and decomposition	?
W D Stock & O A M Lewis	West Coast Lowland Fynbos	Pella	1	<12 mths −	−	−		Processed	Intended: Publication − Nitrogen cycling	?
S M Jongens-Roberts	West Coast Lowland Fynbos	Pella	1	<12 mths + (roots & biomass)	+	−		Processed	Intended: Publication Seasonal changes in biomass and phosphorus in _Leucospermum parile._	?

Key to types of study undertaken:

+ positive

− negative

EVALUATION OF METHODS

In this section, evaluation of phenological methods is restricted to above-ground manifestations of periodicity, focusing on methods used by workers in the fynbos biome, and in southern Africa. Problems encountered in the field and those associated with data analysis are emphasized. The complexity and problems involved in phenology are not apparent until observations are made. There are no standard methods for assessing phenophases by "simple" observation. Often the problems are insoluble and much depends on the discretion and resourcefulness of the observer. In some problematic cases, the only rule is that of consistency. A standard method of data analysis is desirable, however, the variable nature of phenological data necessitates a more flexible approach.

Selection of a phenological method depends on the aims and scope of the study. Two types of phenology are: extensive, non-detailed studies to determine general trends usually within communities or vegetation types; and intensive, detailed studies usually of one or a few species. The former are useful, for example, in drawing up management programmes for fire regimes, determining seasonal availability of resources for birds, animals, insects or for testing hypotheses on the functioning of systems. More detailed studies are needed for eco-physiological as well as plant-animal (grazer, pollinator, disperser) relations.

GENERAL OBSERVATIONS

Phenophases are most often studied by simple observation in the field. Depending on the aim of the study, observations are made at specified time intervals (eg daily, fortnightly, monthly). Species are selected either subjectively or objectively (random numbers on a grid or transect). Phenology of a single species requires observations on replicate plant individuals (eg Moll and Gubb's (1981) work on Staavia dodii). In contrast, phenology of a community might include observations on common species (eg Pierce and Cowling (1984a)) or account for the cover/abundance of the component species (eg Sommerville's community phenology in Siegfried (1982)). The aim of this latter study was to determine plant-bird

interactions. Observations were therefore made on plants occurring, at set intervals along transects, with the result that, each month, there were many, replicate observations made on common species, and perhaps only one on rare species. Data from Pierce and Cowling's (1984a) study, and Sommerville's work (see Siegfried 1982) describing community phenology in terms of community growth, flowering and fruiting, are expressed in two ways in this synthesis: (see Figures 1-5).

1. Number of individuals at a particular phenophase as a percentage of total number of individuals observed;

2. Number of species at a particular phenophase as a percentage of total number of species observed;
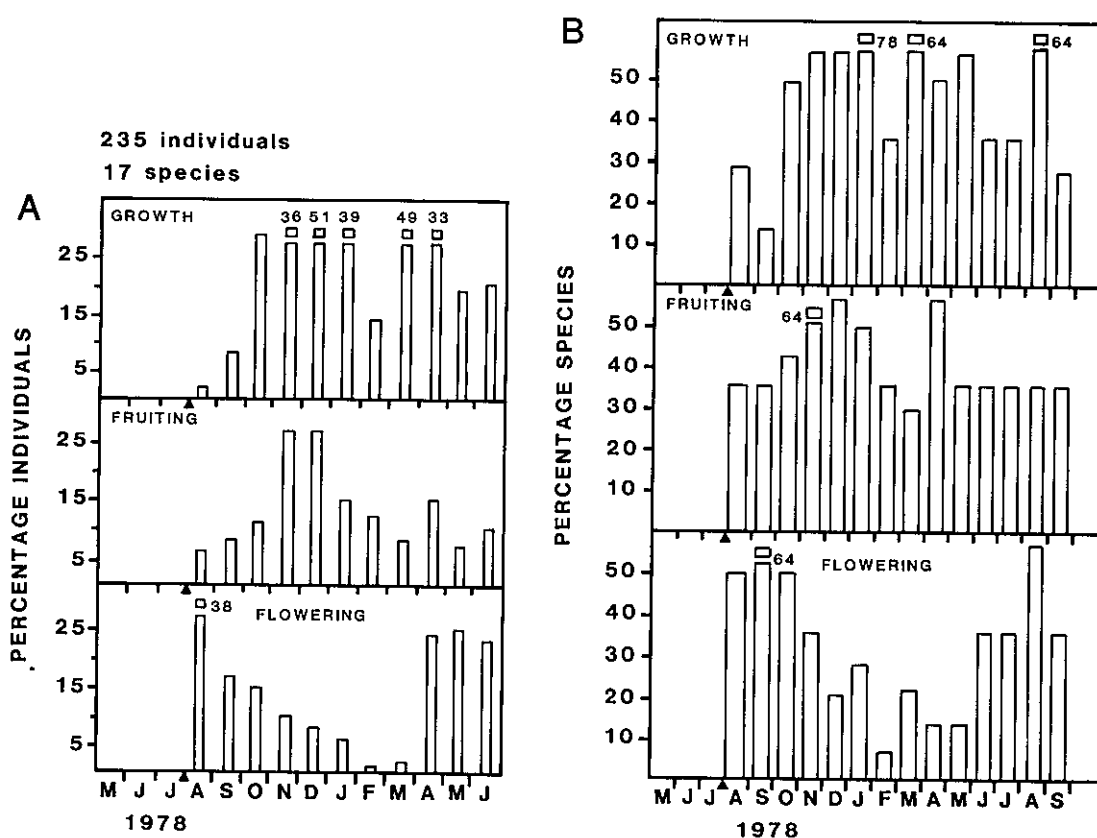
Figure 1.   Phenophases of (A) individuals and (B) species in West Coast Lowland Fynbos at Barhuis.   (Sommerville data in Siegfried 1982). ▲ indicates start of sampling.

The apparent simplicity of phenophase observation is misleading. Phenophases such as shoot elongation, leaf initiation, bud development, flowering, seed development, maturation and set are often extremely difficult to interpret in the field. Kummerow (1983) noted the difficulty in distinguishing between active and resting buds, and even between vegetative and flowering buds. Kharin (1976) asserted that an intimate knowledge of a species' phenophases is a prerequisite to a periodicity study. This prerequisite may seem absurd, but a prior field knowledge is essential if accurate assessments are to be made. Therefore, phenology

GEELBEK
410 individuals
44 species

MELKBOSCH
735 individuals
52 species

1978

1978
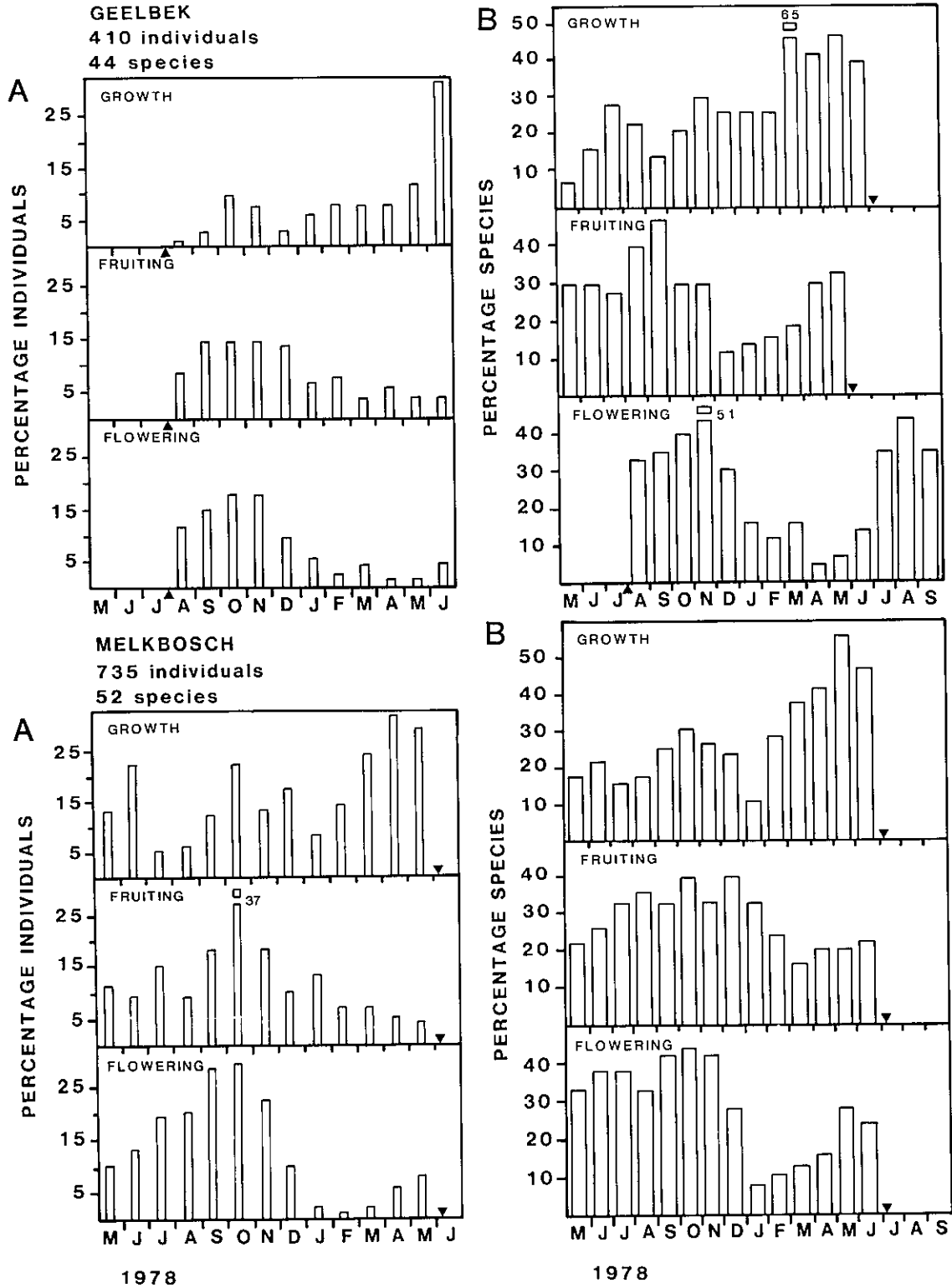
Figure 2. Phenophases of (A) individuals and B (species) in Dune Thicket
at Geelbek and Melkbosch. (Sommerville's data in Siegfried
1982).

