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Aspects of plant dispersal in the southwestern Cape with particular reference to the roles of birds as dispersal agents

by

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Contents

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General Abstract

The dispersal of plants with particular attention to the roles birds play as dispersal agents was studied in the southwestern Cape, South Africa from 1983 to 1985. The research was organized as ten inter-related studies, each with an independent data base. Each chapter focused on a different scale of plant dispersal processes ranging from regional assemblages of plant species to individual species. At the largest scale, the seven vegetation types commonly occurring in the southwestern Cape were examined for incidence of vertebrate-dispersed plants. Coastal Thicket and Afromontane Forest were found to be the richest in these species. The colonization of vertebrate-dispersed plants was examined in an artificially cleared area of Mountain Fynbos vegetation. Enhanced densities of vertebrate-dispersed species were found in areas where perches had been provided. The seasonal availability of vertebrate-dispersed species was found to be most continuous in Coastal Thicket vegetation. Fruit displays of vertebrate-dispersed indigenous plants were found to vary from those that were sporadic and inconspicuous, to those that were conspicuous and predictable, whereas those of alien plants were usually large and conspicuous. Avian use of these fleshy fruits in Coastal Thicket was examined and found to be proportional to their availability. A study of fruit presentation in relation to leaf number and stem thickness suggested that sessile, stem attached fruits have fewer local leaves at time of ripening than fruits which are presented in panicles. This may enhance accessability and conspicuousness of stem attached fruits for dispersal by birds. Four autecological studies tested certain predictions arising from models developed to describe fruit/frugivore interactions. The dispersal of the alien *Acacia cyclops* seeds by the indigenous Black Korhaan *Eupodotis afra* suggested that successful fruit/frugivore relationships are not necessarily the product of reciprocal evolution. The study on *Chrysanthemoides monilifera* found that efficient dispersal systems are not limited to plants producing small quantities of lipid-rich fruits and to dispersal by obligate frugivores. The abiotic dispersal of *Quercus robur* was found to be efficient in relation to vertebrate-dispersal. The study on *Protasparagus aethiopicus* found that the morphology of fleshy fruits may also reflect attempts to overcome the effects of non-dispersing seed predators. It is concluded that a gradient from a predictable to unpredictable fruit availability provides a better basis for studying fruit/frugivore interactions than the coevolutionary models previously presented.

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General introduction

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Dispersal syndromes

Plants being sessile organisms, require mechanisms for the dispersal of their propagules if they are to colonize new areas. In addition the dissemination of their propagules in space may facilitate greater genetic interchange between plant populations and thus enhance their potential for speciation. The use of vertebrates, and in particular birds, is among the most important mechanisms promoting seed-dispersal (Regal 1977). The vertebrate-dispersal syndrome has been considered to represent one of the more obvious evolutionary interactions existing between plants and animals (McKey 1975). Although vertebrate-dispersal of plants is widespread (Ridley 1930) other dispersal mechanisms may be locally predominant. Xeric conditions have been associated with a high incidence of plant species with abiotic dispersal mechanisms (van der Pijl 1969). However, the regional distribution of different dispersal syndromes has received little scientific investigation. The only African study of this nature is a biogeographical analysis of dispersal syndromes occurring in southern African trees (Knight 1983, 1984). On a smaller geographical scale, the southwestern Cape region of South Africa has a number of functionally very dissimilar vegetation types (Moll _et al_. 1984) which include Afromontane Forest, subtropical Coastal Thicket, mediterranean type shrublands (Strandveld), semi-arid Karoo, heathlands (Mountain and Coastal Fynbos) and bush encroached grasslands (Renosterveld). Since each of these vegetation types has a different natural disturbance regime (Cowling _et al_. 1987) different requirements for seed-dispersal will exist. This thesis therefore examines dispersal syndromes occurring in different vegetation types of the southwestern Cape in the context of vegetation dynamics. Particular attention has been paid to identifying interactions between animals and plants with respect to the successful dispersal of plant propagules.

Vertebrate-dispersal of plants

Fruits possessing either a fleshy covering around the seed (usually a pericarp, sarcotesta, etc.) or a fleshy appendage (aril or pseudaril) are usually associated with vertebrate-dispersal and occur worldwide (Ridley 1930; van der Pijl 1969, 1972; Regal 1977). The consumption of such fruits by vertebrates (usually birds, mammals or reptiles) has been documented by Ridley

(1930) and van der Pijl (1972). However, few data exist on the actual dispersal process carried out by such agents, and virtually none on the post-dispersal establishment of these plants (Herrera 1985). Relationships between fleshy fruits and avian frugivores have been described by the theoretical models of Snow (1971), McKey (1975) and Howe & Estabrook (1977). This research predicted that plants producing fleshy fruits for bird-dispersal could be divided into two categories. One category includes species possessing large, nutritious fruits produced in relatively small quantities, whereas the other category includes species producing large quantities of small-sized but relatively unnutritious fruits. Large, nutritious fruits usually contain a single or very few large-sized seeds, and are thought to be used by specialist frugivores. To maintain these specialist birds the fruits would need to be available throughout the year. Consequently many of these plants would possess long fruiting seasons. On the other hand, small and un-nutritious fruits usually contain large numbers of minute seeds and are thought to be used by non-specialist frugivores. Since such birds usually use fruits as a supplement to their insectivorous diet a continuous availability of fruit is not required. Consequently these fruits would probably be available for short periods only. Recent studies suggest that there is little evidence supporting these models (Howe 1977, 1980, 1981, 1983; Kantak 1978; Frost 1980; Herrera & Jordano 1981; Herrera 1982; Howe & Smallwood 1982; Jordano 1982; Moore & Willson 1982; Morden-Moore & Willson 1982; Herrera 1984). To date, no other framework has been presented for testing interactions between plants and their avian dispersal agents.

Alien plants

The avian-dispersal of alien plants has been studied in even less detail than indigenous plants, even though they may pose serious ecological and environmental problems. Most research of this nature has been undertaken in Africa (Glyphis et al. 1981; Alexandre 1982; Oatley 1984; Dean 1985; Knight 1986a). In southern Africa alone the indigenous tree flora (ca 1 300 species) has been complemented by ca 722 alien tree species (Anon. 1981), many of which are potentially vertebrate-dispersed (Knight 1986b). Since vertebrate-dispersed alien plants are abundant both in southern Africa and the southwestern Cape region, they were integrated with the research undertaken on the dispersal processes of indigenous plants. More particularly alien plants may represent experimental controls where the interaction between frugivore and fruit is independent of coevolutionary processes. These artificially created conditions can then be compared to interactions occurring between indigenous fruits and their avian dispersal agents.

Research in southern Africa

In the southern African tree flora at least 23% of species have fleshy fruits that are apparently suitable for bird-dispersal (Knight 1983), whereas less than 14% of the 600 terrestrial bird species are frugivorous, and less than 4% could be considered as specialist frugivores (e.g. barbets, fruit pigeons and some hornbills) (Snow 1981; Knight & Brooke in press). Field-studies carried out in the Dune Forest of Zululand (Frost 1980) suggest that there is little selection by frugivorous birds for the large and nutritious fruits, contradicting the theoretical predictions of McKey (1975) and Howe & Estabrook (1977). Although Snow (1981) and Knight & Brooke (in press) have divided the African avifauna into specialist and opportunist frugivores, there are only two well documented examples of genuine fruit specialization by the African avifauna (van Someren 1957, Godschalk 1983).

Objectives

1) To evaluate the models of McKey (1975) and Howe & Estabrook (1977) with respect to the indigenous vegetation of the southwestern Cape.

2) To determine the ecological importance of avian seed-dispersal mechanisms in relation to other dispersal mechanisms occurring in the different vegetation types of the southwestern Cape.

3) To relate seed-dispersal processes to the establishment of new generations of plants. This aspect of seed-dispersal has been neglected (see Herrera 1985), probably because of the difficulty in designing appropriate field experiments.

4) To integrate dispersal processes with other ecological processes, such as the effects seed-predators (both vertebrate and invertebrate) have on seed-dispersal processes through pre- and post-dispersal predation of seed.

5) To describe and predict the influence alien plants may have in disrupting the vertebrate-dispersal processes occurring in indigenous plants.

Scope

This thesis is arranged as ten inter-related chapters, with each chapter having a particular theme and addressed at a different scale ranging from large assemblages of plant species to individual species. Each chapter has been written as an independent scientific paper in the format of South African Journal of Botany. Plant nomenclature follows Bond & Goldblatt (1984) and bird nomenclature follows Maclean (1985). The first six chapters examine inter-relationships between plant species, whereas the final four chapters examine the interactions of individual plant species with both their dispersal agents and seed predators. Two of these chapters examine alien plants, one of which contrasts abiotic with biotic dispersal processes.

Chapter contents

Chapter 1: The differences in the species richness and abundance of different dispersal syndromes were examined for seven vegetation types occurring in the southwestern Cape (Mountain Fynbos, Coastal Fynbos, Renosterveld, Karoo, Strandveld, Coastal Thicket and Afromontane Forest). A total of 721 plant species were classified according to four mutually exclusive categories of potential dispersal agents: vertebrates (birds and mammals), ants, wind and other mechanical methods. A high species richness and abundance of vertebrate-dispersed plants was found in Afromontane Forest and Coastal Thicket vegetation.

Chapter 2: The relationships between dispersal agents and re-establishment was examined for all plant species found to be colonizing an artificially cleared 0,3 ha Mountain Fynbos site adjacent to a remnant Afromontane Forest patch. In particular the role of perches in promoting local recruitment of bird-dispersed plants was examined during this two-year field experiment. Although reseeding bird-dispersed plants contributed little to the total colonizing flora, their pattern of occurrence was markedly associated with the provision of perches.

Chapter 3: The fruiting phenology of 58 indigenous and nine alien plant species was studied over a two year period in a Coastal Thicket, a Mountain Fynbos site adjacent to a remnant Afromontane Forest patch and an Afromontane Forest site. In particular an attempt was made to identify species which provided a predictable supply of fruit and therefore could be exploited by itinerant frugivores such as the Rameron Pigeon _Columba arquatrix_ and Redfaced Mousebird _Colius indicus_. Two groups of species possessing predictable fruiting were identified; those providing an almost continuous supply of fruit (e.g. _Colpoon compressum_) and those species providing a seasonally predictable supply of fruit (e.g. _Chironia baccifera_).

Chapter 4: The use of fruits of 22 plant species by ten species of avian frugivores was studied over a year in a Coastal Thicket. Aggressive interactions between bird species in the vicinity of fruit crops were also studied. For each plant species an index representing actual fruit availability was related to avian use of that species. This approach was useful for identifying those fruit resources preferred by avian frugivores. The use of most plant species by avian frugivores was found to be proportional to their availability. Those species with fruits preferentially eaten by avian frugivores either provided continuous or seasonally predictable fruit crops.

Chapter 5: Fruit displays of eight indigenous and six alien woody plant species at five sites within the southwestern Cape were described with respect to two proposed theoretical models. The alien plant species were predicted and found to have larger and more conspicuous fruit displays, whereas indigenous plants were predicted and found to include plants with relatively small but long duration fruit displays. Overall, indigenous plant species had a greater variety of fruit displays than alien species.

Chapter 6: Relationships between fruit production, stem thickness and leaf and stem abundance were examined in nine indigenous, evergreen plant species common to Coastal Thicket and Afromontane Forest vegetation of the southwestern Cape. Visual conspicuousness and accessibility of fruit displays was predicted and found to be associated with a limited local reduction of leaves. Sessile fruits were predicted and found to exhibit the greatest loss of leaves, and thereby make the fruits more accessible to frugivores. Thicker stems were predicted and found to support larger fruit crops.