▲ indicates start and ▼ indicates end of sampling.
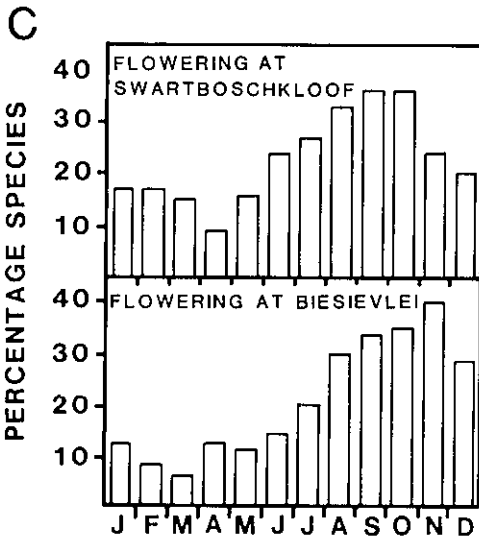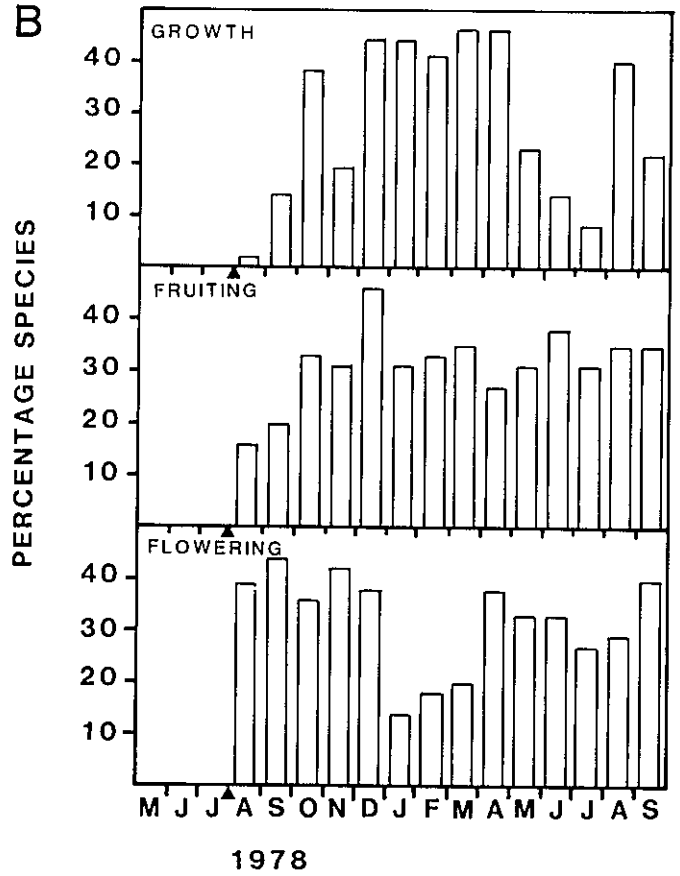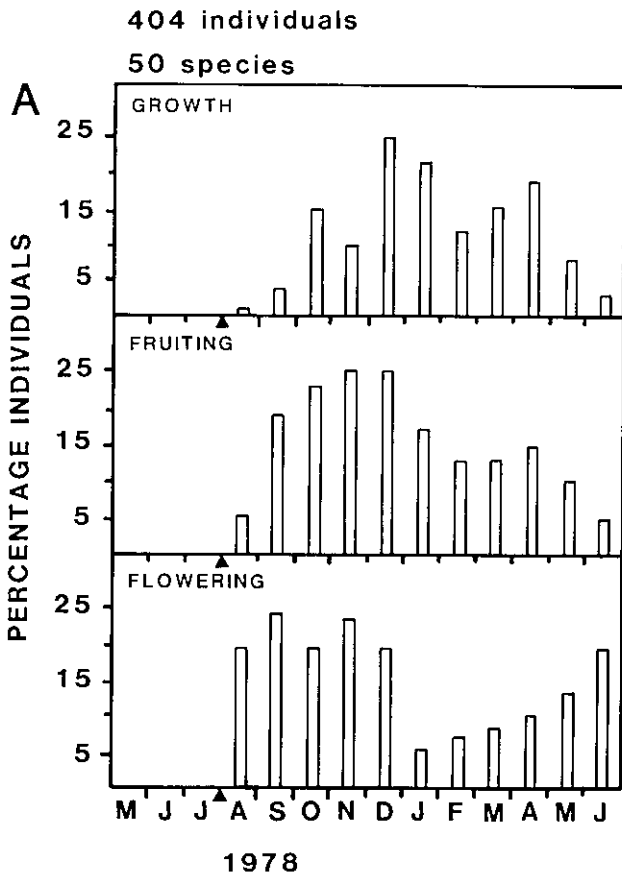
Figure 3. Phosphorus of (A) individuals and (B) species of Mountain Fynbos at Swartboschkloof (Sommerville's data in Siegfried 1982) and (C) species flowering at Swartboschkloof (Van der Merwe 1966) and Biesievlei (Rycroft 1950).
▲ indicates start of sampling.
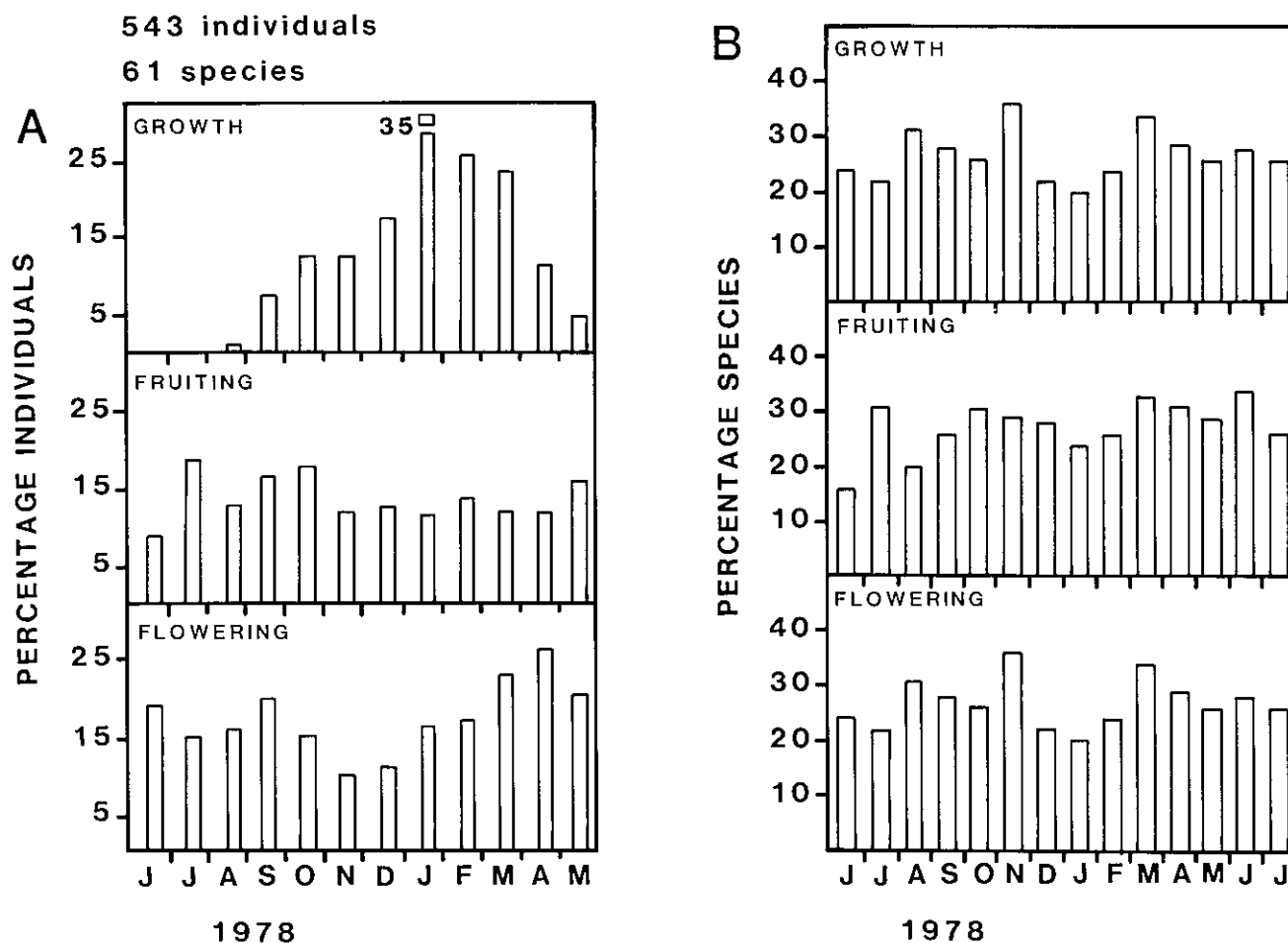
Figure 4. Phenophases of (A) and (B) species in Mountain Fynbos on Sir Lowry's Pass (Sommerville's data in Siegfried 1982).

should continue for at least two years. This applies particularly in the temperate fynbos biome where a single marked growth flush is often lacking (eg the sporadic growth of Erica species, Table 2). Two-year studies have the further advantage of showing between-year variation. An example of the extent of this variation is shown in Low's (personal communication 1982) study on vegetation of the Cape Flats (Figure 6).

General observations may be depicted purely qualitatively as phenodiagrams of coded blocks for each phenophase in each month (eg Van Rooyen et al 1979). More information is provided by semi-quantitative bar graphs of percentage individuals or species showing a particular phenophase at each month of the year (eg Figures 2-7). Shading of bar graphs can indicate the abundance or paucity of a particular variable (eg buds, fruits) (eg Guy et al 1979). Bars may also be divided into proportions of percentage occurrence of phenophases such as new leaf, mature leaf, leaf discolouration, bare etc (eg Tinley 1977).

275 individuals
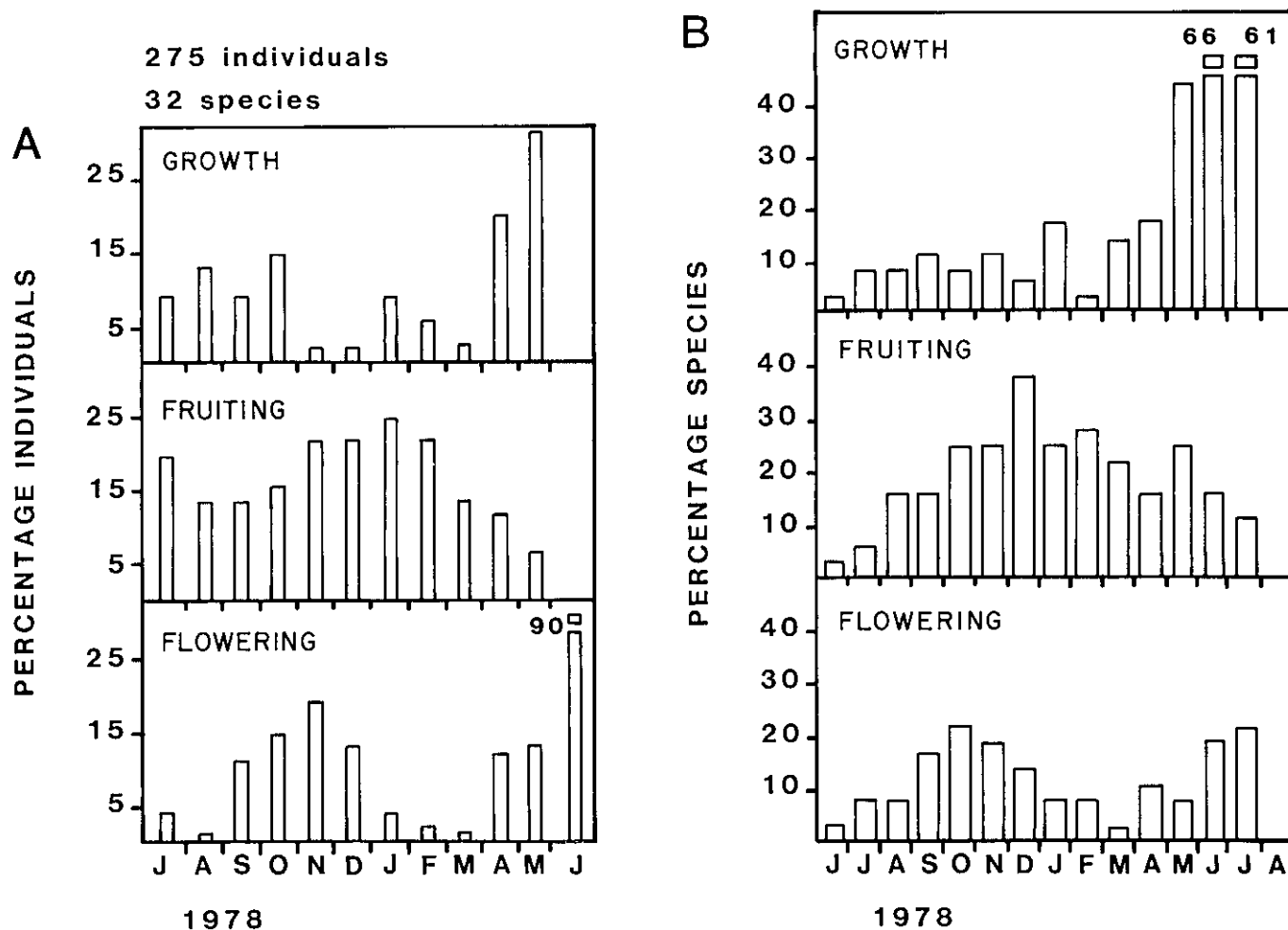
32 species

Figure 5.   Phenophases of (A) individuals and (B) species in West Coast Renosterveld at De Grendel (Sommerville's data in Siegfried 1982).

Bar graphs are prone to different interpretations. For example, community growth of Dune Thicket is interpreted as peaking "during autumn-winter" by Siegfried (1982) whereas I would interpret community growth as variable, peaking in June, October, March and April at Melkbosch, and having an isolated June peak at Geelbek (Figure 2). The interpretation of winter and spring blooming times of the community at Swartboschkloof (Figure 3A)(Siegfried 1982) could equally be called spring/summer phenophases, while the summer and autumn flowering at Sir Lowry's Pass (Figure 4A) could be called spring and autumn peaks.

Pierce and Cowling (1984a) compared the qualitative assessment of growth (bar graphs of percentage individuals growing) with detailed measures of growth of two selected species. They showed that the latter method had distinct advantages over the former in revealing subtleties in growth behaviour.

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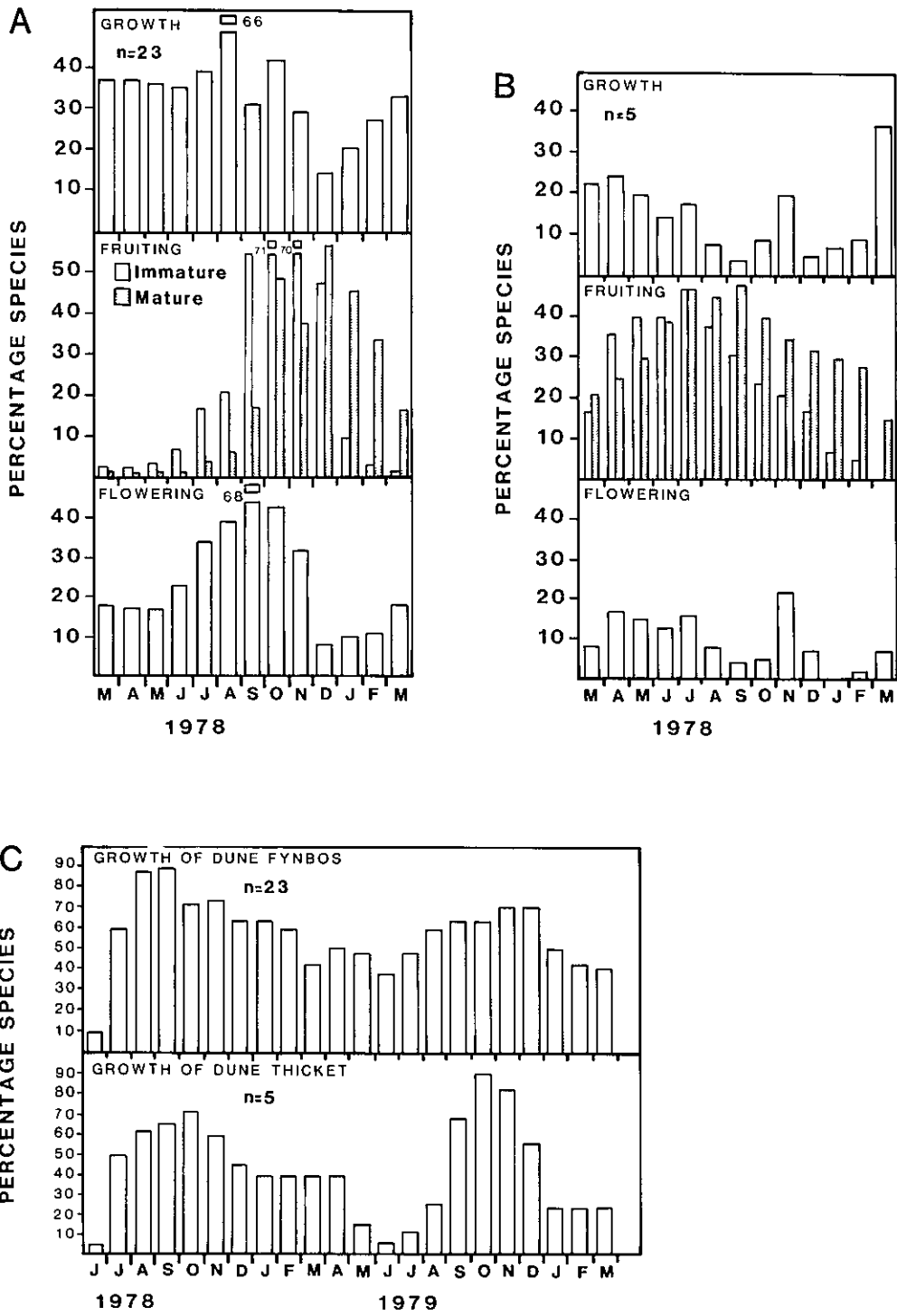
Figure 6.   Phenophases of species in Dune Fynbos (A), Dune Thicket (B) and
Dune Fynbos and Thicket (C) in the Cape Flats Nature Reserve
(A B Lows's data, unpublished).