Chapter 7: Seed-dispersal of two introduced *Acacia* species by Black Korhaans *Eupodotis afra* was studied in relation to their post-dispersal establishment. The seeds of *Acacia cyclops* which possess a large, colourful pseudaril were eaten in preference to *A. saligna* which lacks a functional pseudaril. The successful dispersal system established between *Acacia* plants and Black Korhaans is fortuitous and is not consistent with the coevolutionary models proposed by McKey (1975) and Howe & Estabrook (1977).

Chapter 8: Avian frugivory, seed-dispersal, seed predation and seedling establishment were examined for *Chrysanthemoides monilifera*; a common coastal plant of the southwestern Cape. Since *C. monilifera* has been introduced, and become invasive in Australia, the results obtained in this study have implications for the introduction of biocontrol of this species in Australia. The efficient dispersal systems reported for *C. monilifera* both in South Africa and Australia (Weiss 1983) is in conflict with the coevolutionary models proposed by McKey (1975) and Howe & Estabrook (1977).

Chapter 9: This study examined the role of both abiotic (water) and biotic (an alien squirrel; Sciurus carolinensis) dispersal agents in promoting the naturalization of the oak Quercus robur. The abiotic agent, although episodic, dispersed considerable numbers of acorns to sites suitable for the initial establishment of oaks. Since this dispersal is restricted to downstream translocation of seeds, the low efficiency seed-dispersal carried out by squirrels is still required for maintaining upstream populations of oak. Consequently the two contrasting dispersal processes complement each other.

Chapter 10: The coevolutionary models of McKey (1975) and Howe & Estabrook (1977) suggest that among other morphological features the ratio of pericarp-to-seed would influence the pattern of dispersal carried out by frugivorous birds. Intra-specific changes in ratios of pericarp-to-seed have been related to interspecific plant competition for avian dispersal agents (Herrera 1981). Protasparagus aethiopicus, a common coastal vine occurring in the southwestern Cape, was found to exhibit site-specific and seasonal variations in seed-to-pulp ratios that are apparently unrelated to inter-specific competition for dispersal agents. It is suggested that these variations in pericarp-to-seed ratios were an attempt to overcome the effects of heavy parasitism by a species of lepidopteran larva.

Integration

The relationship between the five objectives and the ten thesis chapters are summarized in Table 1. The thesis aims to contribute to the field of dispersal biology, by proposing alternative theoretical models for fruit presentation (chapters 5 and 6) and suggesting alternative sampling methodologies for identifying fruit resources that are preferred by frugivorous birds (chapter 4). The four autecological studies (chapters 7, 8, 9 and 10) are specific tests of the coevolutionary models proposed by McKey (1975) and Howe & Estabrook (1977). The first three chapters are basic background studies identifying the spatial and temporal availability of fruit resources available in the southwestern Cape. The synthesis draws together these research results and suggests a new framework for addressing further research in the field of bird-dispersal of plants.

Table 1 The relationship between the five objectives and the 10 inter-related chapters dealing with aspects of seed-dispersal of plants occurring in the southwestern Cape

Objectives	**Chapters**									
	1	2	3	4	5	6	7	8	9	10
Evaluate theoretical coevolutionary models describing fruit-frugivore interactions				X			X	X	X	X
Determine the importance and abundance of bird-dispersed plants	X	X	X							
Relate dispersal processes with plant establishment		X					X	X	X	
Integrate dispersal processes with other ecological processes						X	X	X	X	X
Describe effects alien plants have on the dispersal processes of indigenous plants			X		X					

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CHAPTER 1

Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Dispersal syndromes in different vegetation types of the southwestern Cape, South Africa

Contents

Discussion

Dispersal syndromes in different vegetation types of the southwestern Cape, South Africa

Abstract

This study investigates the species richness and abundance of biologically (birds, mammals and ants) and mechanically (ballistic pods and capsules, gravity, wind and mechanical attachments to animals such as hooks and burs) dispersed plant species (N = 721) occurring in seven vegetation types of the southwestern Cape, South Africa. The vegetation types sampled were Mountain Fynbos (36 plots), Coastal Fynbos (81), Renosterveld (55), Karoo (78), Strandveld (24), Coastal Thicket (40) and Afromontane Forest (163). A high species richness and abundance of vertebrate-dispersed plants were found in Afromontane Forest and Coastal Thicket, whereas in the Karoo a high incidence of non-wind, but mechanically-dispersed plants, was found. Coastal and Mountain Fynbos were characterized by a low representation of vertebrate-dispersed plants.

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Introduction

The regional distribution of different plant dispersal syndromes has received little scientific investigation. The only African study of this nature is a biogeographical analysis of dispersal syndromes occurring in southern African trees (Knight 1983, 1984). This study identified a dominance of wind-dispersed nut/achene fruit types occurring in the southwestern Cape. However, within the southwestern Cape a number of functionally dissimilar vegetation types exist (Moll et al. 1984), the most extensive being Mountain Fynbos. Most Mountain Fynbos plants are characterized by canopy-stored (Le Maitre 1987) and soil-stored seeds (Pierce 1987) which are dispersed over relatively short-distances (Bond 1980; Moll & Gubb 1980; Brits 1987; Manders 1986). Vertebrate-dispersal is largely absent in Mountain Fynbos plants (Milewski & Bond 1982), whereas ant-dispersal is common (Bond & Slingsby 1983). Vertebrate-dispersed plant species are, however, common in Afromontane Forest (Milewski 1982, 1985, Phillips 1927, 1931), Strandveld and Coastal Thicket (Tinley 1985; Knight in prep., Chapter 4). Differences in dispersal syndromes between vegetation types is thought to reflect nutrient availability of soils (Milewski 1982, Milewski & Bond 1982) or the absence of fire (Midgley 1987). To date no quantified comparisons of dispersal syndromes in different vegetation types of the fynbos biome have been undertaken, although Midgley (1987) has suggested some general trends. The first aim is to compare the incidence (species richness and abundance) of biologically (birds, mammals and ants) and mechanically (ballistic pods and capsules, gravity, wind and mechanical attachments to animals such as hooks and burs) dispersed plant species in seven vegetation types (Mountain Fynbos, Coastal Fynbos, Renosterveld, Karoo, Strandveld, Coastal Thicket and Afromontane Forest) occurring in the southwestern Cape. The second aim is to compare the colour of fleshy fruits (black/purple/blue, red/orange, white/yellow, brown/green) occurring in the flora of the southwestern Cape with the invasive and indigenous floras of South Africa (Knight 1986) and other floras of the world (Wheelwright & Janson 1985).

Materials and Methods

Published and unpublished phytosociological tables using Braun-Blanquet (1932) cover abundance scales (Table 1) were amalgamated to create a basic data matrix of species abundance (N = 721) at 13 sites representing the seven vegetation types. Data from 477 sampling plots was accumulated from Mountain Fynbos (36 plots), Coastal Fynbos (81), Renosterveld (55), Karoo (78), Strandveld (24), Coastal Thicket (40) and Afromontane Forest sites (163). Each of the 721 plant species were classified according to four mutually exclusive categories of potential dispersal agents: vertebrates (birds and mammals), ants, wind and other mechanical methods according to information in Adamson & Salter (1950), Bond & Slingsby (1983), Siegfried (1983), Bond & Goldblatt (1984), and by examining plant material in the Hermanus and Bolus herbaria. This information was supplemented by consultation with other ecologists (see acknowledgements). Additional information was obtained from field observations and data collected on vertebrate-dispersed plant species associated with Mima-like earth mounds in a Dry Mountain Fynbos and Karoo ecotone (Knight, Rebelo & Siegfried 1988). Only those plant species that possess an edible fleshy appendage (pericarp, aril, elaisome, etc.) were recorded as vertebrate-dispersed. Plant species with hooks and burs were classified as mechanical-dispersal. Annuals and geophytes, where recorded in the phytosociological tables, were included in the analyses.

Colours of fleshy fruits were determined by field observations of all plant species possessing fleshy fruits and compared with data presented by Knight (1986) and Wheelwright & Janson (1985).

Patterns occurring in the data matrix of species by sites were identified using a cluster analysis (Anderberg 1973; Field & McFarlane 1968) based on the Bray & Curtis (1957) measure of similarity and Lance & Williams (1967) group-average sorting method. Percentage representation within the cover abundance classes (Braun-Blanquet 1932) for different dispersal syndromes and vegetation types was analysed using correspondence analysis (Greenacre 1984; Underhill & Peisach 1985). Statistical differences in the representation of dispersal syndromes in different vegetation types were determined using maximum likelyhood values.

Table 1 Data sources used in the assessment of the representation of dispersal syndromes (vertebrate, ant, wind and other mechanical methods) of species in plant assemblages at 13 sites in seven vegetation types in the southwestern Cape. The localities of sites 1, 2, 4, 6, 9, 10 are given in Siegfried & Crowe (1983)

	Site	Vegetation type	Data source
1.	Sir Lowry's Pass	Mountain Fynbos	FitzPatrick Institute (unpublished)
2.	Swartboschkloof	Mountain Fynbos	FitzPatrick Institute (unpublished)
3.	Orangekloof	Mountain Fynbos	McKenzie, Moll & Campbell (1977)
4.	Barhuis	Coastal Fynbos	FitzPatrick Institute (unpublished)
5.	Pella	Coastal Fynbos	Boucher & Shepherd (in press)
6.	De Grendel	Renosterveld	FitzPatrick Institute (unpublished)
7.	Tygerberg	Renosterveld	Paterson (1982)
8.	Worcester Botanical Garden	Karoo	Norton (1977)
9.	Melkboschstrand	Strandveld	FitzPatrick Institute (unpublished)
10.	Geelbek	Strandveld	FitzPatrick Institute (unpublished)
11.	Hermanus	Coastal Thicket	FitzPatrick Institute (Chapter 4)
12.	Orangekloof	Afromontane Forest	McKenzie, Moll & Campbell (1977)
13.	Table Mountain	Afromontane Forest	Campbell & Moll (1977)

Results

Difficulty was encountered with respect to distinguishing mammal- from bird-dispersed species, since many species are probably dispersed by both agents. Consequently these two categories were combined into a single vertebrate-dispersed category for the analyses. Plant species bearing small (< 10 mm length) black, purple, orange or red coloured fleshy fruits are normally dispersed by birds (van der Pijl 1972). Such species accounted for 55% of the 91 species which were found to produce fleshy fruits in the southwestern Cape. Larger (> 10 mm length), but dull coloured (green or brown), fleshy fruits are characteristic of species dispersed by mammals (van der Pijl 1972) and occurred in only 3% of the species. Other species of fleshy fruit are probably dispersed by both mammals and birds. Consequently few species possessing fleshy fruits in the southwestern Cape were found to be unsuitable for bird-dispersal.

The representation of dispersal syndromes (vertebrate-, ant-, wind-dispersed, and other mechanically-dispersed species) vary significantly ($G^2_{18} = 145,6$; $P < 0,001$; Figure 1) among the different vegetation types (Mountain Fynbos, Coastal Fynbos, Strandveld, Renosterveld, Karoo, Coastal Thicket and Afromontane Forest). Much of this variation can be explained by the high representation of vertebrate-dispersed plants occurring in Afromontane Forest and Coastal Thicket (standardized deviations are 5,4 and 4,7 respectively). Also of importance is the relatively high representation of non-wind, but mechanically dispersed species in Karoo vegetation (standardized deviation = 3,9), and the very low representation of vertebrate-dispersed species in Coastal Fynbos (standardized deviation = -3,5).