DETAILED OBSERVATIONS

The phenophases of leaf expansion, leaf loss and shoot elongation are suited to detailed quantitative measures. Leaf expansion may be determined by destructive sampling (clipping) of randomly selected shoots and recording of leaf number and size. Growth may then be depicted as histograms showing number of juvenile leaves (eg smaller than x mm^2) for each month (Specht and Brouwer 1975). However, this method is unreliable for species which lack a distinct growth flush (Milton and Moll 1982), a common phenomenon in the fynbos biome.

The measurement of growth of grasses is difficult when the growth habit of the species obviates simple measurement of shoot elongation and leaf growth (cf Pierce 1983). The number of tillers per tagged shoot may be monitored (eg for the growth habit of <u>Themeda triandra</u>), or the number of leaves per tagged shoot (eg <u>Stenotaphrum secundatum</u>) (Pierce and Cowling 1984a).

Growth, expressed as leaf area per shoot, of different species is difficult to compare due to: differing number of shoots per shrub volume; new foliage not being limited to the current year's growth; and variation in the duration of growth flushes (Kummerow 1982). Therefore Kummerow uses leaf area produced by one shoot during the week of most rapid extension. However, the initial problem remains of which shoot to choose for detailed observation (see below).

Litter traps are a useful means of measuring leaf loss, though the growth forms of some species precludes their use (eg certain restioids, most grasses). Leaf loss (and leaf growth) of certain species can be monitored by numbering leaves with water-insoluble felt-tipped pens. A standard litter trap cannot be recommended as specifications will vary with growth forms and study requirements.

Shoot elongation is the simplest parameter to measure but is also problematic. Accuracy of length measurement can be a problem in the field eg difficulty in distinguishing shoot tip due to apical buds. Selection of which shoots to tag and measure is difficult (growing or dormant shoot?) even by objective means (random points on a grid held over a plant?). There is often a sampling bias towards accessible shoots. Tags tend to damage plant shoots and are sometimes attractive to and damaged by birds. A further problem in choice arises when a tagged shoot ceases growth and develops actively growing laterals.

Ideally, the number of shoots measured should be sufficient to yield a low variance. However, growth is extremely variable. I carried out a pilot study on shoot increment data from one species and it showed that for a variance of less than 10 percent at the 95 percent confidence level, some 200 - 2 000 shoots per species should be measured. This sampling intensity is beyond the scope of most studies.

Table 2. Phenograms of species of the Proteaceae, Ericaceae and
Restionaceae

SPECIES	SITE	AUTHOR	FLOWERING J F M A M J J A S O N D	GROWTH J F M A M J J A S O N D
PROTEACEAE				
Protea repens	Swartberg	Bond (1980a)		
P. repens	Swartboschkloof	Slabbert		
P. repens	Swartboschkloof	Sommerville		
P. neriifolia	Swartboschkloof	Le Maitre		
P. neriifolia	Sir Lowry's Pass	Sommerville	none	
P. nitida	Swartboschkloof	Le Maitre		
P. nitida	Swartboschkloof	Sommerville		
P. nitida	S W Cape	Haynes 1976 in Kruger 1981		
P. burchelli	Pella	Sommerville	juvenile	
P. cynaroides	Sir Lowry's Pass	Sommerville		
Leucadendron pubescens	Pella	Sommerville		
L. lanigerum	Pella	Sommerville		
L. uliginosum	Outeniqua mtns	Bond (1980a)		♀
L. xanthoconus	Jakkalsrivier	Slabbert		
L. laureolum	Kogelberg	Durand (1981)		
L. salignum	Barhuis	Sommerville		
L. salignum	Sir Lowry's Pass	Sommerville		
L. salignum	Humansdorp	Pierce & Cowling (1984a)		
L. adscendens	Sir Lowry's Pass	Sommerville		
L. spissifolium	Swartboschkloof	Sommerville		
Leucospermum tottum	Jonkershoek (cultivated)	Le Maitre		
L. tomentosum	Barhuis	Sommerville		
L. cuneiforme	Jonkershoek (cultivated)	Le Maitre		
L. cuneiforme	Humansdorp	Pierce & Cowling (1984a)		
L. parile	Pella	Sommerville		
L. conocarpodendron	Sir Lowry's Pass	Sommerville		
L. oleifolium	Sir Lowry's Pass	Sommerville		
ERICACEAE				
Erica pulchella	Kogelberg	Durand(1981)		
E. seriphiifolia	Outeniqua mtns	Bond (1980a)		
E. diaphana	Humansdorp	Pierce & Cowling (1984a)		
E. pectinifolia	Humansdorp	Pierce & Cowling (1984a)		
E. articularis	Sir Lowry's Pass	Sommerville		?
E. corifolia	Sir Lowry's Pass	Sommerville		?
E. imbricata	Sir Lowry's Pass	Sommerville		
E. massonii	Sir Lowry's Pass	Sommerville		
E. plunkenetti	Sir Lowry's Pass	Sommerville		
E. plunkenetti	Swartboschkloof	Sommerville		?
E. pulchella	Sir Lowry's Pass	Sommerville		
E. sphaerocephala	Swartboschkloof	Sommerville		?
E. hispidula	Swartboschkloof	Sommerville		
Philippia leeana	Sir Lowry's Pass	Sommerville		?
Scyphogyne muscosa	Sir Lowry's Pass	Sommerville		
Sympieza articulata	Kogelberg	Durand (1981)		

Table 2 continued

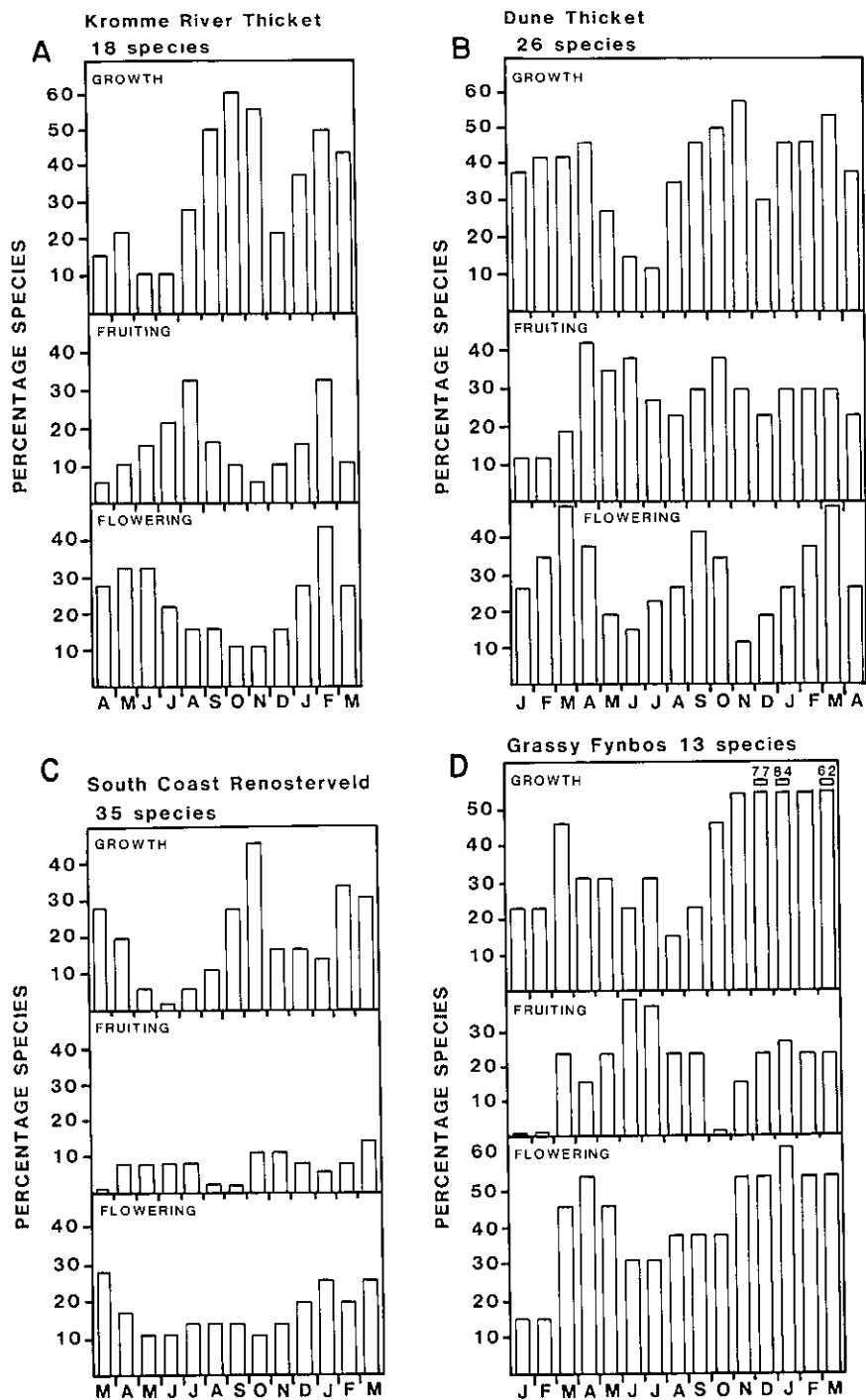| SPECIES	SITE	AUTHOR	FLOWERING J F M A M J J A S O N D	GROWTH J F M A M J J A S O N D
RESTIONACEAE				
Restio egregius	Sir Lowry's Pass	Sommerville		
Restio egregius	Kogelberg	Durand (1981)		
R. gaudichaudianus	Worcester	Olivier (1966)		
R. monanthus	Pella	Sommerville		
R. fruticosus	Swartberg	Bond (1980a)		
R. leptoclados	Cape St Francis	Pierce & Cowling (1984a)		
R. triticeus	Humansdorp	Pierce & Cowling (1984a)		
R. triticeus	Sir Lowry's Pass	Sommerville		
R. sieberi	Humansdorp	Pierce & Cowling (1984a)		
R. cuspidatus	Sir Lowry's Pass	Sommerville		
R. filiformis	Sir Lowry's Pass	Sommerville		
Wildenowia argenteum	Sir Lowry's Pass	Sommerville		
W. arescens	Barhuis	Sommerville		
W. teres	Cape Flats	Low		
Leptocarpus membrynaceus	Sir Lowry's Pass	Sommerville		
Thamnochortus gracilis	Sir Lowry's Pass	Sommerville		
T. dichotomus	Swartboschkloof	Sommerville		
T. dichotomus	Sir Lowry's Pass	Sommerville		
T. punctatus	Pella	Sommerville		
T. erectus	Cape Flats	Low		
T. fruticosus	Humansdorp	Pierce & Cowling (1984a)		
T. spicigerus	Melkboschstrand	Sommerville		
T. spicigerus	Cape Flats	Low		
Elegia parviflora	Outeniqua	Bond (1980a)		
E. juncea	Jakkalsrivier	Slabbert	?	
E. vaginulata	Humansdorp	Pierce & Cowling (1984a)		
E. parieflora	Sir Lowry's Pass	Sommerville		
E. racemosa	Sir Lowry's Pass	Sommerville		
E. racemosa	Swartboschkloof	Sommerville		
Hypodiscus aristatus	Sir Lowry's Pass	Sommerville		
H. aristatus	Swartboschkloof	Sommerville		
Staberoha cernua	Sir Lowry's Pass	Sommerville		
S. cernua	Swartboschkloof	Sommerville		

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Figure 7.   Phenophases of species in Kromme River Thicket (A), Dune Thicket (B), South Coast Renosterveld (C), and Grassy Fynbos (D) at Cape St Francis (Pierce and Cowling 1984a).