A subdivision of the plant species representing particular dispersal syndromes into Braun-Blanquet cover abundance categories (r, +, 1, 2, 3, 4 and 5) indicated significant differences between vegetation types ($G^2_{162} = 2830,6$; $P < 0,001$; Table 2). The greatest representation of vertebrate-dispersed plants occurred in Coastal Thicket at a BB cover abundance of 2 (standardized deviation = 22,4) and in Afromontane Forest at a BB cover abundance of 1 (standardized deviation = 13,7). This analysis also indicated

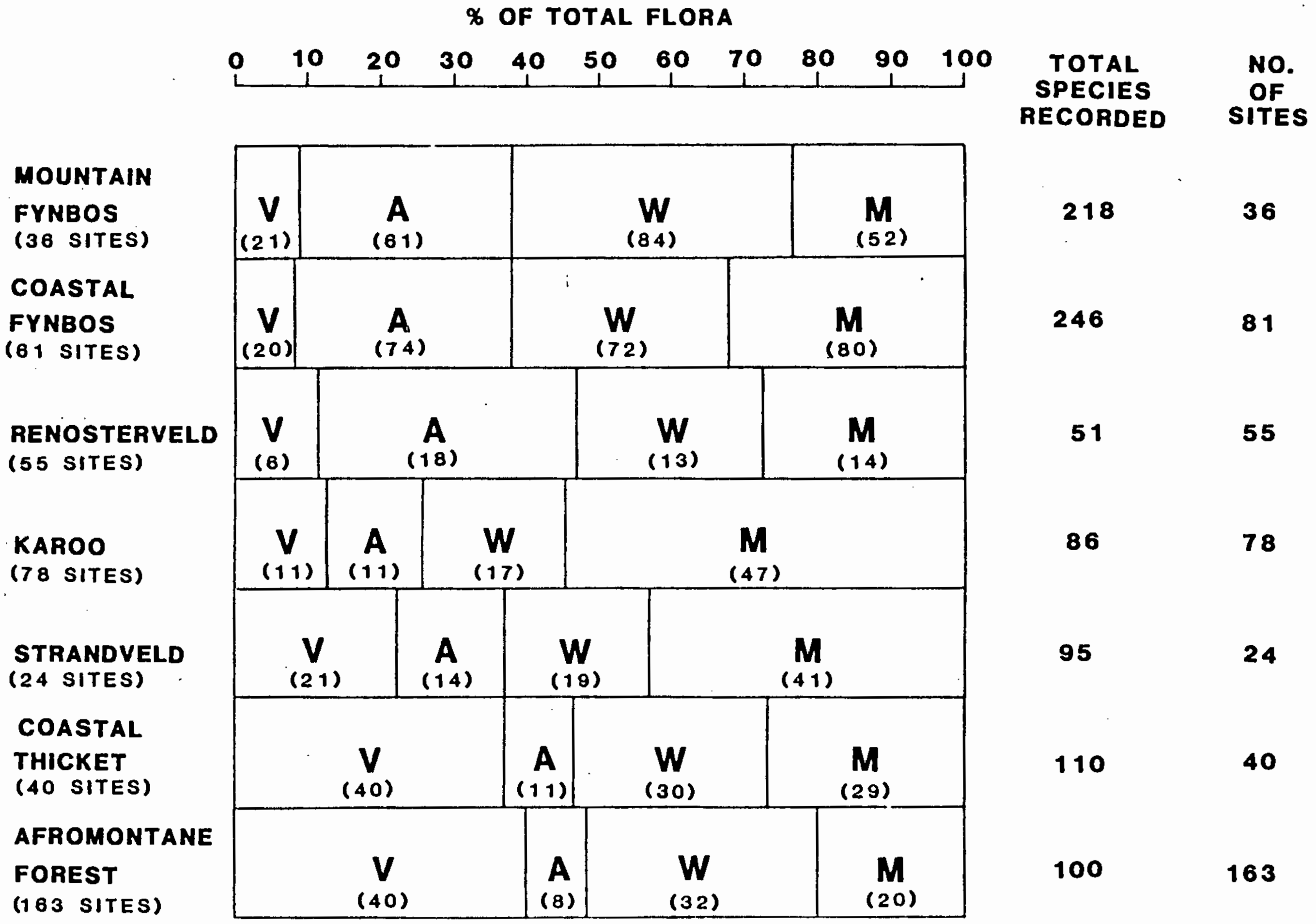

Figure 1 Percentage frequency of vertebrate-, ant-, wind-, or mechanically-dispersed (V, A, W and M, respectively) plant species in seven vegetation types in the southwestern Cape. Actual numbers of species are in parentheses.

a high representation of both wind- and vertebrate-dispersed plants in the Karoo vegetation in the higher BB cover abundance classes (4 and 5 respectively) (Table 2).

The relationship between dispersal syndromes, BB cover abundance categories, and vegetation types are represented by a dendrogram (Figure 2) and a correspondence analysis ordination plot (Figure 3). In the ordination plot, a gradient of increasing plant cover abundance occurs from the top to the bottom and a second gradient represents an increasing proportion of vertebrate-dispersed plants from left to right. Hence, a clear dichotomy exists between the fynbos vegetation types (coastal and mountain), with their low representation of vertebrate-dispersed plant species, and the thicket-forest types with their relatively high representation of vertebrate-dispersed plant species. Strandveld, and to a lesser extent, Karoo vegetation types are intermediate between the fynbos and thicket-forest vegetation types, with regard to the representation of particular dispersal syndromes in different cover abundance classes.

The representation of vertebrate-dispersed plant species possessing black, purple or blue coloured fruit in the flora of the southwestern Cape is greater than that in the indigenous tree-shrub flora of southern Africa, but is similar to that of the southern African alien flora (invasive and non-invasive species), and lower than that in the New World floras (Table 3). A smaller proportion of species producing red or orange coloured fleshy fruit occurs in the indigenous flora of the southwestern Cape than in either the invasive alien or indigenous tree-shrub floras of southern Africa. These proportions, however, are similar to comparable ratios for the New World floras (Table 3). There is a large variation in brown/green fruits, with the European flora having a particularly high representation.

Discussion

Dispersal syndromes and vegetation dynamics

Milewski (1982) and Milewski & Bond (1982) suggested that in the fynbos biome soil nutrients are the most important factor determining the distribution of

Table 2 The 20 most significant deviations in the representation of four categories of dispersal syndromes (vertebrate, ant, wind and other mechanical methods) of species in Braun-Blanquet cover classes in seven vegetation types in the southwestern Cape

Vegetation type	Dispersal agent	Braun-Blanquet plant cover classes	Standardized deviation
Coastal Thicket	Vertebrate	2	22,4
Afromontane Forest	Vertebrate	1	13,7
Coastal Fynbos	Mechanical	r	12,8
Coastal Fynbos	Wind	r	12,5
Karoo	Vertebrate	5	11,7
Karoo	Wind	5	10,8
Karoo	Wind	4	10,6
Coastal Fynbos	Wind	+	-9,8
Coastal Fynbos	Mechanical	+	-9,6
Afromontane Forest	Vertebrate	r	-9,5
Coastal Thicket	Wind	2	9,0
Karoo	Mechanical	2	9,0
Coastal Thicket	Vertebrate	+	-8,3
Coastal Thicket	Vertebrate	4	8,3
Strandveld	Ant	+	7,8
Renosterveld	Wind	1	7,7
Karoo	Wind	2	7,4
Coastal Fynbos	Mechanical	1	-7,3
Karoo	Mechanical	+	6,8
Coastal Fynbos	Ant	2	6,7

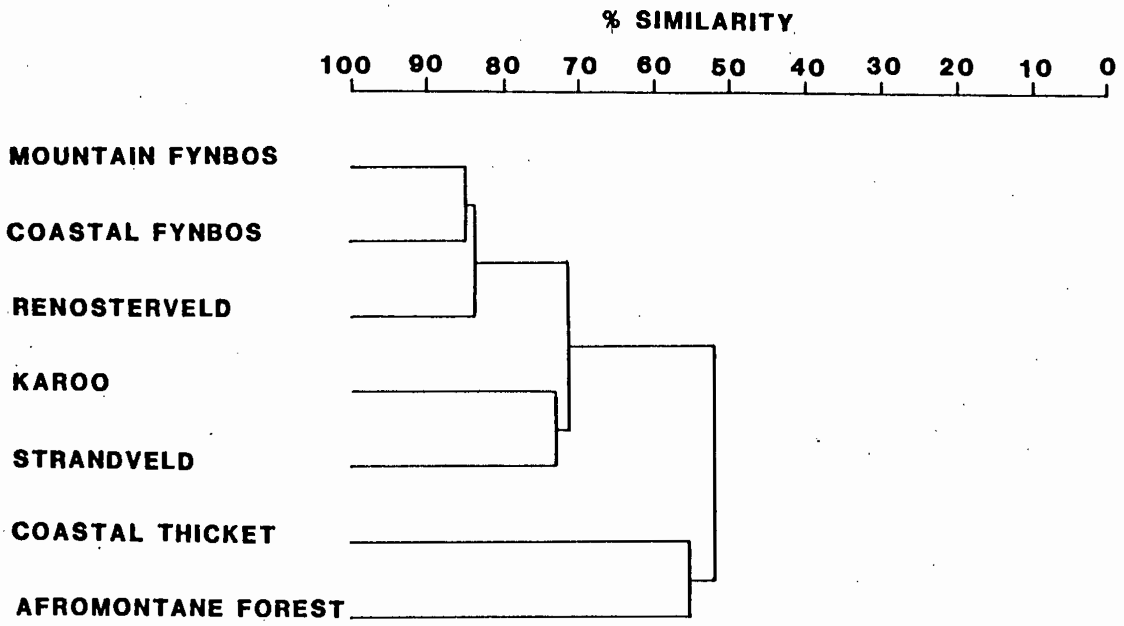

Figure 2 Dendrogram showing relationships between seven vegetation types in the southwestern Cape, based on the representation of dispersal syndromes (vertebrate, ant and wind and other mechanical methods) of plant species in Braun-Blanquet (1932) cover abundance classes (r - 5).

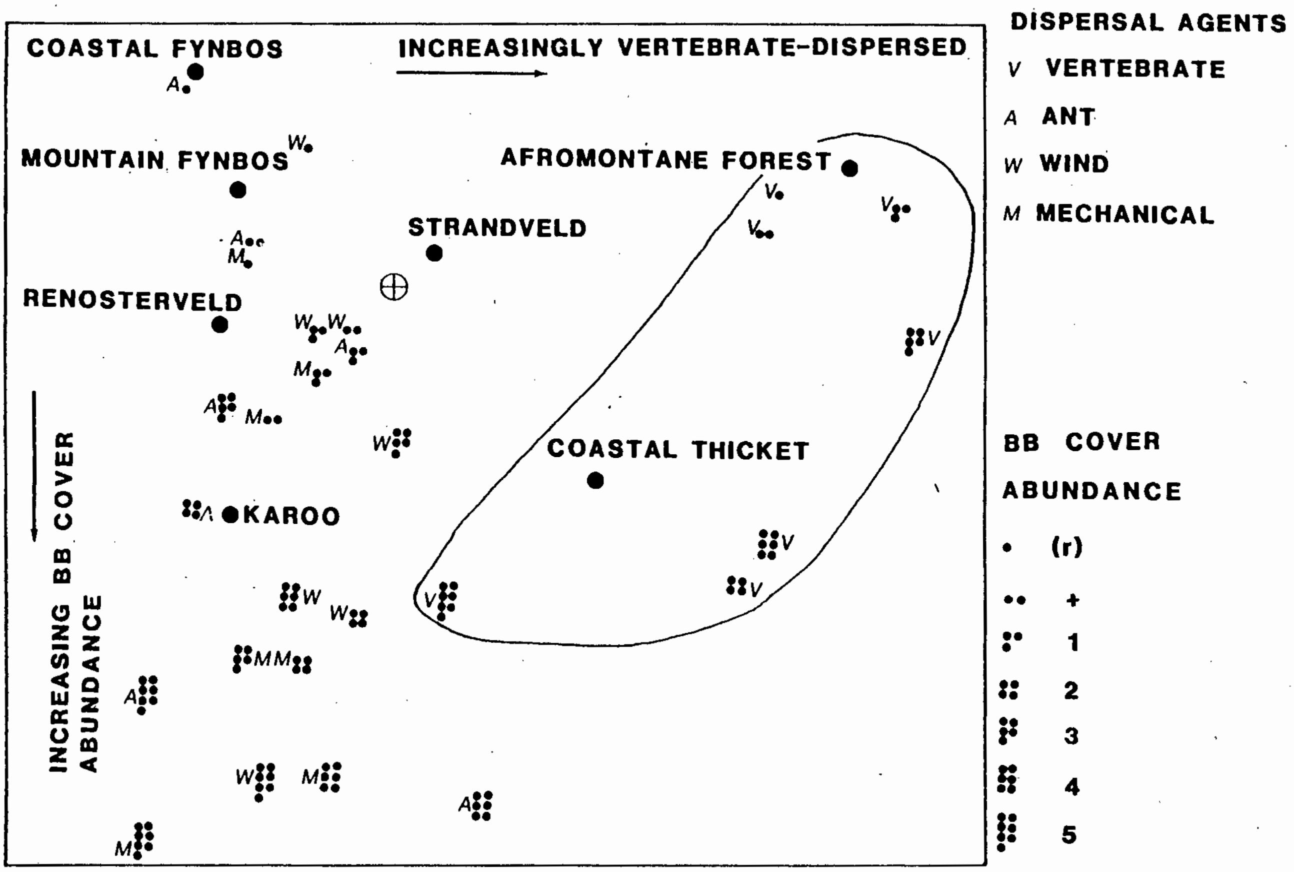

Figure 3 Ordination representing relationships between dispersal syndromes (V = vertebrate, A = ant and W = wind, or M = other mechanical methods) of plant species in Braun-Blanquet (1932) cover abundance classes (one to seven dots representing r - 5) for seven vegetation types in the southwestern Cape.

Table 3 The percentage frequency of vertebrate-dispersed plant species producing fleshy fruit in different regions of the world

Region	Black/Purple/Blue	Red/Orange	White/Yellow	Brown/Green	No. spp.	Source
Peru	40,2	35,8	21,7	2,2	134	Wheelwright & Janson (1985)
Costa Rica	47,2	35,8	12,3	4,7	252	
Florida	43,8	29,0	18,2	9,0	137	
Europe	33,6	40,8	6,7	18,9	137	
Southern Africa						Knight (1986)
Indigenous	27,2	42,7	19,2	10,9	349	
Invasive alien	35,0	42,5	20,0	2,5	40	
Non-invasive alien	39,2	31,7	23,4	5,7	148	
southwestern Cape	35,2	34,1	14,3	16,3	91	This chapter

plants possessing fruits suitable for bird-dispersal. Midgley (1987) argued that protection from fire is more important for the establishment of these species. Van Daalen (1984) found few major differences in the occurrence of nutrients in the soils of Mountain Fynbos (which is depauperate in vertebrate-dispersed plant species) and Afromontane Forest (which is rich in vertebrate-dispersed species). Those differences found in soils viz. calcium and potassium (Van Daalan 1984; Masson & Moll 1987) largely reflect differences in nutrient cycling processes. Further evidence against the soil nutrient hypothesis of Milewski & Bond (1982) is the artificial establishment of an Afromontane Forest in the Elgin district of the southwestern Cape on a site that formerly supported Mountain Fynbos (Knight & Masson 1987). This forest, presently with a canopy exceeding 15 m in height, was established only 30 years ago without the aid of fertilization or watering. Consequently forest development is unlikely to be limited solely by the nutrient deficiencies of the soils.

Since young forest plants are not usually resilient to fire (pers. obs) a frequent burning regime such as occurs in Mountain Fynbos would, however, prevent their establishment. Once mature, however, most of these forest species are able to resprout after fire (C.J. Geldenhuys, pers. comm.) and therefore become resilient to this type of disturbance. In conclusion, given sufficient soil moisture (Schimper 1903) and initial protection against fire (Kruger 1979; Midgley 1987) there is no apparent restraint on the expansion of Afromontane Forest into Mountain Fynbos.

A second argument against the nutrient deficiency hypothesis of Milewski (1982) and Milewski & Bond (1982) is the abundance of resprouting plants producing fleshy fruits during the immediate post-fire period in Mountain Fynbos (e.g. unnamed Colpoon spp. and Euclea polyandra (L.f.) E. Meyer ex Hiern; see Chapter 2). The restriction of these species to a single post-fire fruiting may, however, be related to the lack of available nutrients in periods other than those immediately after a fire. Since these plants are able to cope with fairly frequent disturbances it is difficult to substantiate either hypothesis (soil nutrient availability or long-term protection from fire) for all vertebrate-dispersed plant species in the southwestern Cape.

The frequent occurrence of fires in Mountain Fynbos (Cowling et al. 1987) suggests that there is little need for complex or efficient dispersal systems since propagules generally germinate in a post-fire environment that is free of competition from parent plants (Manders & Cunliffe 1987). To overcome the lack of efficient dispersal sytems in fynbos plants, either the plant propagules or plants themselves must be resilient to fire. The nature of resilience (parent plant or propagule) has considerable implications for the speciation of the taxa (Wells 1965). The comparative scarcity of plant species which persist after a fire through resilience of the parent plants may reflect their reduced potential for speciation (viz. a lower turnover of generations). In contrast ant-dispersal may facilitate post-fire survival of the propagules (Bond & Slingsby 1983) and such species have an enhanced potential for speciation through a greater turnover of generations.

The comparative dominance of vertebrate-dispersed propagules in Strandveld and particularly Coastal Thicket may well reflect greater availability of nutrients, particularly calcium and phosphorous (Witkowski & Mitchell 1987). Given that these vegetation types are likely to carry less fire than fynbos (van Wilgen 1987), there is a greater potential for the establishment of long-lived woody species possessing fleshy fruits (see Cowling & Pierce in prep.). The differences in the dominance of vertebrate-dispersed woody species in Strandveld of the west coast and Coastal Thicket of the south coast may reflect both the greater availability of moisture in the south (amount and seasonality) and that the Coastal Thicket plants are geographically closer to the probable centres of origins for broad-leafed woody evergreen species in southern Africa (Cowling 1983). Both Coastal Thicket and Strandveld vegetation types have much in common with tropical rain forests (e.g. phenology; chapter 3), and consequently Acocks' (1975) description of this type of vegetation as a "lilliputian forest" is appropriate.

Since Levyns (1929, 1935), little research has been undertaken on Renosterveld with respect to vegetation dynamics and disturbance regimes, and therefore the results obtained (Figures 1 & 3) are difficult to interpret. The evidence for the assumed resilience to disturbance by 'migration' (Cowling et al. 1987) was not found whereas a high incidence of ant-dispersal (indicative of 'in situ' resilience) was found. Some of the ambiguity found in the results obtained for this vegetation type may be the product of intense fragmentation, isolation and extinction that has recently occurred in Renosterveld vegetation (McDowell in prep.).

The Karoo vegetation showed high representation of mechanically-dispersed plants, and these plants occurred at particularly high BB cover abundance levels. This suggests that species packing (alpha diversity) would probably be relatively low. Since much of the dynamics of the karoo vegetation is related to environmental cues such as rainfall, mechanical dispersal syndromes may be favoured. Many species of the Mesembryanthemaceae have seed capsules that only release seeds in the presence of sufficient moisture and thereby may ensure a better seedling recruitment. The presence of persistent soil-stored seed banks rather than mode of dispersal may be important for determining the abundance of particular karoo plant species (Ivey & Cowling 1987).

Colours of fleshy fruits in the southwestern Cape

The flora of the southwestern Cape is distinguished by its relative scarcity of fleshy fruits suitable for dispersal by mammalian agents. Since fruits in the invasive and indigenous floras have similar representation with respect to size and colour of fleshy fruits (Knight 1986) it may be predicted that alien plants that become invasive in the southwestern Cape are more likely to be suitable for bird-dispersal than mammal-dispersal. Nevertheless, similarities in the proportions of some fruit colours (e.g. red) are sufficiently similar to suggest convergence in the morphology of fleshy fruits, irrespective of phylogenetic or geographical origin (Knight 1986).

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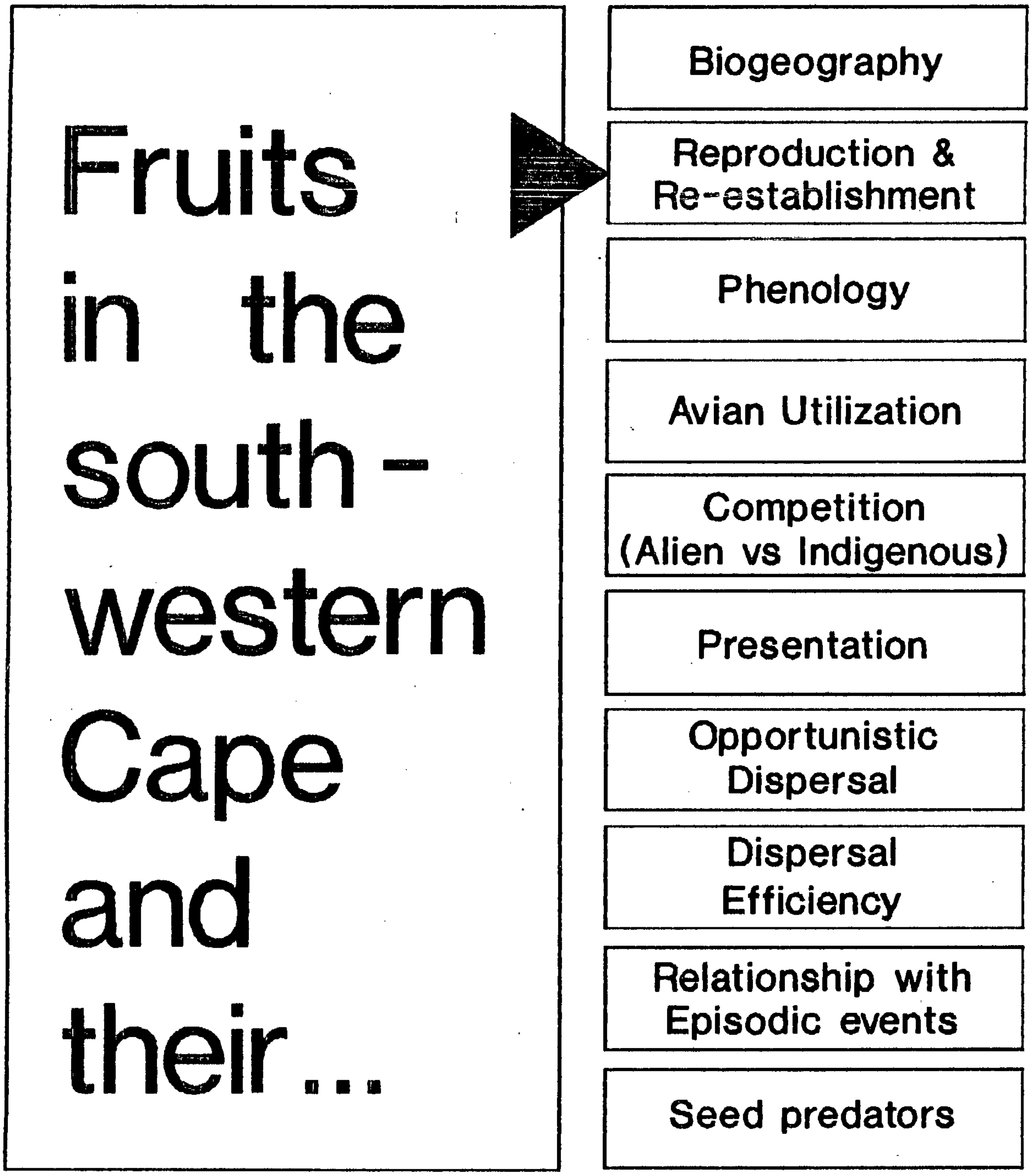
CHAPTER 2



Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Reproductive strategies of plants in relation to their re-establishment in the vegetation of the southwestern Cape, South Africa

Contents

Reproductive strategies of plants in relation to their re-establishment in the vegetation of the southwestern Cape, South Africa

Abstract

Recruitment of plant species, with particular attention to bird-dispersed reseeding species, was monitored in an artificially cleared area formerly dominated by Mountain Fynbos vegetation of the southwestern Cape region of South Africa. Sampling was undertaken using 62 1 x 1 m^2 quadrats, 27 of which were positioned under potential avian perches. Approximately 179 plant species were recorded with 154 occurring in quadrats not under perches and 123 occurring in quadrats under perches. Bird dispersed reseeding species accounted for 2,8% of the total number of recolonizing species, but were more abundant in areas under perches (4,1%). Abundance of vertebrate dispersed plants was also better represented in sites occurring under perches than not under perches (2,2% and 0,6% of all plants recorded respectively). Woody and semi-woody, non-vertebrate dispersed species had the highest representation of the total colonizing flora (38,5%). All colonizing species found were categorized into a reproductive/re-establishment classification, and the results are interpreted in the light of current theory on plant succession.