QUANTITATIVE DATA ANALYSIS

There are numerous methods of analysis of phenological data but each method has limitations. Sommerville (personal communication 1982) found that percentage of previous sampling length gives a misrepresentation of the growth phenophase. For example, if growth rate is constant over a number of sampling periods, relativization has the effect of diminishing growth values over sampling times because each equal increment is expressed as a percentage of a larger previous length. This problem may be obviated theoretically by expressing each new increment as a percentage of the original length (instead of previous sampling length). Also, growth may be expressed as a percentage of the total of all summed growth for the year. However, both these forms of analysis are dependent on the same tagged shoot being measured throughout the study period. This is uncommon and death or damage to tagged shoots necessitates the continual tagging of new shoots during the study period (Sommerville, personal communication 1982; personal observation).

Absolute values may be used instead of increments. However, there is great variation in length amongst shoots on any one shrub. Therefore comparisons amongst shoots are difficult due to differences in scale. These scale differences in absolute growth values result in extremely wide ranges in values when average growth is calculated.

Increments may be averaged and represented as mean histograms with vertical lines representing standard errors (eg Milton and Moll 1982). However, many growth data are not normally distributed and their ranges are widely spread. Therefore they are poorly represented by means and standard errors. A clear, non-ambiguous method of depicting such data are five-number summaries (Underhill 1981) which are recommended for representing growth trends (Pierce and Cowling 1984a; Sommerville, personal communication 1982). The chief disadvantage in this form of analysis is that it is not amenable to statistical tests of significance. However, ranking non-parametric statistical tests (Mann-Whitney) can be used on the same data, with the five-number summaries providing graphical depiction.

F J Kruger of the Department of Environment Affairs strongly proposes that growth curves should be fitted to the experimental data by computer. An advantage of this kind of analysis would be the ready inclusion of growth data into models of the autecology of species and eventually the synecology of vegetation. Unfortunately no processed data are available for discussion here. Problems to be overcome include: adequate expression of the variation i) within the plant; ii) within the plant species population; and determining the shapes of growth curves of best fit peculiar to each species (eg Dieckman 1978; Pierce 1983). Species growth rate comparisons may aid in studies on "why plants grow where they do" (Parsons 1968). However, this falls beyond the scope of this synthesis. Comparisons of growth rates of species of the different growth forms characteristic of the fynbos biome are dubious (eg the validity of comparing growth rates of proteoids and restioids).

A need exists for a computerised phenological data base for the fynbos biome. At present, no standardized method of data collection exists largely as a result of the differences in growth habit of fynbos species and also the enormous variation in the nature of growth. The data base

should include those phenophases recommended for inclusion in the proposed Mediterranean Ecosystems Data Source Book (1981), which has the aim of collating world-wide data to ascertain effects of perturbations (eg fire, grazing, fertilizers) on mediterranean-type ecosystems by computer modelling. On a smaller scale, a phenological data base may be of similar use in the fynbos biome. The monthly data for each species should include activity of: buds, flowers, fruits, leaves, shoot increment, leaf fall, stem girth and stem starch, root girth and root starch, rootlets and litter decomposition. The MTE Data Source Book suggests that data on buds, flowers and fruits should be based on small quadrat samples over stratified grids, but the practicalities of this approach are not explained. Leaf production and loss and shoot increment should be based on tagged shoots. Leaf loss should be measured by means of litter traps.

The ideals of the Source Book are commendable but its data requirements are obviously beyond the scope of available data on the fynbos biome (see Table 1). However, once the Department of Environment Affairs have resolved the problems of processing and storing phenological data by computer, and current studies are completed (see Table 1), all these data should be collated and stored in a computer data base. The extensive phenology by Kirstenbosch horticulturalists (Table 1) and also the wealth of information contained in certain taxonomic revisions (eg Williams 1972; Rourke 1980) and other works (Adamson and Salter 1950; Vogts 1982) are valuable sources of information which should also be included.

PHENOLOGICAL THEORY

INTRODUCTION

Many periodicity studies are purely descriptive and comprise lists of phenophases with little interpretation. But for phenological data to provide meaningful explanations of biological phenomena, they must be placed in a theoretical framework. There exist a number of theories, some general and some specific to mediterranean-type ecosystems. Determinants of phenophases include environmental factors (eg temperature, soil moisture, radiation accumulation) biological factors (pollinators, dispersers, predators) and competition for resources, and disperser and pollinator vectors (staggering of phenophases). The problems of treating these determinants as different subjects are manifold as exogenous and endogenous cues are often inextricably bound. Nevertheless, in this section, for ease of discussion, I have made artificial separations of environmental determinants (climate, nutrients, 'old climate theory') and competition for resources (by temporal partitioning).

ENVIRONMENTAL DETERMINANTS OF PHENOPHASES

The cues which cause organisms to change from one activity to another may be direct, such as the changing resource level itself (eg soil moisture) or indirect such as photoperiod or temperatures which "forewarn" the organism of an impending change in resource level, or a possibly unfavourable thermal period (Mooney and Kummerow 1980). For example, the leaf fall of a southern Californian summer-deciduous shrub is correlated with drought coinciding with long days (Nilsen and Muller 1980). This combination of cues prevents leaf loss during an unseasonable drought.

There is much speculation over the cues for phenophases which range from environmental to endogenous rhythms, though the latter are ultimately related to environment. Over a period of 40 years, studies in chaparral have claimed various factors as the specific controllers of phenophases, but no one study can explain the findings of another study. Variables offered as controlling factors are soil moisture depletion, minimum air

temperature, favourable soil temperature, low soil and air temperature, diurnal temperature, insolation, relative humidity and lowered starch reserves. Hanes (1965) concluded that though resumption and cessation of growth are influenced by some of these variables, the two species he studied had internal physiological rhythms which operated more or less independently of physical factors. Inherent rhythms may explain the behaviour of some fynbos species eg certain Protea species, indigenous to the south western Cape show the same flowering times (within the four to six week period of expected variation) when cultivated in the summer rainfall region of the Transvaal (J Winter, personal communication 1982) and even in the northern Hemisphere (Vogts 1982).

In recent studies on chaparral shrubs, regression analyses on percentage population which initiated flowering or shoot elongation as a function of warming hours (sum of hours greater than or equal to 15°C from the day preceding autumn after which soil moisture was greater than $0,1g$ cm^{-3}) accounted for more than 90 percent of total variation in phenophases of almost all species (Kummerow et al 1981). Difficulties encountered in determining controlling factors include cognizance of the species specific time lag between budding and flowering.

There are numerous factors which influence phenophases, such as: critical soil moisture and cumulative warming hours (as well as photoperiod) for leaf growth and stem elongation (Kummerow 1983); low soil moisture in combination with short days for leaf fall (Nilsen and Muller 1980); photoperiod and light quality for lateral branching and flowering (Healy et al 1980); heat unit accumulation for flowering in a Leucospermum hybrid (Jacobs and Honeyborne 1979); cumulative photosynthetically active radiation for growth and flowering (Erickson et al 1980).

Unfortunately there are almost no detailed studies of phenophase determinants in the fynbos biome. For the purposes of this synthesis, the following quotation is appropriate:- "many climatic impulses are attuned to each other, rendering it almost impossible, without the help of experimental work, to individualize the factor which triggers one particular phenological event" (Monasterio and Sarmiento 1976). The theories concerning factors governing phenophases in mediterranean-type ecosystems other than the Cape (ie the Mediterranean Basin, Chile, California) are not always directly applicable to the fynbos biome, since a distinct spring peak in growth is observed in these regions (Kummerow 1983). Certainly temperature and soil moisture etc must play a role in initiating certain fynbos phenophases, such as the later flowering of high altitude populations of Proteaceae species (Rourke 1980; Vogts 1982).

THE OVERSTOREY/UNDERSTOREY HYPOTHESIS

The major theory forwarded to explain the "anomalous" summer growth patterns peculiar to important species in the mediterranean-type ecosystems of South Africa and Australia (Kummerow 1983) is the overstorey/understorey theory of Specht et al (1983).

The basis of this hypothesis, hereafter referred to as Specht's model, is that soil nutrient status is the major determinant of vegetation structure in the mediterranean-type ecosystems of South Africa and southern Australia. The premise is that an interplay of water availability and

nutrient cycling is the major determinant of growth phenophases in these regions.

Three major soil suites are recognized: moderately leached, strongly leached and calcium-rich/high pH. Hereafter, the first two mentioned soil suites will be referred to as nutrient-poor and base-rich respectively, for reasons given by Pierce and Cowling (1984b), and complying with terminology used in an earlier work (Specht and Moll 1983). Specht's model describes shrublands occurring on base-rich soils as comprising an overstorey of evergreen sclerophyllous tall shrubs (Euclea, Olea, Pterocelastrus, Rhus, Sideroxylon) above an understorey of seasonal grasses and herbs. Heathlands on nutrient-poor soils comprise an overstorey of evergreen sclerophyllous shrubs (Proteaceae); a mid-storey of evergreen sclerophyllous sub-shrubs (Ericaceae) and a ground stratum of evergreen hemicryptophytes.

Briefly, the model's predictions are that on base-rich soils, understorey seasonal grasses and herbs sprout from seed/storage organs in autumn, and complete their life cycle by the end of spring. Overstorey species exhibit shoot growth in autumn and/or spring and leaf fall follows after shoot growth. In contrast, overstorey species on nutrient-poor soils grow in late spring/summer "in order to" utilize nutrients in the soil released from litterfall dropped two years previously, and simultaneously recycle internally nutrients from abscissing leaves. Thus shoot growth is synchronous with leaf fall. Understorey species grow in autumn and/or spring and leaf loss is in summer. The model predicts that shoot phenophases of vegetation on calcium-rich/high pH soils should be similar to those patterns shown by vegetation on nutrient-poor soils.

An analysis of overstorey and understorey growth and leaf fall patterns of vegetation on the three different soil suites (sensu Specht and Moll 1983) but with similar mesoclimate, provided a test for the phenological predictions of Specht's model in the south eastern Cape (Pierce and Cowling 1984b). They found evidence which both supported and refuted the hypothesis. A major criticism was Specht's assumption that nutrients and water alone are of prime importance and other factors such as radiation, temperature, light, and biotic factors are ignored. The model's ecophysiological bias also ignores historical factors such as interpretation of summer growth of Banksia species in Australia as the heritage of having evolved in an earlier tropical climate (Specht and Rayson 1957; see 'old climate' hypothesis).

Other criticisms levelled are that: the predictions are vague; emphasis is placed on long-lived overstorey and short-lived understorey species - both relative, ill-defined terms which do not account for the longevity of restioids; the description of base-rich community structure is inaccurate and renosterveld is dismissed as a "disclimax community"; classification of shrubs into overstorey/understorey components without clear definitions or characteristics is difficult. An example of this lack of clarity is the prediction for growth of overstorey species on base-rich soils "in spring, or sometimes in autumn, while leaf fall follows shoot growth as soil drought increases". However, if growth does occur in autumn, leaf fall following growth would occur in winter when there is, in fact, no soil drought.

A serious flaw in Specht's model is shown by the fact that selected species which grew on all three different soil types - base-rich clay,

nutrient-poor and calcium-rich substrates - showed similar phenophases (Pierce and Cowling 1984a).

Consistencies in their findings with Specht's hypothesis allowed Pierce and Cowling (1984b) to conclude that the model has much merit, but the inconsistencies suggest a re-evaluation. The model is the first real attempt to explain aspects of the functioning of mediterranean-type ecosystems in the Cape and southern Australia. Investigation of the nutrient, water and growth seasonality of fynbos biome species would provide a more rigorous test of the model, but the co-ordinated research by Sommerville, Stock, Brown, Coley and Jongens-Roberts is incomplete at this stage. Preliminary findings suggest that the data (on soil and plant phosphorus, soil and plant nitrogen, litter production and decomposition, soil and plant water potential and root depth) thus far do not provide conclusive evidence for nutrient availability as the cause of the summer growth observed in some species.

However, there is some correlation between root depth and summer growth season - only species with extensive root systems showed summer growth (Sommerville 1983). Other authors (Mooney and Kummerow 1980; Pierce and Cowling 1984a) have also suggested root architecture to explain growth in drier seasons. Data on rooting systems in fynbos are poor. Apart from the rooting spread (4-5 m diameter) and depth (6,06 m) of Elytropappus rhinocerotis recorded by Scott and Van Breda (1937), the work reported by Sommerville (1983) is the first local confirmation for this correlation. Investigation of roots of proteoids and ericoids should reveal if the former have access to deep underground water sources enabling them to show consistent summer growth patterns, while ericoid root patterns might reveal the more opportunistic mechanism of exploiting chance soil moisture, and similarly for restioids. Occasional summer rains are not uncommon in the Cape but are absent in the other mediterranean-type ecosystems, and exploitation of these rains may help to explain the summer growth of some Cape species (Cody and Mooney 1978).

THE 'OLD CLIMATE' HYPOTHESIS

Some mention must be made of historical factors which have been offered as explanations for apparently "anomalous" phenophases, particularly those peculiar to certain species in South African and southern Australian mediterranean ecosystems.