To be submitted to <u>Vegetatio</u>

Introduction

Disturbance processes are fundamental to understanding plant communities and explaining species richness patterns (see Pickett & White 1985). Theories describing and predicting the ecological changes in plant communities following a disturbance have rarely examined the individual ecology of plant species (Clements 1916; Egler 1954; Drury & Nisbet 1973; Connell & Slatyer 1977). A knowledge of both seed bank dynamics, potential for vegetative reproduction and the propagule dispersal of dominant species are essential before such predictions can be justified. In this respect the succession models based on vital attributes (Noble & Slatyer 1980) have partly overcome such deficiencies. However, Noble & Slatyer (1980) did not consider the mode of dispersal (biotic or abiotic). Such an omission may be significant, e.g. the presence of a large, colourful pseudaril in Acacia cyclops seeds can result in a greater potential for dispersal over A. saligna (Macdonald et al. in prep; Knight & Macdonald in prep.; Chapter 7). This paper aims to test if differences in the floral composition occur in the colonization of sites below and not below suitable avian perches. In addition, modifications to the vital attributes scheme (Noble & Slatyer 1980) were identified and applied to all plant species found recolonizing these sites.

Materials and Methods

A 0,33 ha site was artificially cleared of above ground vegetation to simulate plant succession occurring in Mountain Fynbos areas (sensu Moll et al. 1984) adjacent to a remnant Afromontane Forest in Fernkloof Nature Reserve, Hermanus (34° 25'S; 19° 16'E). All vegetation, except for a few fully grown Virgilia oroboides/divaricata and Kiggelaria africana trees was cleared manually. The colonization of the area by all plant species was monitored on eight occasions from March 1984 to July 1985, using 62 permanent 1 x 1 m^2 quadrats. Twenty-seven of the quadrats were under potential avian perches (telegraph lines and fully grown K. africana and V. oroboides/ divaricata trees). Two additional quadrats were netted to prevent both herbivory and seed deposition and acted as control plots. For each species in each quadrat, the number of individual plants, the mode of regeneration (reseeding or resprouting), and the ability to withstand herbivory were recorded. Two pioneer bird dispersed plants species were identified (Chrysanthemoides monilifera and Kiggelaria africana) and their abundance was recorded monthly until September 1985.

Using the above basic information, together with other field knowledge, all plant species were categorized according to the classification scheme presented in Table 1. This scheme represents a modification of Noble & Slatyer's (1980) classification and has been found to be suitable for application to local vegetation (Knight et al. 1987). Each plant species was classified with respect to the longevity of the plant and time to reach reproductive maturity (L), the availability and dispersal potential of seed propagules (S and D respectively), and the ability to reproduce vegetatively (V). All plant species were classified by growth form: woody (reseeding, resprouting, vertebrate and non-vertebrate dispersal), herbaceous, graminoid (alien and indigenous grasses, restios and cyperaceous spp.) and geophytes (including dicotyledonous plants). Seasonal representation of species richness, plant abundance and growth form for perch and non-perch sites were analysed using correspondence analysis (Greenacre 1984; Underhill & Peisach 1985).

Results

General trends

Both the number of species and the total abundance of plants showed an increase from June 1984 to July 1985 (Figure 1). A greater total plant abundance was recorded for sites not under perches than sites under perches. This may reflect the greater number of quadrats in areas not under perches (35 vs 27). The total number of species is only marginally higher in sites not under perches. Within three months of clearing almost 100 plant species were recorded in both sites under and not under perches (Figure 1). At the end of 15 months 154 plant species were recorded from sites not below perches and were represented by ca 2876 individual plants (Table 2). Sites below perches had 123 plant species represented by ca 1976 individual plants.

Table 1 Classification used for identifying patterns of reestablishment in Mountain Fynbos plants found colonizing a cleared one-third ha site Fernkloof Nature Reserve.

Attributes	Symbols	Categories	Symbols
Maturity & Longevity	L	*Time required to reach first seed production	a = annual s = short period m = medium period l = long period
		+Potential life span of parent plant	a = annual s = short period m = medium period l = long period
+Seed availability	S		c = long-lived and canopy stored s = long-lived and soil stored o = short-lived soil and canopy stored cs = long-lived canopy and soil stored
+Vegetative reproduction	V		a = adults survive j = juveniles survive o = neither adults nor juveniles survive i = plants survive intact aj = adults and juveniles survive
+Dispersal potential	D		b = biotically dispersed a = abiotically dispersed o = non-dispersive

* written as superscript + written as subscript

Table 2 Percentage occurrence of total number of species and individual plants in 62 1 m² quadrats, 27 of which were sited under perches and 35 in areas not under perches. Plant species are arranged in 10 suites, based on life-form, seed-dispersal and regeneration mechanism.

Species suites	% species			% abundance		
	Total N=179	Under perches N=123	Not under perches N=154	Total N=4852	Under perches N=1976	Not under perches N=2876
Woody and semi-woody re-seeding vertebrate-dispersed	2,8	4,1	2,6	1,2	2,2	0,6
Woody and semi-woody re-sprouting vertebrate-dispersed	2,2	2,4	2,6	1,5	1,7	1,4
Woody and semi-woody re-seeding and non-vertebrate-dispersed	38,5	43,9	37,7	37,1	36,4	37,6
Woody and semi-woody re-sprouting and non-vertebrate-dispersed	3,4	4,1	3,2	0,7	0,5	0,9
Geophytes	18,4	15,5	19,5	18,2	14,2	20,9
Herbaceous annual and perennial re-seeding and re-sprouting	21,8	13,8	22,1	9,7	9,5	9,9
Grasses (introduced)	1,1	1,6	1,3	15,4	16,7	14,4
Grasses (indigenous)	3,4	4,1	3,9	4,3	3,3	4,9
Restionaceae	2,8	3,3	1,3	7,0	9,9	5,1
Cyperaceae	3,9	4,9	3,9	2,6	3,7	1,9
Unclassified	1,7	2,4	1,9	2,3	1,9	2,6

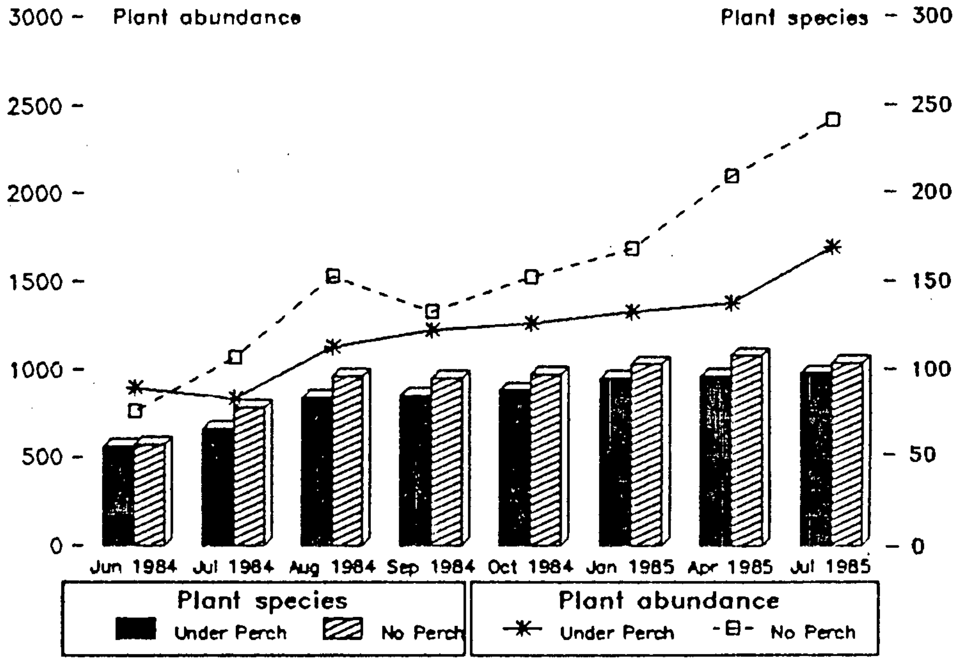


Figure 1 Observed regeneration of both plant species and abundance of individuals at Fernkloof Nature Reserve, Hermanus, during 1984 and 1985.

Seasonality and growth forms

The seasonal occurrence of basic growth forms: woody plants, herbaceous plants, graminoids (including Restionaceae and Cyperaceae) and geophytes (dicots and monocots) showed similar seasonal patterns both under and not under perches (Figures 2 and 3). Woody plants showed a continuous increase in abundance, whereas the other growth forms had cyclical patterns. Three months after the clearing, geophytes were in greatest abundance in areas not under perches, and graminoids in areas under perches. From August onwards woody plants were generally most abundant. Graminoid plants peaked during early summer; largely a reflection of the annual cycle of the alien grass Briza maxima. Herbaceous plants were scarce and peaked during spring (August). Both herbaceous plants and geophytes were more abundant in 1985 than in 1984.

Within the woody flora (Figure 4) the majority of plants were non-vertebrate dispersed and reseeding. Vertebrate dispersed plants were evenly represented between reseeding and resprouting plants. Resprouting and non-vertebrate dispersed species were the least abundant, but their numbers were found to increase markedly during 1985.

Within the graminoid flora (Figure 5), the majority of plants were alien grasses (ca 98% being Briza maxima) and maximum abundance was found in October. Peak abundance of restioids occurred in January. The reduced abundance of restioids found in April was due to foraging (particularly at Elegia filacea) by baboons Papio ursinus. Cyperaceous plants (sedges) were the only graminoid that showed a continuous increase in abundance during the experiment, even though the most common species is an annual (Isolepis antarctica, Appendix 1). The frequencies of plant species occurring in each of these suites of species, based on life-form, seed-dispersal and regeneration mechanism (Table 2) were found not to vary significantly between perch and non-perch sites ($X^2 = 5,82$; df = 9; ns). However, the abundance of individual plants representing these suites of species does vary significantly between perch and non-perch sites ($X^2 = 123,00$; df = 9; $P < 0,01$).