The annual growth rhythms of many important southern Australian plants (eg Banksia species) are said to be "out of phase with the present climate" as maximal shoot growth is in the hot, driest summer months (Specht and Rayson 1957; Groves 1965). This apparently anomalous behaviour is explained as the heritage of a tropically evolved flora, which now, by geographic circumstance, and changing world climates, occupies a mediterranean climate region. Johnson and Briggs (1963, 1975) discuss the implications of the theory concerning the evolution and radiation of the Proteaceae in Australia. Holland (1968) suggests that the timing difference between the winter/early spring growth of field layer species and the summer/autumn growth of the tall shrubs and mallee eucalypts may be ascribed to differences in longevity: field layer species live for six months to five years; eucalypts last up to 500 years. Longer-lived species had fewer opportunities for "better adapted individuals" to be selected for

(Holland 1968). This 'old climate' hypothesis is difficult to test. However, seedling growth experiments under controlled environments have shown that not all <u>Banksia</u> species have high temperature requirements for growth. <u>Banksia</u> <u>ornata</u>, for example, is not necessarily a "relict" species out of phase with the present annual climatic cycle (Groves 1978).

The 'old climate' hypothesis has been used to explain the summer growth of certain important fynbos elements, especially the Proteaceae (Table 2). Bond (1980a) 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 sub-tropical origin for the family Proteaceae (Johnson and Briggs 1975) and the genus <u>Leucospermum</u> (Rourke 1972). Even the genus <u>Leucadendron</u>, for which Williams (1972) has argued a mediterranean-type origin, exhibits summer growth. However, there are contradictions; <u>Protea</u> <u>repens</u> begins growth at relatively low mean daily air temperatures of between twelve to fourteen degrees centigrade (Le Maitre, personal communication 1982).

The inflexibility of the growth phenophase in the Proteaceae to changing climates, even over evolutionary time, must be great, or the "summer water stress" which biologists anthropomorphically ascribe to these plants is not operative, and is obviously not a major limiting factor to growth. I suggest that deep roots reaching underground water supplies might explain this summer growth. Fernandez and Caldwell (1975) found the main factor which allowed a semi-desert shrub to transpire and fix carbon during the driest time of the year was continued root growth down to greater depths.

The proteoid element is one of the few components of the fynbos to grow mainly in summer (see section on Intraspecific phenology; see also Bond 1980a). These data give lie to the myth that fynbos grows in summer and is not at harmony with the present climate. This myth appears to have sprung from Levyns' (1964) rather vague statements that "several members of the (Cape) flora...in their growth rhythm...show that they are strangely ill-adapted to the present dry summers". This at variance with her earlier statement that the majority of Cape plants flower in spring and early summer; shed their seeds in the dry months, germinate later with the onset of the winter rains, and are thus in harmony with their surrounds (Levyns 1956). However, Levyns continues by describing the contrasting growth patterns of <u>Metalasia</u> <u>muricata</u> and <u>Elytropappus</u> <u>rhinocerotis</u>, with active summer growth and delayed seed germination; both aspects suggested to her that these plants have had their origin in a summer rainfall region. I suspect that it is these species to which Levyns was referring in her later discourse (Levyns 1964). Some authors have gone so far as to use this out-of-phase summer growth as evidence of the Cape mediterranean climate being a recent phenomenon (Axelrod and Raven 1978; Westman 1978). The cool season growth of the sub-tropical thicket species, <u>Pterocelastrus</u> <u>tricuspidatus</u> and <u>Sideroxylon</u> <u>inerme</u> (Pierce and Cowling 1984a), exemplifies the danger of interpreting climate of origin from growth rhythms.

TEMPORAL PARTITIONING OF RESOURCES AMONGST SPECIES

The theory of temporal partitioning of resources amongst species has been suggested as a mechanism for reducing competition and allowing the coexistence of species, thus explaining diversity in systems. The basic assumption is that plants compete for resources (eg water, nutrients etc)

and pollinators and dispersers. Staggering in time of phenophases should reduce the intensity of competition and allow greater species packing within a community. An example is the explanation of the co-existence of two Eucalyptus species by differences in seasonality in growth and uptake of essential elements, as well as in morphology and insect attack (Rogers and Westman 1979). Thus phenophases are assumed to represent external manifestations of resource use. However, phenophases such as growth do not necessarily reflect coincident resource uptake and use. Growth may result from re-allocation of metabolites stored prior to shoot growth (Groves 1965).

Temporal partitioning of resources is a simple concept in itself, but actually involves highly complex interactions amongst eco-physiological requirements and reproductive mechanisms. One approach for dealing with this complexity is to isolate niche axes along which species differ in their pattern of use of a critical resource (Whittaker 1969; Rogers and Westman 1979). However, this approach assumes that niche axes "are relatively independent of one another" (Rogers and Westman 1979). Other research suggests that eco-physiology and reproductive mechanisms are inextricably bound. Competition for pollinators should result in a uniform distribution of flowering of species over time, but this uniformity will be limited by the physiological constraints imposed on the plants by the seasonality of the habitat (Stiles 1979) and of the pollinators. A lack of base line information on physiological requirements can cause considerable difficulty in determining the staggering of flowering times as a mechanism for reducing competition for pollinators. Also, an evolutionary commitment to dispersal by one disperser over another carries with it a phenological "commitment" to the timing of fruit ripening or seed release (Thompson 1981). Plant-disperser relations may have co-evolved in such a way that the quality of fruit varies seasonally according to the nutritional requirements of the disperser (Herrera 1982), a commitment which may place further constraints on the physiology of the plant.

Seeds of seventy-eight plant genera (some 20 percent of species) of Cape fynbos are myrmecochorous (ant dispersed) (Bond and Slingsby 1983). Myrmecochory implies an "evolutionary commitment" to produce seeds when ants are active in the warmer periods. However, further "commitments" are imposed on flowering times by nectarivorous bird pollinators. There is further selective pressure to time seed release so that seed predation (eg by rodents) is minimised. Phenophase interpretation is further complicated by the fact that spread in flowering phenophases is also apparent in species pollinated and dispersed by wind (Pemadosa and Lovell 1974; Grubb 1977).

In opposition to the theory that temporal partitioning of resources reduces competition, are the assertions of Fagerström and Agren (1980). They suggest that increased temporal segregation of flowering times of co-occurring species can lead either to increased seed production (through decreased competition for pollination) or to decreased competition amongst seedlings - but the latter is negatively related to increased seed production which in turn leads to competition. They suggest instead that phenological spread is the result of competition pressure at seedling establishment. In fynbos, however, which is a fire-prone vegetation, germination is often synchronous after a fire (Kruger 1983) and this theory is not entirely applicable here.

COMPARISONS OF FYNBOS BIOME PHENOLOGY

In synthesizing the available phenological data of the fynbos biome, I have classified the information under different headings to facilitate comparison and discussion. Phenological data are compared intraspecifically, interspecifically and within communities - both at the specific and individual level, and amongst growth forms. Furthermore, comparisons are made amongst individuals and also amongst communities to determine the existence of patterns of phenological behaviour across the extent of the fynbos biome from the western winter rainfall region to the eastern non-seasonal rainfall region. Where possible, phenological theory discussed in the previous section, is applied to the data.

INTRAPLANT PHENOLOGY

In general, all parts of plants do not grow simultaneously, possibly because of the limitation of building materials and because priority is given at any time to the most critical growth phase (Mooney 1983). In certain South African and Australian Proteaceae more than one quarter of the aboveground biomass consists of reproductive organs (Specht et al 1958; Kruger 1979). However, Mooney et al (1977) have reported that low proportions of total annual terminal shoot production are allocated to flowering (eg 5,3 percent for eight chaparral species and 2,3 percent for seven matorral species). The time separation between phenophases (such as growth and flowering) may be the result of synchronization with other selective factors eg flowering patterns may have co-evolved with pollination and dispersal vectors (cf Herrera 1982) or there may be a strong selective force to avoid excessive seed predation, while growth may occur earlier to coincide with favourable environmental conditions. The lateral and proteoid roots of Leucospermum parile grow during the moist winter/spring months, which is out of phase with aboveground summer growth (Sommerville, personal communication 1982).

In many fynbos species growing on nutrient-poor soils, growth and flowering are often synchronous or at least overlapping eg Paranomus bracteolaris, Protea neriifolia, P. nitida, Leucadendron cuneiforme, Leucospermum parile

(Le Maitre, personal communication 1982) which indicates that "building materials" may not be limiting. A possible explanation is the constraint of the growth form of the plant itself. For example, the inflorescences of restioids are borne terminally and growth must precede anthesis (Table 2).

A special case exists in species which initiate buds in one season and develop them in the next: eg Protea repens shows shoot growth in September-November/December and then develops a terminal flower bud in December; the following spring, shoot growth occurs and the flower bud begins expansion in November/December so that only in the autumn of the third year does the terminal bud fully develop as a flower (Le Maitre, personal communication 1982). Le Maitre has observed that in the genus Protea growth occurs prior to flowering in the same year. However, he reports that for Leucospermum, flowering is on the previous year's shoots and immediately precedes the following season's growth. It is difficult to determine in the field if flowering (which is axillary) marks the termination of the growth of that shoot, or if it precedes the next season's growth. Without anatomical studies and pruning experiments the sequence is not readily understood.

INTERSPECIFIC PHENOLOGY

The importance of phenology in the understanding of species diversity is evident in the flowering rhythms which determine gene flow and the population dynamics of plants. Interbreeding is only possible if flowering is synchronous (Griffin 1980); eg many sympatric species at least within subgenera, of the genus Eucalyptus are interfertile and asynchrony in flowering is a major isolating factor responsible for the maintenance of the integrity of these species (Pryor 1959).

Flowering rhythms, unique to each of three groups of populations of Virgilia (V. oroboides subsp. oroboides; V. oroboides subsp. ferruginea and V. divaricata), have been suggested as isolating mechanisms preventing crossing between the groups (Van Wyk 1982). The genus is distributed across the extent of the fynbos biome from Cape Town to Port Elizabeth and there is variation across this east-west gradient in terms of time, duration and colour of flowers and also floral morphology, including pollen and nectar guides. Van Wyk (1982) suggested that speciation may have been the result of different pollinators operating at different times of the year.

Niche complementarity in seasonal rhythms of growth and mineral uptake, amongst other factors, has been used to explain the lack of hybrids amongst co-existing eucalypts in Australia (Rogers and Westman 1979). If the converse holds, then the evidence of prolific hybridization (eg in Euphorbia; White et al 1941) in the eastern part of the Cape Region should indicate a lack of partitioning of resources, temporal or otherwise. Analysis of the phenology of succulents in the south-eastern Cape (Pierce and Cowling 1984a) and the eastern Cape (Palmer 1982) showed a coincidence of spring and autumn growth (as well as some summer growth for two species) which suggests a lack of temporal partitioning of resources. Cowling (1984a) has proposed that during the last glacial, valley conditions were drier and experienced more erratic rainfall than at present, and considerable diurnal temperature fluctuations due to temperature inversions (Deacon 1983). These are the conditions which favour CAM succulents

(Osmond et al 1976). Since then, moderation of the climate would have favoured invasion of the valleys by non-succulent, subtropical thicket species. This invasion would have been facilitated by the apparently low competition of the succulents as shown by their synchronous growth patterns, as opposed to the more flexible, "opportunistic" growth patterns of thicket species.

The subtropical elements which are dominant members of the Kaffrarian Thicket (sensu Cowling 1984a) can show temporal variation in flowering and particularly fruiting amongst individuals of the same species (Pierce and Cowling 1984a; Liversidge 1972), a phenomenon well documented for certain tropical tree species (Frankie et al 1974; Grubb 1977). According to the theory discussed earlier, that synchronous flowering is necessary for interbreeding, there should be reduced interbreeding, less gene flow and the maintenance of species integrity amongst thicket species. However, these species are predominantly bird dispersed (Liversidge 1972; Siegfried 1982) which should result in extensive gene flow since fruits are dispersed over relatively large areas. This wide dispersal may help to explain the extensive distribution of certain subtropical thicket species occurring in coastal thickets as far west as the Cape Peninsula (Sideroxylon inerme, Pterocelastrus tricuspidatus). The theory of asynchronous flowering may explain in part the existence in coastal dune thickets of a few local endemics which are very closely allied to more widespread elements eg Rapanea gilliana (from R. melanophloeos), Olea exasperata (from O. europeae), Euclea racemosa subsp racemosa (from E. racemosa subsp schimperii), Maytenus lucida (from M. procumbens) (see Cowling 1984b).

Although individuals of thicket species can flower and fruit asynchronously, when total species are considered there are spring and autumn peaks (Liversidge 1972; Pierce and Cowling 1984a; K L Tinley personal communication). There is much variability in the quantity of fruit produced but there are unfortunately no data on seasonality in quality of fruits. In mediterranean Spain, species ripening at different times of the year differ in their nutritional properties to match the seasonally changing demands of their bird dispersers, which suggests a closely co-evolved system between the birds and the evergreen sclerophyllous vegetation (Herrera 1982).

Frost (1976) found low calorific values of dune thicket fruits at Swartklip (False Bay) dispersed by opportunistic rather than specialized feeding birds. She suggested displaced fruiting periods as a means of reducing competition for dispersers (eg Pterocelastrus tricuspidatus). In contrast, Euclea racemosa produced fruit in a short compact period (April-June) and Frost reasoned that a broad range of bird dispersers could be catered for by sheer abundance of fruit, an alternate strategy to ensure adequate dispersal (cf McKey 1975). These patterns of Swartklip thicket differed from those in the south-eastern Cape where E. racemosa produced unripe fruit over a long period culminating in a short period of mature fruit (October-December). Also P. tricuspidatus produced unripe fruit in midsummer only (Pierce and Cowling 1984a). Of nine species common to both Cape St Francis (Pierce and Cowling 1984a) and Cape Recife (Liversidge 1972), seven showed marked reproductive phenophase differences between the two sites.