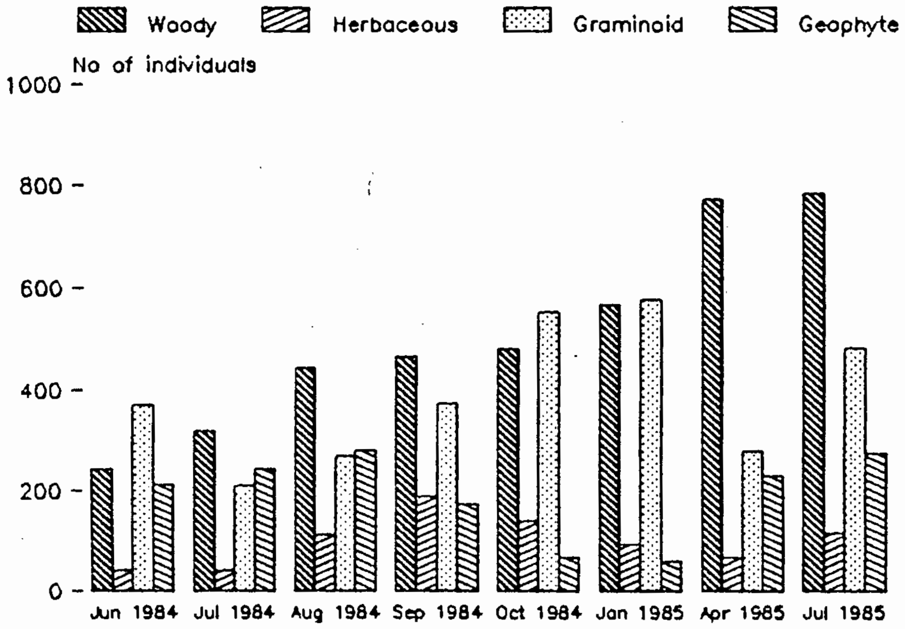


Figure 2 Observed regeneration of plants by growth form for sites below perches at Fernkloof Nature Reserve, Hermanus.

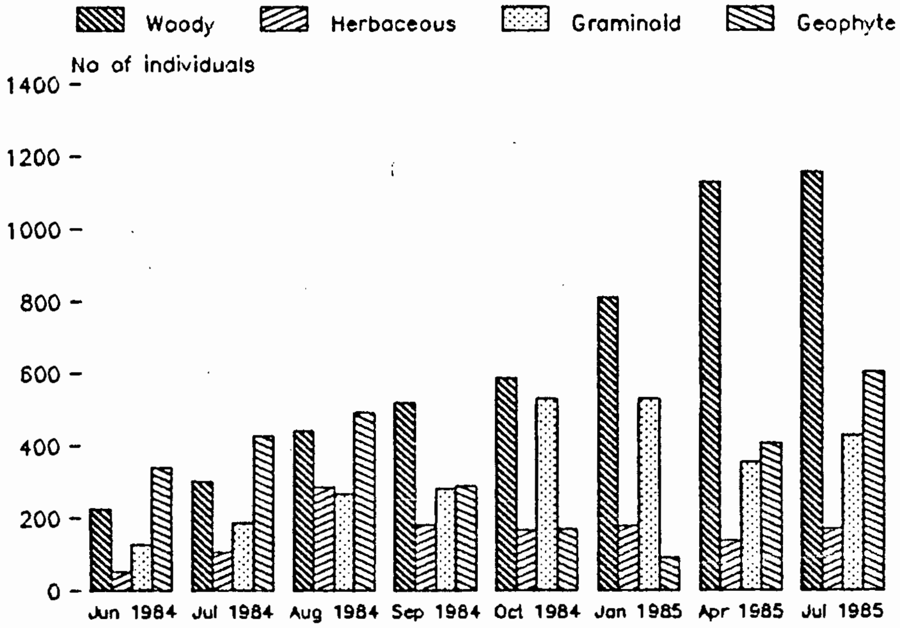


Figure 3 Observed regeneration of plants by growth form for sites not below perches at Fernkloof Nature Reserve, Hermanus.

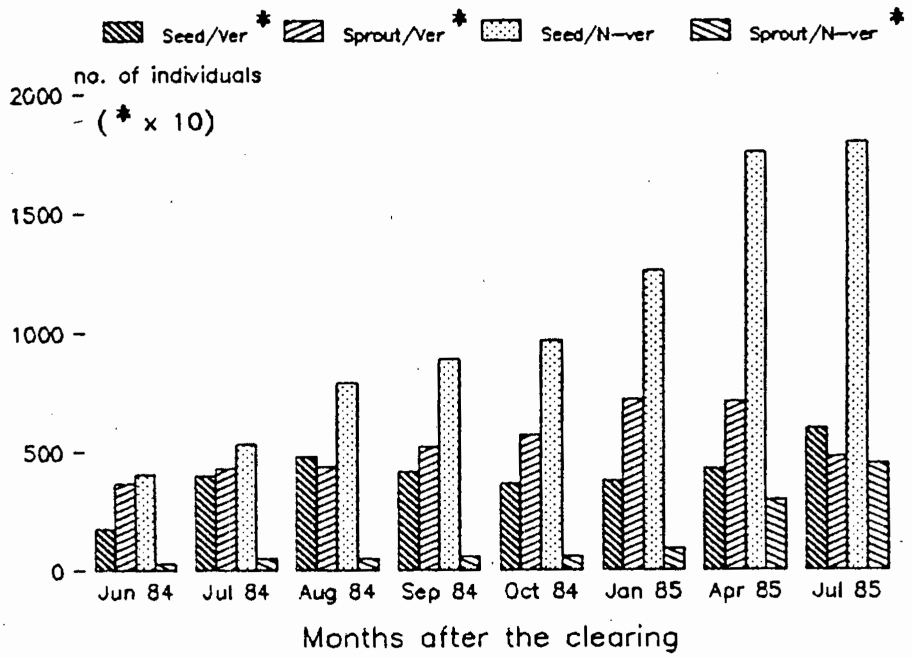


Figure 4 Obseved regeneration of all woody plants at Fernkloof Nature Reserve, Hermanus.

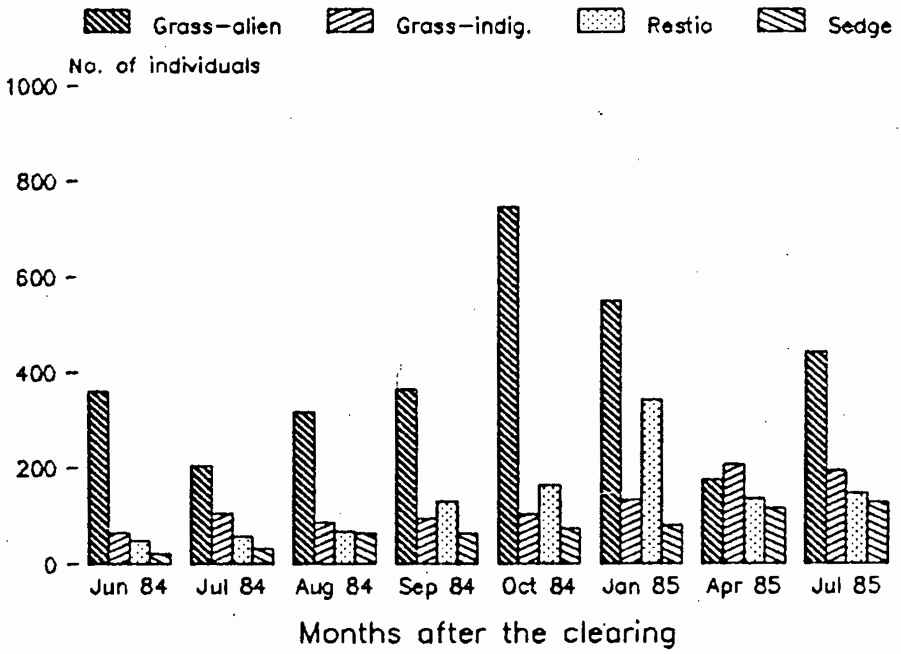


Figure 5 Observed regeneration of all graminoid plants at Fernkloof Nature Reserve, Hermanus.

Bird dispersed species

The recruitment of the two bird dispersed pioneer species (Chrysanthemoides monilifera and Kiggelaria africana) was greater in sites under perches (Figures 6 and 7). Recruitment of C. monilifera commenced in June and maximum seedling densities occurred in July 1984 and May 1985 (41 and 48 plants per 100 m^2 respectively) for sites under perches. For sites not under perches maximum seedling densities were recorded in the same month but were considerably lower (20 and 14 seedlings per 100 m^2 respectively). Seedling recruitment of C. monilifera ceased from August 1984 until the following year's recruitment in May 1985 (Figure 6). Seedling mortality in C. monilifera was restricted to the immediate post-germination periods (Figure 6). The recruitment of Kiggelaria africana seedlings commenced in June 1984 for sites under perches, and in July 1984 in sites not under perches (Figure 7). A maximum density of 104 K. africana seedlings per 100 m^2 occurred in August 1984 in sites under perches, and in July 1984 in sites not under perches (23 plants per 100 m^2). Maximum seedling mortality in sites under perches occurred soon after germination and again in late summer. No new seedlings were observed between October 1984 and the next years's recruitment in July 1985. Perching sites appeared to facilitate the seedling recruitment of bird dispersed plants and confirmed the hypothesis that compositional changes in plant assemblages occur in the presence of such perches.

Vital attributes

Twenty-five suites of vital attributes were identified and accounted for over 95% of plant species and 99% of all plants found in the 62 quadrats. The specific vital attributes appropriate for each plant species (Appendix 1) are based on the reproductive biology of plants found in this particular experiment. Different forms of disturbances can result in a different suite of vital attributes occurring for the same species. Data on seed banks (particularly if persistent soil-storage occurs) and the dispersal potential of propagules are particularly difficult to obtain, and therefore their categorization largely reflects value judgements. Without this type of information, no predictive understanding of successional changes in total plant assemblages occurring in fynbos vegetation can be achieved. The

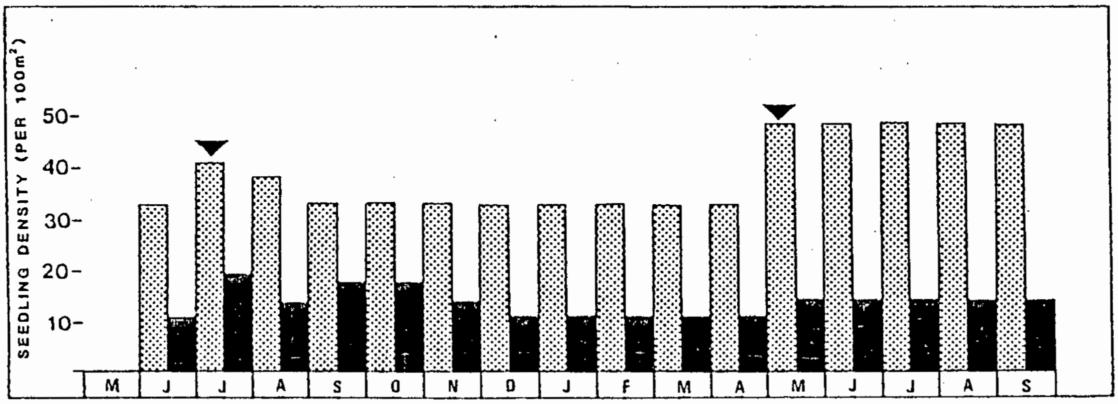


Figure 6 Monthly (May 1984 to September 1985) densities of *Chrysanthemoides monilifera* seedlings in sites under potential bird perches (shaded histogram) and not under perches (solid histogram) at Fernkloof Nature Reserve, Hermanus. The arrows indicate the two winter recruitment seasons.