A comparison of thicket species in the south-western and south-eastern Cape (Rhus crenata, Olea exasperata, Euclea racemosa, Putterlickia pyracantha, Pterocelastrus tricuspidatus - in Table 3) similarly reveals great

Table 3.   Phenograms of species occurring at more than one site in the fynbos biome.

SPECIES	SITE	AUTHOR	FLOWERING / GROWTH (J F M A M J J A S O N D)
Rhus incisa	Cedarberg	Le Maitre	
Rhus incisa	Humansdorp	Pierce & Cowling (1984a)	
R. rosmarinifolia	Swartboschkloof	Le Maitre	
R. rosmarinifolia	Pella	Sommerville	
Diosma hirsuta	Swartboschkloof	Le Maitre	
D. hirsuta	Cedarberg	Le Maitre	
Themeda triandra	Swartboschkloof	Lamb	
T. triandra	Humansdorp	Pierce & Cowling (1984a)	
T. triandra	Fish River valley	Palmer (1982)	
Elytropappus rhinocerotis	Signal Hill	Kyriacou	
E. rhinocerotis	De Grendel	Sommerville	yr 2 / yr 1
E. rhinocerotis	Humansdorp	Pierce & Cowling (1984a)	
Metalasia muricata	Swartboschkloof	Sommerville	
M. muricata	Humansdorp	Pierce & Cowling (1984a)	
M. muricata	Melkboschstrand	Sommerville	
M. muricata	Cape Flats	Low	
Rhus crenata	Cape Flats	Low	
R. crenata	Humansdorp	Pierce & Cowling (1984a)	
Olea exasperata	Cape Flats	Low	none
O. exasperata	Melkboschstrand	Sommerville	
O. exasperata	Humansdorp	Pierce & Cowling (1984a)	
Euclea racemosa	Cape Flats	Low	
E. racemosa	Melkboschstrand	Sommerville	
E. racemosa	Cape St Francis	Pierce & Cowling (1984a)	
Helichrysum teretifolium	De Grendel	Sommerville	
H. teretifolium	Humansdorp	Pierce & Cowling (1984a)	
Anthospermum aethiopicum	Geelbek	Sommerville	
A. aethiopicum	Cape St Francis	Pierce & Cowling (1984a)	
Putterlickia pyracantha	Geelbek	Sommerville	
P. pyracantha	Cape St Francis	Pierce & Cowling (1984a)	
Pterocelastrus tricuspidatus	Melkboschstrand	Sommerville	
P. tricuspidatus	Geelbek	Sommerville	
P. tricuspidatus	Cape St Francis	Pierce & Cowling (1984a)	
Elegia racemosa	Sir Lowry's Pass	Sommerville	
E. racemosa	Swartboschkloof	Sommerville	

variation in timing of reproductive activity. Irregular timing of reproduction has been noted in tropical trees and has been explained as a strategy for decreasing competition for pollination (Stiles 1977) and possible escape from seed predation (Janzen 1969, 1970). Asynchrony in fruit production and dispersal within a species may represent a way to limit competition (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 1983c). 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 (Pierce and Cowling 1984a).

Further west, in the south-western Cape, dune thickets are often dominated by a few species of thicket shrubs (viz Sideroxylon inerme, Euclea racemosa, Pterocelastrus tricuspidatus, Olea exasperata). Pierce and Cowling (1984a) argue that this is an historical consequence of the westwards depauperization in the temperate Cape Region of subtropical thicket. The sub-tropical thicket species would have migrated into the Cape Region from the north-east possibly during the warmer, wetter conditions after ±12 000 bp.

Only those species with wide phenological tolerances would have been able to penetrate the non-seasonal rainfall area, as insufficient summer rainfall would severely restrict strictly summer growth season species, and winter deciduous thicket species (eg some Acacia species); none of which penetrate west of Grahamstown. Pierce and Cowling (1984a) suggest that flexibility in the growth phenophase of deep-rooted, "high cost – low profit" sclerophyll (Orians and Solbrig 1977) shrubs would pre-adapt them for penetration of the non-seasonal rainfall area of the eastern Cape. Ability to exploit bimodal and winter rains has led to the successful penetration into the south and south western Cape of two subtropical thicket species in particular. Sideroxylon inerme gains importance further westwards from the south-eastern Cape area as a dune thicket element as far as the Cape Peninsula and Pterocelastrus tricuspidatus penetrates the very dry summer area of the Cape West coast as far as Elands Bay, where summer rain is less than 20 percent total rainfall.

The "generalist strategy" of opportunistic growth whenever the combination of soil moisture, temperature and photoperiod is suitable (Morrow and Mooney 1974) is characteristic not only of thicket species, but also of very prominent components of the fynbos, eg the Ericaceae (Table 2). Bond (1980a) has suggested that the ability of ericoid and narrow sclerophyll shrubs for variable growth through the year would seem sufficiently flexible to allow more subtle seasonal partitioning of resources and hence a large number of species within the life form. Pierce and Cowling (1984a) found small-leaved shrubs growing primarily in summer (Erica pectinifolia, Metalasia muricata, Elytropappus rhinocerotis). However, a comparison of the latter two species growing in different environments (Table 3) shows a greater flexibility in growth rhythms than they reported for the south-eastern Cape. Bond's (1980a) theory would help to explain the high speciation in certain taxa with small-leaves eg Erica, Agathosma, Phylica, Aspalathus, Cliffortia. Agathosma apiculata and A. stenopetala coexist and have similar flowers but asynchronous flowering and fruiting, possibly as a result of selection for lowered competition for pollinators and dispersers (ants) (Pierce and Cowling 1984a).

Analysis of flowering in Erica in the three regions of winter, non-seasonal, and summer rainfall, shows that there is a number of species flowering through the year (Figure 8). (This is in marked contrast to the peaked distribution for the proteoids.) This temporal staggering of flowering within the genus may also help to explain the high speciation in this taxon. Many Erica species are bird-pollinated, though only two bird species appear responsible (Rebelo 1982). The staggering in flowering may help to reduce competition for pollinator vectors.
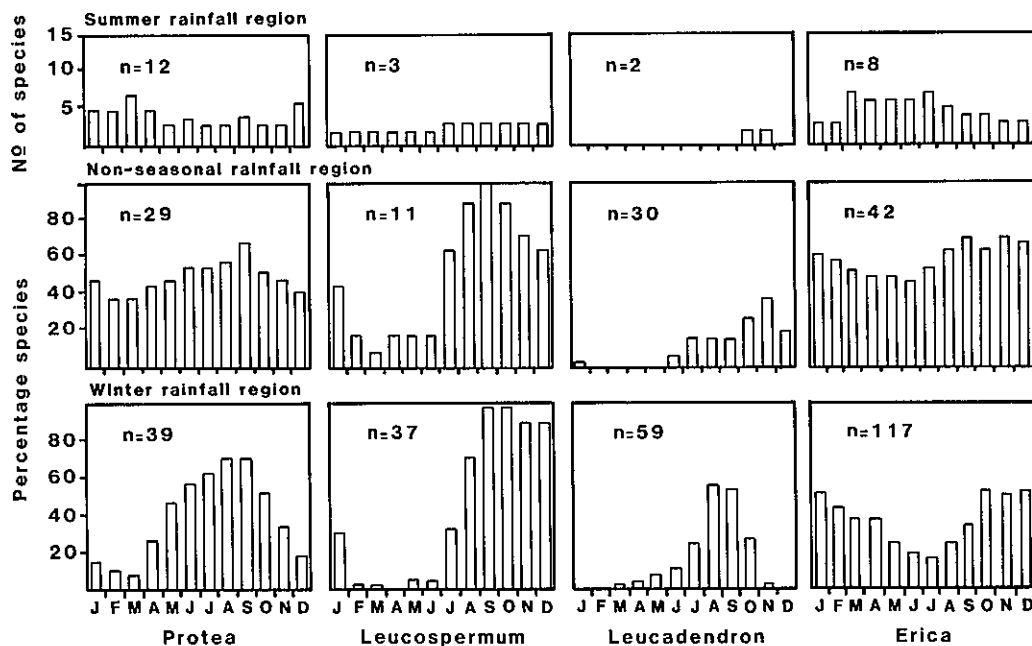
Figure 8. Seasonal flowering of species in winter, non-seasonal and summer rainfall regions (see Introduction for definitions). Data from Baker and Oliver 1967 (Erica); Williams 1972 (Leucadendron); Rourke 1972 (Leucospermum); Rourke 1980 (Protea).
n = total number of species. Totals for summer rainfall area considered too low to be expressed as percentages.

Analysis of the available data on proteoids shows a marked trend for species of Protea, Leucadendron and Leucospermum to grow in summer/early autumn (Table 2). Species which deviate from this pattern are those which have the widest distributions within their respective genera eg Leucadendron salignum (Williams 1972) and Leucospermum cuneiforme (Rourke 1972).

Bond (1980a) argues from the limited data available at that stage, that growth in summer is apparent in few fynbos species and the difficulties of summer growth during the period of maximal water stress is reflected in the low number of species in any community occupying the proteoid niche. Subsequent data and the validity of the statement concerning low numbers of summer growers in fynbos are discussed later. However, the low number of proteoid species in any community is explored here from the reproductive point of view.

Proteoids are conspicuous components of fynbos communities and certain aspects of their reproductive biology are fairly well known (see Vogts 1982). I attempted to show temporal partitioning of flowering within congeneric species in communities of known composition, including those studied by Boucher (1978) in the Cape Hangklip region of the south western Cape, by Bond (1981) in the Swartberg mountains of the southern Cape, and by Cowling (1984a) in the Elandsberg mountains of the south-eastern Cape (Table 4). Flowering rhythms given in Table 4 are from Rourke (1972, 1980), Williams (1972) and Vogts (1982). As the patterns are generalized for each species throughout its distribution, comparisons are not strictly valid. However, within the limitations of the data, certain trends are apparent. In each community described, congeneric species show a certain amount of staggering of blooming times (Table 4). Where there is some overlap, the pollinators are different eg in the Protea-Tetraria Dry Short Fynbos community, Protea scabra is putatively rodent-pollinated while P. repens is bird-pollinated, though both species' flowering times overlap in July-October. Obviously reproduction is just one aspect where temporal partitioning of resources can operate. Growth may also be staggered, and nutrient and water use staggered as a result of different root architecture.

Almost all species of Leucospermum in the winter-rainfall region, flower in spring/summer (Figure 8, Table 2), and all species are bird pollinated and the seeds are ant dispersed (Slingsby and Bond 1982). Seed ripens and is released from outer flowers while the innermost are still immature (Vogts 1982). Thus flowering and seed release are synchronous. Evolution of myrmecochory must have resulted from selection for flowering and seed ripening to suit the period of ant activity. This constraint on reproductive patterns would lead to competition for dispersers (ants) and result in few Leucospermum species coexisting at any one site. This prediction is borne out by the community data in Table 4, where only one species of this genus is recorded in each community.

Congeneric species flowering synchronously and requiring the same pollinator should, according to the theory of temporal partitioning of resources, result in increased competition for the pollination vector. Instead of the pressure of competition promoting segregation of flowering times of coexisting species, it may select for a different pollination vector. For example, in the genus Leucadendron there is a trend from more primitive entomophily towards more recently evolved anemophily (Williams 1972).

Leucadendron shows even more marked flowering peaks - late winter/spring in the winter rainfall region and spring in the non-seasonal rainfall region (Figure 8). Compared to Leucospermum this genus has a greater variety of pollination vectors (Williams 1972) and at least three dispersal mechanisms (Slingsby and Bond 1982). These differences might explain the greater richness of Leucadendron in any community (see Table 4).

All Mimetes species are ant dispersed (Slingsby and Bond 1982) but flowering time is variable although most species flower in late winter/early spring (data from Vogts 1982). Seed is retained for 2-6 months (Vogts 1982) and the period of retention is probably dependent on flowering time since seed release in all species should coincide with the summer season when ants are active. Competition for dispersers should result in few or no congeneric species in a given habitat. The latter is true of the Ruitersbosch community described in Table 4.

Table 4. Phenograms of proteoid species occurring in different communities.

COMMUNITY	SPECIES	Pollina-tion	Disper-sal	Mode of Regen-eration	FLOWERING J F M A M J J A S O N D
Protea-Tetraria Dry Short Fynbos at Cape Hangklip (Boucher 1978)	Protea nitida	bird	wind	sprout	
	P. scabra	rodent	wind	sprout	
	P. repens	bird	wind	seed	
	P. lepidocarpodendron	bird	wind	?	
	P. cynaroides	bird	wind	sprout	
	P. longifolia	bird	wind	seed	
	Leucadendron salignum	insect	wind	sprout	
	L. xanthoconus	insect	wind	seed	
	Leucospermum oleifolium	bird	ant	? seed	
Tetraria-Thamnochortus S E Cape Mountain Fynbos (Cowling 1984a)	Protea mundii	bird	wind	seed	
	P. neriifolia	bird	wind	seed	
	P. foliosa	bird	wind	sprout	
	P. eximia	bird	wind	seed	
	Leucadendron eucalyptifolium	insect	wind	seed	
	L. salignum	insect	wind	sprout	
	L. loeriense	insect	wind	seed	
	Leucospermum cuneiforme	bird	ant	sprout	
Protea neriifolia - Leucadendron eucalyptifolium -Erica triceps community at Ruitersbosch (Bond 1981)	P. neriifolia	bird	wind	seed	
	P. cynaroides	bird	wind	sprout	
	P. aurea	bird	wind	seed	
	Leucadendron salignum	insect	wind	sprout	
	L. eucalyptifolium	insect	wind	seed	
	L. uliginosum	insect	wind	seed	
	L. spissifolium	insect	wind	sprout	
	Mimetes cucullatus	ant	?	?	
Protea lorifolia-Simocheilus multiflorus community in the Swartberg mountains (Bond 1981)	Protea repens	bird	wind	seed	
	P. exima	bird	wind	seed	
	P. lorifolia	bird	wind	seed	
	P. punctata	bird	wind	seed	
	Leucadendron rubrum	wind	wind	seed	
	L. salignum	insect	wind	sprout	
	L. barkerae	insect	ant	seed	
	L. spissifolium	insect	wind	sprout	
	Leucospermum cuneiforme	bird	wind	sprout	

COMMUNITY PHENOLOGY

In order to facilitate comparisons within communities, particularly of fynbos, species are often classified into growth forms (eg Bond 1981, Campbell 1984a). Below I present the available data on the phenology of growth forms within the fynbos biome. Growth form definitions are given in Pierce and Cowling (1984a).