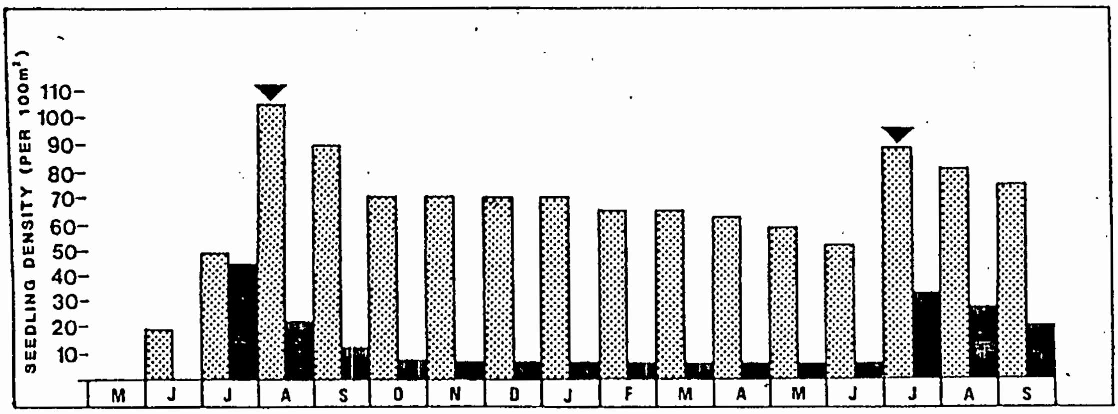


Figure 7 Monthly (May 1984 to September 1985) densities of *Kiggelaria africana* seedlings in sites under potential bird perches (shaded histogram) and not under perches (solid histogram) at Fernkloof Nature Reserve, Hermanus. The arrows indicate the two winter recruitment seasons.

following categories of vital attributes were identified as contributing most significantly (Table 3) to the total recolonizing flora:-

$L_m^s \quad S_s \quad V_a \quad D_o$

This suite of vital attributes accounted for approximately 11 % of the flora and was represented in similar proportions in both perch and non-perch sites (Appendix 2). These species include rapidly growing, perennial plants that have a combination of soil stored seeds and an ability to resprout once reproductive maturity is reached. The frequent presence of an elaiosome such as found in many sedges suggested a short distance dispersal (Bond & Slingsby 1983). Many <u>Ficinia</u> seedlings succumbed to herbivory by tortoises, antelope and invertebrates, and in their juvenile state are unlikely to overcome such disturbances. Some geophytes and many orchids were included in this category. Although most orchids have very fine seeds their highly localized distribution may reflect poor dispersal to sites suitable for establishment except in the immediate vicinity of parent plants.

$L_a^s \quad S_s \quad V_o \quad D_o$

This suite of vital attributes is represented by virtually all the annual plants and is particularly well represented at the abundance level (Table 3) by the common alien grass <u>Briza maxima</u> found throughout the experiment. Apart from <u>Briza maxima</u>, this suite of species contribute little in way of biomass and species richness, but are well represented with respect to number of families (Cyperaceae, Poaceae, Campanulaceae, Caryophyllaceae, Crassulaceae and Gentianaceae). Most of these plant species will have an early, but ephemeral appearance following a disturbance and are likely to be highly reliant on persistent seed banks. Judging by both their pattern of establishment and the structure of the propagules these plants appear to lack adaptation for long-distance dispersal and establishment, yet many of these species are widespread. This largely reflects our lack of understanding of plant dispersal processes.

Table 3 Percentage occurrence of the total number of species and individual plants in 62 1 m² quadrats, 27 of which were sited under perches and 35 in areas not under perches. Plant species are arranged in suites based on the modified vital attributes classification presented in Table 1.

Vital attributes				% species			% abundance		
				Total N=179	Under perches N=123	Not under perches N=154	Total N=4852	Under perches N=1976	Not under perches N=2876
L_m^m	S_c	V_a	D_o	2,2	2,4	0,6	0,6	0,6	0,6
L_m^m	S_c	V_a	D_o	1,7	1,6	1,9	0,8	0,9	0,7
L_m^m	S_o	V_a	D_a	0,6	0,8	0,6	1,9	1,5	2,2
L_m^m	S_o	V_{aj}	D_o	1,7	2,4	1,9	1,1	1,7	0,7
L_m^m	S_o	V_{aj}	D_b	2,2	1,6	1,9	1,3	1,4	1,2
L_m^m	S_s	V_a	D_o	7,3	9,8	7,1	5,5	7,0	4,4
L_m^m	S_s	V_o	D_o	3,4	4,1	3,2	2,5	1,8	3,0
L_m^s	S_s	V_a	D_o	0,6	0,8	0,6	5,1	6,2	4,3
L_a^s	S_o	V_o	D_a	2,8	4,1	2,6	2,5	4,3	1,3
L_a^s	S_s	V_o	D_a	1,1	1,6	1,3	0,4	0,3	0,5
L_a^s	S_s	V_o	D_o	8,4	7,3	8,4	16,4	18,0	15,3
L_m^s	S_o	V_a	D_a	2,2	0,8	2,6	0,8	0,7	0,9
L_m^s	S_o	V_a	D_o	5,0	4,9	5,2	6,9	6,3	7,3
L_m^s	S_o	V_{aj}	D_o	7,3	5,7	8,4	8,0	6,4	9,1
L_m^s	S_o	V_o	D_a	6,7	9,8	5,8	4,4	4,6	4,3
L_m^s	S_s	V_a	D_o	11,7	11,4	11,0	7,3	4,4	9,3
L_m^s	S_s	V_{aj}	D_o	1,1	1,6	0,6	1,6	0,1	2,6
L_m^s	S_s	V_o	D_o	6,1	6,5	5,8	14,4	19,9	10,6
L_m^s	S_o	V_a	D_a	2,8	2,4	3,2	1,1	0,9	1,2
L_s^s	S_o	V_{aj}	D_o	1,7	1,6	1,3	1,0	0,5	1,4

Table 3 continued

				% species			% abundance		
				Total N=179	Under perches N=123	Not under perches N=154	Total N=4852	Under perches N=1976	Not under perches N=2876
L_s^s	S_o	V_o	D_a	2,2	3,3	2,6	1,9	2,1	1,7
L_s^s	S_s	V_a	D_a	2,2	3,3	2,6	1,9	1,7	2,0
L_s^s	S_s	V_a	D_o	4,5	0,8	4,5	3,7	2,7	4,4
L_s^s	S_s	V_o	D_o	8,4	8,1	9,1	8,0	4,8	10,2
Other species				3,9	0,8	4,5	0,5	0,7	0,3

L_m^s S_s V_o D_o

This suite of vital attributes represents the largest number of species and are reseeding but non-vertebrate dispersed (Table 2). Species with this set of vital attributes are found in Ericaceae, Fabaceae, Rubiaceae and Thymelaeaceae and common genera include Anthospermum and Aspalathus. Many of the species included in this group have seeds with elaiosomes and are soil-stored.

Since this suite of woody species have little or no potential for resprouting they rely heavily on producing large quantities of soil-stored seed. It was apparent that germination following a disturbance was not synchronized, but occurred in a series of recruitment waves. The size of seed bank and lack of synchrony in germination ensures that this suite of species will remain persistent given very frequent disturbance regimes and therefore are frequently dominant in highly disturbed fynbos vegetation.

L_s^s S_s V_o D_o

This suite of vital attributes is represented by species that tend to be short-lived and heavily reliant on persistent soil-stored seed banks, and also occurs in a variety of plant families including Apiaceae and Aizoaceae, Asteraceae (Corymbium and Othonna), Mesembryanthemaceae and Campanulaceae. In successional processes these species occupy periods between recruitments of annual plants and the woody, reseeding plants. Reproductive maturity is reached within the year, but the plants rarely exceed three years in total lifespan. No apparent adaptations for long-distance dispersal were found, but this group of species is often found after considerable disturbances such as fires and even after alien vegetation has been cut down and burnt. This suggests that large, persistent soil-stored seed banks exists.

Correspondence analysis

Patterns of plant assemblages found at the eight different sampling periods were distinct for sites below and not below perches, based on both

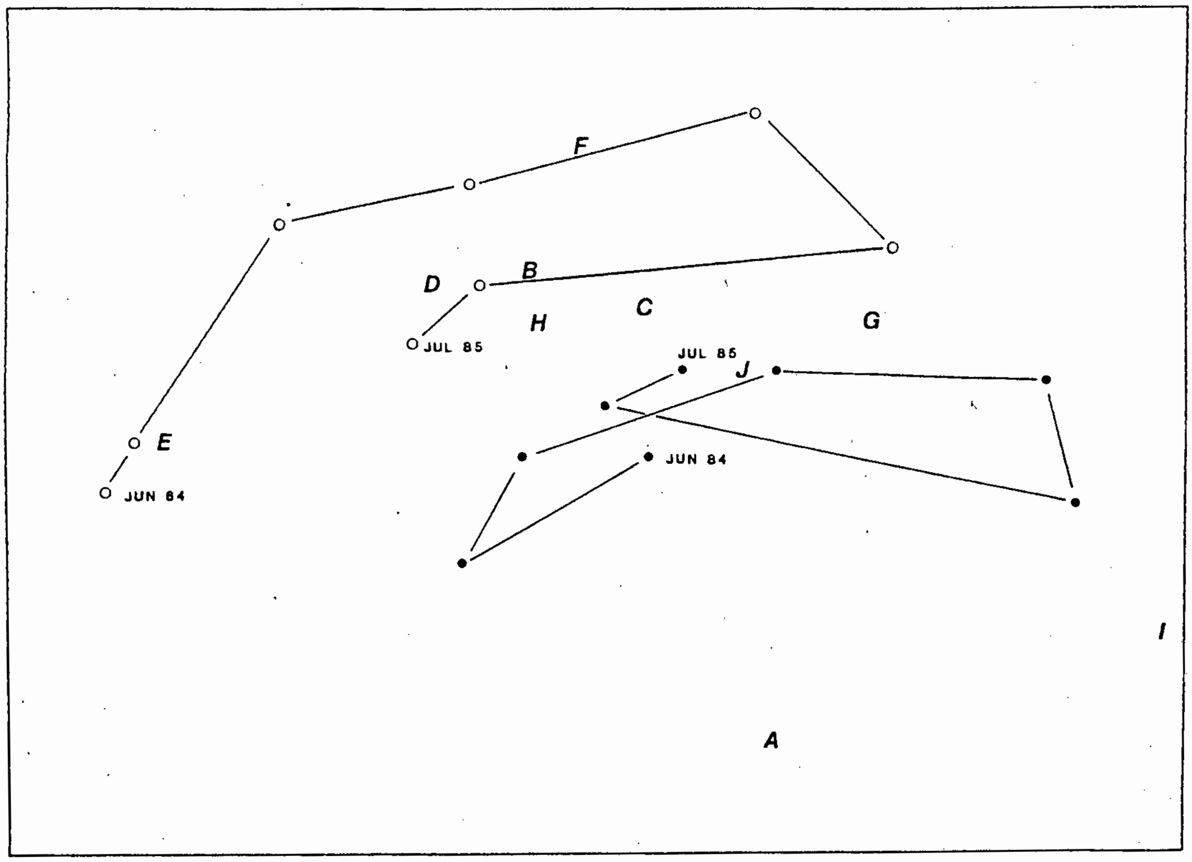


Figure 8 A correspondence analysis of all re-establishing plant species by growth form for both sites under perches (dots) and not under perches (circles) during June 1984 to July 1985. A = woody, reseeding and vertebrate dispersed plants, B = woody, resprouting and vertebrate dispersed, C = woody, reseeding and non-vertebrate dispersed, D = woody, resprouting and non-vertebrate dispersed, E = geophytes, F = herbaceous, annual and perennial plants, G = introduced graminoids, H = indigenous graminoids, I = restioids, J = cyperaceous plants.