I compare two other methods of analysing community phenology - by percentage species and by percentage individuals comprising the communities, and I discuss their respective information yield.

(i) Growth forms

In his synthesis of seasonality in mediterranean-type ecosystems, Kummerow (1983) noted the summer/autumn growth phases of South African and southern Australian species in contrast to the spring peak of the other mediterranean-type ecosystems. Kummerow stated that although similarities amongst mediterranean-type ecosystems have been recognized, it is not possible to predict synchronous growth in all these systems, but rather a staggering in space and time ie comparable growth forms occupying different spaces should show phenological similarities. However, Mooney (1983) states that "if the same resources are utilized by all species, such as water and nutrients of a given rooting zone, there cannot be a time separation in use, since the resource would be depleted by the first user" eg species of the the same growth form co-occurring in Californian warm deserts have different temperature requirements for growth so that each species has a "chance" of depleting soil moisture reserves.

Mooney (1983) further suggests that the greater variety of growth forms in Australian and south African mediterranean communities indicates a greater variability of resource-gathering "strategies" present, possibly due in part to the low nutrient status of the soils. Presumably he is implying that the "stressed" situation of infertile soils decreases competition and therefore allows greater diversity (see Grime 1977). In the chaparral, shallow-rooted herbs start growing at the start of winter rains, followed by deeper-rooted drought-deciduous shrubs, and finally the deep-rooted evergreen shrubs and trees. The phenophases are thus explained in terms of root architecture and water accessibility. However, some situations in the chaparral are not always so neatly explained (cf Hanes 1965).

The theory is that diversity in communities is maintained by staggering of utilization of resources in space (growth forms) and time (phenophases). This approach has been discussed for Mountain Fynbos (Kruger 1981) and mediterranean shrublands in the south-eastern Cape (Pierce and Cowling 1984a). I would expect that because of the morphological constraints placed on a particular growth form, a similar pattern of periodicity would be displayed by members of that growth form. However, because of these constraints, I would also expect the individuals within these groups or guilds to be competing directly for resources (cf Peet 1978). Therefore, within the expected phenophase of a life form, I would predict further, more subtle partitioning of resources.

Geophytes

There has been little additional data collection on this group since Kruger's (1981) synopsis. Maximum flowering is in spring, with leaf initiation in autumn/early winter but there is much variation as regards time of flowering and death of leaves (Kruger 1981; Pierce and Cowling 1984a).

Therophytes

Information on this group is lacking. In the south-eastern Cape almost all therophytes grew and flowered in spring (Pierce and Cowling 1984a). In the Cedarberg and Kogelberg, therophytes have been observed to germinate in autumn and flower in spring (Le Maitre, personal communication 1982).

Cypes

Few data are available on this group. Growth and flowering appear to be variable in the south-eastern Cape (Pierce and Cowling 1984a).

Restioids

A comparison of restioid growth suggests a trend for earlier growth eastwards across the fynbos biome (Pierce and Cowling 1984a). In the south-eastern Cape the restioids studied grew in autumn, winter and spring and an occasional species in summer. In the southern Cape, growth coincided with the wetter periods from early winter to spring (Bond 1980a). In the south-western Cape, species grow in spring/early summer (Kruger 1981), and also throughout summer (Sommerville, personal communication 1982, Table 2). Bond (1980a) stated that a combination of high soil moisture, low temperatures and low light conditions are a prerequisite for restioid growth. However, subsequent data on summer growth within the group refutes this. Although the relatively shallow roots of restioids could exploit any chance summer rain, low temperature and low light conditions are highly unlikely in the midsummer of the south-western Cape. Bond (1980a) further predicted that the winter drought of the summer rainfall region would limit the eastward distribution of restioids and reduce their competitive advantage. Presumably he is referring to competition with grasses. Obviously a winter drought is not entirely a limiting factor as some restioids show such distinctive summer growth (Sommerville, personal communication 1982, Table 2). Pierce and Cowling (1984a) suggest that the trend for growth occurring earlier in the east than in the west of the fynbos biome could be related to climatic differences other than rainfall, such as a lower (by 2,2°C) mean winter temperature in the west and 1-2 hours more bright sunshine per day in the east (Fuggle 1981). Furthermore, the distribution of restioids, limited largely to the fynbos biome may be the result of unsuccessful competition with grasses on the more fertile soils of the eastern Cape relative to the soils of the south and south-western Cape reported by Campbell (1983) and Cowling (1983d). Distribution could also be limited by the absence or rarity of ants essential for seed dispersal.

Grasses

Unfortunately, apart from the work of Pierce and Cowling (1984a), almost no other phenology on grasses has been carried out in the fynbos biome. The only comparable data are those for Themeda triandra, which shows much variation in growth season (Table 3). The possibility that this variation is due to differences in Themeda ecotypes (Downing and Marshall 1980) is not overruled.

In the south-eastern Cape, C_3 grass species grow in the cooler months from spring to autumn which agrees with the notion of cool season growth of C_3 species (Teeri and Stowe 1976; Boutton et al 1980). This explains the predominance of C_3 grasses over C_4 species in the south-western Cape (Vogel et al 1978) since the region is characterized by a cool growing season which meets the ecophysiological requirements for the C_3 photosynthetic mode (Bouton et al 1980; Ellis et al 1980).

In contrast, C_4 grass species showed either a single, summer growth season, or an additional autumn/winter growth season. The former pattern is associated with species which do not penetrate into the winter rainfall region (eg Diheteropogon filifolius), while species with the latter pattern are able to do so (eg Themeda triandra).

In the south-eastern Cape there are approximately equal numbers of species of C_3 and C_4 grasses (Cowling 1983d) 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 predominate over C_3 species in our study area (Cowling 1983d). Pierce and Cowling (1984a) 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 non-seasonal rainfall throughout the year.

There are no indicators of distinct seasonal temporal partitioning of resources amongst grasses and restioids. The C_4 grasses with more than one growth season, the C_3 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 appear to favour the moderately warm, wetter months. These data refute the hypothesis that greater grass cover in eastern fynbos communities is due to a temporal separation of growth activities amongst grasses and restioids in a given community (Cowling 1983c). There may be temporal partitioning of resources such as biotic factors or germination requirements or even growth requirements, but at more subtle divisions of time.

Succulents

Succulents are not a prominent feature in the fynbos biome vegetation (Day et al 1979; Kruger 1979). They are particularly conspicuous in the Kaffrarian Succulent Thicket (sensu Cowling 1984a) (Valley Bushveld, Spekboomveld) of the eastern end of the biome. Growth is mainly in autumn and spring and in some species, additionally in summer. Flowering in the species studied was in late summer/autumn. Pierce and Cowling (1984a) have speculated about the role of modes of carbon metabolism (C_3, C_4, CAM) in

determining growth patterns of succulents. The relevance of these rhythms and their biogeographical implications are discussed earlier (see section on Interspecific phenology).

Small-leaved sclerophyll shrubs

This growth form includes ericoids and all shrubs with narrow or small leaves less than ±15 x 10mm. No particular pattern of periodicity is characteristic of this group. Growth and flowering seasons are very varied. This may be expected in view of the wide taxonomic and growth habit diversity within the group. Its validity as a category and its relevance to phenology is questionable. Although there is an inferred and measurable adaptive significance of small leaves in terms of heat budget (Gates 1968; Taylor 1975) and tolerance of low nutrient soils (Small 1972), the importance of these properties to phenophases is not readily apparent. I suggest instead that when the information becomes available, rooting structure should be used as a criterion for classification.

There are few data on the phenophases of small-leaved sclerophyll shrubs in the fynbos biome, therefore I have focused mainly on ericoids (sensu Specht 1979), and more specifically, the Ericaceae as most data are available from this group (see Table 2).

Bond (1980a) and Pierce and Cowling (1984a) found that ericoid species showed variable growth throughout the year in the south and south-eastern Cape respectively. A synthesis of Ericaceae shows similar variation in growth (Table 2). Bond interpreted the aseasonality as a "generalist" strategy (cf Morrow and Mooney 1974) of growth occurring whenever soil moisture, temperature and photoperiod is suitable. Bond's explanation of the high speciation amongst small-leaved shrubs as a consequence of this flexible growth pattern is discussed earlier (see section on Interspecific phenology).

However, no neat explanation, such as the "generalist" strategy, exists for species which have growth peaks during the hottest, driest summer months. In contrast, growth rhythms of mediterranean-scrub vegetation are clearly related to soil moisture availability, with most growth in spring (Rundell 1977). Productivity gradually decreases as summer drought progresses (Mooney and Dunn 1970). In the southern Cape, Bond (1980a) 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.

A comparison of the two small-leaved shrubs, Metalasia muricata and Elytropappus rhinocerotis at different sites within the fynbos biome, shows a similar tendency for summer growth, except for the second year's growth at De Grendel in Table 2.

Summer growth by these species is easier to explain by their extensive rooting 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 and Van Breda 1939); the latter are probably effective exploiters of chance summer rains. Levyns (1956) noted that their summer growth 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. Their ability, however, to tap underground water reserves does not limit their growth during summer drought. These species' phenology is difficult to explain in terms of temporal partitioning of resources with the present lack of autecological and eco-physiological information.

Broad-leaved sclerophyll shrubs

Thicket species: Analysis of available information shows much variation in growth and reproductive timing within thicket species (Liversidge 1972; Pierce and Cowling 1984a; Tinley, personal communication 1982), and the implications of this on thicket diversity have been discussed earlier (see section on Interspecific phenology). However, percentages of thicket species show bimodal peaks in reproductive activity in spring and autumn (see Kromme River Thicket, Figure 7). Pierce and Cowling (1984a) ascribe this pattern to the bimodal pattern of rainfall in the south-eastern Cape which was very marked in their year of study. However, other environmental factors may be important in determining this bimodal pattern (see Tinley 1977).

The variation in growth patterns may be explained by the "generalist" strategy (Morrow and Mooney 1974; see Interspecific phenology). Leaf fall is strikingly synchronous over the hottest, driest months of December, January, February. The predominance of midsummer leaf loss is usually associated with low soil moisture (Frankie et al 1974; Kummerow 1983). This phenomenon amongst thicket shrubs, sufficiently deep rooted to reach underground water sources, may be the result of a "self-induced" soil water deficit from enhanced evapotranspiration during the hottest months (cf Groves 1965) by a large thicket canopy.

Proteoid species: Proteoids flower in spring and summer (Figure 8) and show maximal growth in midsummer and autumn (Proteaceae in Table 2). Even the broad-leaved deep-rooted "generalists" of Californian chaparral grow in the moister springtime, and not in midsummer (Morrow and Mooney 1974; Rundel 1982). This "anomalous" growth is discussed earlier as are the implications of the flowering patterns (see Interspecific phenology).

From the data available, it would appear that there is considerable variation within growth forms. I question the validity of these groups as they ignore underground root structure and behaviour. I suggest that a "whole growth form" approach be made before attempting a comparison of phenophases. Water use is largely unknown and detailed studies such as the current work of Sommerville and Schütte on water uptake and available soil moisture are required to understand seasonality.

(ii) Individuals and species

Determination of community seasonality either by analysing species' behaviour or, alternatively, by analysing individuals' behaviour reveals very different patterns (Figures 1-7). Analysis of phenophases of species reveals patterns of theoretical interest allowing speculation about evolutionary and biogeographic patterns. Alternatively, analysis of phenophases of whole communities (ie of all individuals, where some species are represented by many, and some species by only one individual) gives a

more realistic idea of community dynamics and is of more practical benefit.
Kruger (1981) points out for example that the autumn and early winter
flowering of the dominant proteoids, Protea repens and P. neriifolia is of
importance to the fynbos consumers (nectarivorous birds), an effect not
evident from recording numbers of species flowering in a given time. The
approach of recording individual behaviour was used by Sommerville in
studying the phenophases of plant communities in relation to bird
communities (Siegfried 1982).

Data available on community phenology, according to species or individual
behaviour, is limited (Figures 1-7). Analyses should be interpreted with
caution as there is only one sample area for each community. I discuss
here a comparison between species and individual analysis of phenology to
show the differing results. The example is a Lowland Fynbos (sensu Cowling
1984a; Acock's Coastal Fynbos in part) community sampled by Sommerville
(Siegfried 1982) (see Figure 1). Percentage individual data showed most
growth was in December 1978 and March 1979. Expression of the data as
percentage species showed much growth in March 1979, but peak growth in
January 1978. Timing of individuals flowering was maximal in August 1978,
but in terms of species, flowering peaked in September 1978. Fruiting of
individuals showed a more marked seasonality than for the percentage
species.

A comparison of West Coast Dune Thicket (Figure 2) reveals that all three
phenophases of individuals show more distinctive peaks than at the species
level, where activities are more evenly spread through the year.

Most species in Grassy Fynbos in the south-eastern Cape grow in midsummer
(Figure 7). Mountain Fynbos at Swartboschkloof (Figure 3A) and Sir Lowry's
Pass (Figure 4A) in the south-western Cape also shows maximal growth of
individuals in summer. However, in terms of species, all three phenophases
of growth, flowering and fruiting are more evenly spread throughout the
year. This may contribute to the diversity of these types. A comparison
of flowering data of species from two Mountain Fynbos sites at
Swartboschkloof (Van der Merwe 1966; Sommerville in Siegfried 1982) and one
at Biesiesvlei (Rycroft 1950) showed marked differences (Figure 3). The
latest study shows activity in April which is not apparent in the earlier
works. This indicates the need for more than one community sample.

Analysis of community phenology shows that sampling should include more
than one replicate. Generalizations concerning community behaviour should
state explicitly whether species or individual seasonality is being
referred to due to the differences indicated here. No generalizations
concerning growth of fynbos as a whole can be made. This synthesis shows
for example, that although most species of Grassy Fynbos in the south-
eastern Cape grow in summer, Mountain Fynbos species can show growth
throughout the year.

PHENOLOGY ACROSS THE FYNBOS BIOME

Because of the east-west gradient from a non-seasonal to a winter rainfall
regime across the fynbos biome, one would expect a corresponding pattern of
response in the behaviour of plants (Kruger 1979). Therefore I have
synthesised phenological data on individual species, genera and communities
occurring across the extent of the fynbos biome to determine any regional

patterns. Altitudinal patterns should also be determined, however, data are too scarce for comparisons to be made. Flowering records for proteoids growing at both low and high altitudes show a distinct time lag for the higher altitude species (Rourke 1980; Vogts 1982).

A comparison of individual species studied at sites across the biome (Table 3) does not show any pattern related to the climatological gradient. Instead, it appears that characteristic of these species is a flexibility in growth and reproductive phenophases, which enables the plants to exploit suitable conditions whenever they occur. This may explain their wide distributions.

Comparisons of flowering times of selected genera dominant in the fynbos biome show that proteoids tend to have marked peaks in the winter rainfall region, and slightly less marked peaks in the non-seasonal rainfall region (Figure 8). (Proteoids in the summer rainfall region are too few for any pattern to be discerned.) This slight tendency for a uniform spread of flowering through the year in the non-seasonal rainfall region is also apparent for members of the genus Erica (Figure 8). The trend for restioids in the eastern end of the fynbos biome to start growing earlier than species in the west has been related to higher winter temperatures and longer hours of bright sunshine (Pierce and Cowling 1984a; see section on Growth forms - restioids).

A comparison of patterns in similar communities is also limited by paucity of data, and I doubt the validity of single sample comparisons. Nonetheless, I draw attention to certain trends. In West Coast Renosterveld, most species grew in winter of 1979 (Figure 5B), while in South Coast Renosterveld, there are spring and autumn growth peaks (Figure 7). Reproductive patterns of species in this community type also differ across the extent of the biome, with marked seasonality in the south-western Cape and a more even spread through the year in the south-eastern Cape. In the South Coast Dune Thicket most species grow in autumn and late spring, and similarly for fruiting and flowering (Figure 7). This equinoctial bimodality in phenophases is much less marked in the reproductive activity of the West Coast Dune Thicket (Figures 2 and 6).

MANAGEMENT AND THE ROLE OF PHENOLOGY

The ultimate aim of the Fynbos Biome Project is to "provide sound scientific knowledge of the structure and functioning of constituent ecosystems as a basis for........conservation and management" (Kruger 1979). In managed natural systems, particularly if fire-prone, a predictive knowledge of community dynamics provides the soundest basis for long term management (Slatyer 1976). Phenology is an essential component of dynamics since it reveals the timing of events such as growth, flowering, fruiting, predation etc. In this section I examine the role of phenology in understanding vegetation dynamics and discuss the implications for management.

There are two approaches to study the dynamics of a system in order to develop a management programme for either the maintenance of species richness (conservation) or the elimination of undesirable, usually unpalatable species (pasture management). One approach is inductive and based on trial and error experiments and the use of controls. Trollope (1971) used this approach to determine the optimum season of burn for the elimination of the fynbos component in the grassland for the Amatole Mountains in the eastern Cape. The disadvantage of this inductive approach is a lack of generality (Goodall 1977). Predictions cannot be extrapolated confidently to areas outside where the experiments were conducted. The alternative deductive approach is to study the properties of individual species and use these data to predict the effects of different management practices. For example, a study of the phenophases of desirable grasses and undesirable shrubs in the renosterveld of the Humansdorp region in the south eastern Cape has indicated that late summer burns would be most effective in eliminating shrubs and increasing grass cover (Pierce et al 1984, in preparation). These predictions can be tested by observing vegetation subjected to different fire regimes and also by experiments. Similarly Krüsi (1981) successfully used phenology to predict the effect of time of mowing of limestone grassland in Switzerland. He concluded that phenology provided a sensitive meter indicating the possible unfavourable effects of different treatments.

In fire-prone fynbos communities, where the management goal is usually the maintenance of species richness (Kruger 1982a), a knowledge of the phenophases should theoretically be crucial for the effective management of these systems. A number of workers have recognized "safe" and "unsafe" fire seasons on the basis of phenological data. Jordaan (1949) was the first worker in the Cape to draw attention to the importance of phenology in determining species' responses to fire (see also Jordaan 1965, 1972, 1982). He inferred from embryological and phenological work that seed regeneration of Protea repens would occur only if populations were burnt in the period January-June; burns after this period would be particularly harmful to the regeneration of this species. However, P. repens is serotinous in most localities and good regeneration after winter and spring burns has been observed at Jonkershoek (Kruger et al 1977).

Wicht (1948) observed that a late summer or autumn burn caused resprouting species to miss the spring flowering and concluded that autumn was an unsafe period for burning. Both Bond (1980b) and Durand (1981) assert that spring burns are unfavourable for the regeneration of certain species (mostly Proteaceae) but the reasons for this remain unclear. With serotinous species (Bond 1980b, 1984), or species with long lived seeds stored in the soil (eg Staavia dodii in Moll and Gubb 1981), phenological considerations may not be critical in determining the fire regime. Information on other biological parameters such as youth period, fecundity, "safe" reproductive condition etc is necessary in planning a fire regime so that seed stores can be replenished in between burns (Kruger 1982b). Germination cues and variation in the timing of seed and seedling predation are also important. Effects of season of burn are due more to seed predation by rodents than to phenology in some communities (Bond personal communication). Because of the viable seed reserves accumulated in serotinous Proteaceae, Bond (1984) suggested that "phenological hypotheses are inadequate explanat⸱⸱ns for seasonal differences in seedling establishment". However, flowering and fruiting phenophases and time of burn are important for seed regenerating species with very short-lived propagules. Ultimately a knowledge of a species' phenology as well as its life history are important in determining responses to fire (Jordaan 1965; Kruger et al 1977).

The threat of invasive plants in the fynbos biome is well documented (Hall 1979) and is a major problem in management (Kruger 1982a). In southern Australia the success of exotics has been ascribed to their earlier growth compared to indigenous plants (Specht 1975). Sommerville's (1981) findings in the south-western Cape agreed with this theory, with three of five exotics studied growing earlier than three cohabiting indigenous species.

Milton and Moll's (1982) phenology on the Australian acacias in the south western Cape yielded inconclusive management programmes for eradication. Although there were similarities in phenophases between species growing in Australia and in the south-western Cape, no guarantee of success with biological control was offered due to the possibility of new "races" having evolved in the Cape. These authors did not develop any fire regime programme relating to the phenology of the acacias and in fact burning was not recommended at all for reasons of fuel wastage and sand erosion.

CONCLUSIONS AND RECOMMENDATIONS

This synthesis shows that no generalizations may be made about seasonal rhythms of the vegetation in the fynbos biome as a whole. The components of the different vegetation types and even communities show variable patterns both in terms of percentage individuals and percentage species. Statements describing phenological behaviour of vegetation should therefore state explicitly the vegetation type, community and analysis (ie by individuals or species) in question, and not refer vaguely to "fynbos". Certainly the Cape and also southern Australian vegetation differs from that of other mediterranean type ecosystems in having dominant species showing peak growth during the hottest, apparently driest summer/early autumn period. This behaviour has been known for proteoids; however, this synthesis revealed that summer growth is also a characteristic of certain ericoids and even restioids.

Phenophases have been assumed to be manifestations of utilization of resources and hence evidence of the temporal partitioning of resources as an extension of competition theory in explaining diversity in systems. However, this synthesis revealed that phenophases do not necessarily reflect resource use and that because of the complexity and interdependence of environmental as well as biological resources, this theory is practically untestable, and serves simply as a framework for interesting speculation. The same can be said for biogeographic inferences drawn from phenology. Even the old climate theory, offered as an explanation for the"anamolous" summer growth of certain Cape elements is untestable and serves as an easy explanation without involving detailed studies of the plants' functioning. The only testable theory regarding phenology and more particularly, this puzzling phenomenon of summer growth, is Specht's overstorey/understorey model. Pierce and Cowling (1984b) have shown that not all of the phenological predictions of Specht's model hold for south-eastern Cape mediterranean communities. Recent evidence (Jongens-Roberts 1982; Sommerville 1983) indicates that the model's ecophysiological predictions concerning nutrient seasonality are not valid. Also, the model ignores biological interactions. Instead I suggest studies on water relations, and root architecture to understand seasonal plant functioning in conjunction with plant-animal interactions.

The diversity in growth form and within that, growth habit, precludes the presentation of standardized specifications for phenological methods. There is no easy solution to field problems. However, for accurate observations and also to account for some of the between-year variation, I strongly recommend that future phenology be carried out over at least two years to ensure the researcher's familiarity in recognizing phenophases. Also, sampling must include as many replicates of individuals or communities as is practically possible because of the enormous variation inherent in plant behaviour. Selection of a method of data analysis is dependent on the scope and goals of a study; however, it is hoped that the Department of Environment Affairs will develop a computer programme which can deal adequately with the variance in growth data. Once this is operative, all future quantitative phenological data can be stored for easy access in a fynbos biome data bank. Considerable unprocessed phenological data have already been collected at Kirstenbosch Botanic Gardens and priority should be given to the processing of these raw data.

Generalizations about seasonal patterns characteristic of growth forms are not really valid as variation is too great. This is to be expected when one considers the extent of taxonomic diversity encompassed within each of the selected growth form groups. I have questioned the validity of determining the phenology of growth forms as competition theory would suggest a more subtle temporal partitioning of resources even though a similar phenological pattern would be expected in view of similar morphological constraints. Again, an attempt to categorize plants in terms of types of phenological pattern also reveals no general statement. The pattern of summer growth is seen in such diverse forms as proteoids, certain ericoids and restioids. The opportunistic behaviour of growing at different times throughout the year is shown by sub-tropical thicket species, certain ericoids and a very diverse group which appears flexible enough in its phenophases to occur across the east-west climatological gradient of the fynbos biome (Table 3). There is a tendency amongst certain species of the Proteaceae and the genus <u>Erica</u> for a seasonal flowering in the non-seasonal rainfall region, in contrast to a more strongly seasonal trend in flowering in the winter rainfall region (Figure 1). Synthesis of seasonal data of fynbos biome species suggests that regardless of environment, many phenophases are initiated more by endogenous rhythms than environmental cues (see also Hanes 1965). There are some indications that the behaviour of proteas growing in the northern hemisphere corresponds closely to their seasonality in the Cape (Vogts 1982).

The possibility of endogenous rhythms overriding environmental stimuli makes the study of causal factors extremely difficult. The range of suggested environmental determinants is vast - from accumulating hours of warmth to varying light quality - and the formidable task of experimentation involved may explain the reluctance amongst biologists to do causal studies (see inventory). However, the studies of Sommerville, Brown, Jongens-Roberts and Stock may indicate seasonality in nutrient and water balance in relation to phenophases. I suggest that more of these detailed ecophysiological studies, taking into account cumulative radiation effects, and with particular emphasis on root behaviour and water balance (cf Schütte 1982) be undertaken, so that although we may not be able to determine causal factors, we may at least explain mechanisms.

In conjunction with this ecophysiological work there should be more seasonality studies on plant-animal interactions such as pollination, dispersal and predation. Also, work on populations and genetics should not preclude flowering phenology which determines the extent of possible interbreeding (cf Van Wyk 1982).

A further suggestion is a plea to taxonomists who possess a wealth of phenological information but who seldom collate it into an easily accessible form. Exceptions are the invaluable works of Rourke (1972, 1980) and Williams (1972). Revisions of taxa can impart immeasurable information in terms of floral descriptions, flowering times, pollinators, dispersers, and time of growth.

Finally, phenology on its own is of little value but is an essential facet of the biology of a species. In combination with other autecological data such as seed germination requirements, seed viability etc, phenological information can be a very important management tool. Even though Grubb (1977) precludes phenological spread in advocating the prime importance of regeneration niches in species diversity, phenophases are actually implicit in his examples of differentiation in the regeneration niche. For example, production of viable seed, dispersal and germination are all delimited by their dependence on flowering time. Therefore the inclusion of phenology is essential in most studies on the maintenance of species diversity.

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