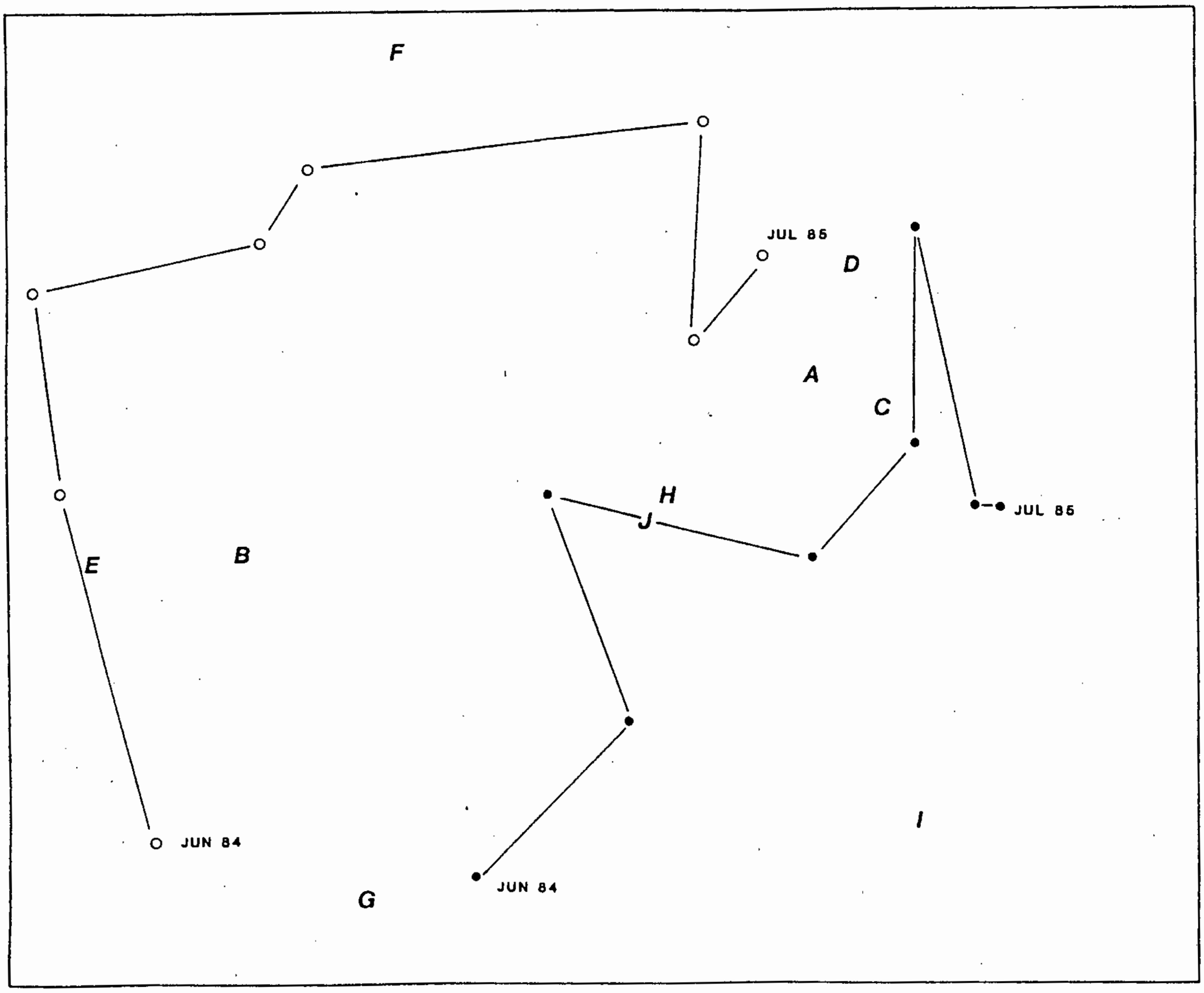


Figure 9 A correspondence analysis of all re-establishing plants by growth form for both sites under perches (dots) and not under perches (circles) during June 1984 to July 1985. A = woody, reseeding and vertebrate dispersed plants, B = woody, resprouting and vertebrate dispersed, C = woody, reseeding and non-vertebrate dispersed, D = woody, resprouting and non-vertebrate dispersed, E = geophytes, F = herbaceous, annual and perennial plants, G = introduced graminoids, H = indigenous graminoids, I = restioids, J = cyperaceous plants.

representation of species and their abundance (Figures 8 and 9). Reseeding and vertebrate dispersed and restionaceous plants were markedly associated with perch sites (Figure 8). Geophytes were the earliest recruits, with herbaceous and graminoid plants following soon after. Of the woody plants, resprouting and vertebrate dispersed species were the earliest recruits, whereas both groups of reseeding species (vertebrate and non-vertebrate dispersed) appeared only during and after the rainy winter season. Resprouting and non-vertebrate dispersed species appeared last. With respect to the overall pattern of succession there is a pronounced pattern created by the annual cycles of geophytes, herbaceous and graminoid plants and is best represented by the loop created on the ordination plot (Figure 8) for sites under perches.

Discussion

Patterns of plant occurrence following a disturbance are graphically represented in Figure 10 and are based on both the succession study and empirical observations before and after two fires (December 1985 and February 1986). The curves are generalized, and both vertical and horizontal exaggeration can either be enhanced or compressed depending on the precise nature of the vegetation and the disturbance. Periods of maximum reproductive effort are identified by shaded areas, whereas inputs to seed banks are identified by arrows. Solid arrows represent either transient or persistent seed banks whereas the open arrows represents only transient seed banks. The attempts to use vital attributes clearly identified the need for greater knowledge of seed banks (Pierce 1987). Even the basic datum on whether seed banks are transient or persistent is little more than educated guesswork. The patterns presented (Figure 10) do not include the dispersal potential of propagules since plant establishment following long distance propagule dispersal is largely stochastic.

Little evidence was found for facilitation succession (Clements 1916), except for the presence of perching sites prior to any significant recruitment of reseeding bird dispersed plants (Figure 10). Regular and frequent disturbances found in fynbos communities (Cowling et al. 1987) may prevent facilitation succession.

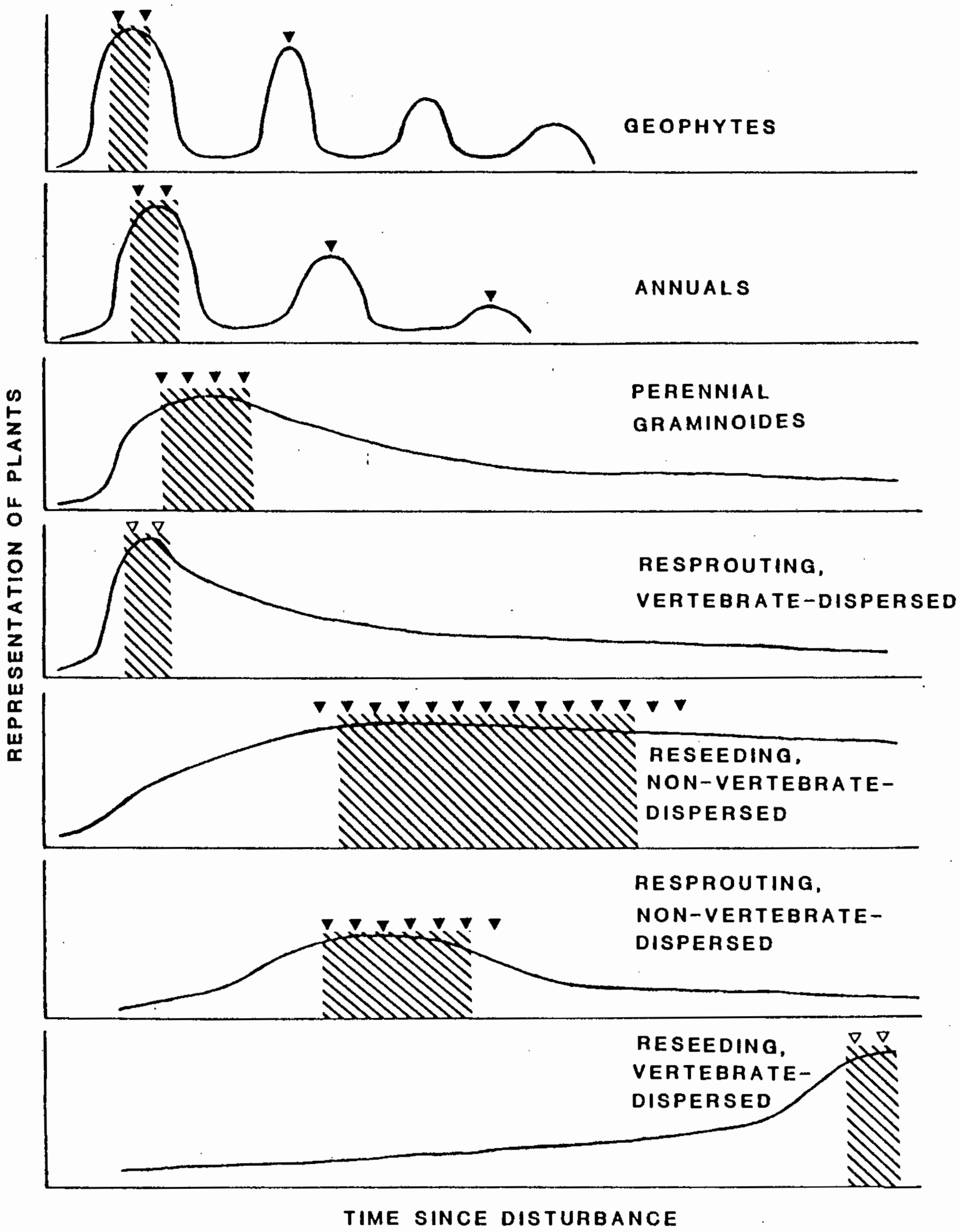


Figure 10 Hypothesized temporal patterns for the re-establishment of different growth forms in Mountain Fynbos vegetation. Shaded areas represent periods of maximum reproductive effort. A solid arrow represents seed inputs into either a transient or a persistent seed bank. An open arrow represents seed inputs into transient seed banks only.

Although recruitment of different growth forms were seasonal (Figures 8, 9 & 10), all were present within 15 months of the disturbance. This pattern is consistent with Egler's (1954) concept of "initial floristic composition". Apparent compositional turnover was the product of differential development of biomass occurring in each growth form (Peet & Christensen 1980; Kruger & Bigalke 1984; Cowling & Pierce in prep.). Since pre- and post-disturbance plant communities differed in composition, and germination was usually restricted to immediate post-disturbance periods, no clear autosuccession (Hanes 1971) was identified (see van Wilgen & Kruger 1981; Hoffman _et_ _al_. 1987; Cowling & Pierce in prep.).

A variety of plant responses were recorded (Appendix 1) even within individual growth forms (e.g. geophytes possessing dispersive and non-dispersive propagules). Consequently the lack of variety in post-disturbance responses reported by Richardson & van Wilgen (1986) and Le Maitre (unpublished) may have reflected incomplete knowledge of the plant's reproductive biology and/or a lack of refinement in the original Noble & Slatyer (1980) scheme.

The seasonal presence of geophytes is represented by a cyclical pattern of waves with diminishing amplitudes (Figure 10). The large initial recruitment of geophytes (Figure 2) usually evident in Mountain Fynbos (Taylor 1978; Kruger 1977, 1981; Kruger & Bigalke 1984) was sustained for a comparatively long post-disturbance period (Figure 10). Similar persistence of geophytes has also been observed in Lowland Fynbos (Hoffman _et_ _al_. 1987). Reappearance of geophytes may occur in the absence of disturbances and when new gaps have been created by senescent woody plants. However, the species composition may vary from that occurring immediately post-disturbance (e.g. _Eriospermum_ _nanum_ is more common in moribund vegetation than immediately post-disturbance, pers. obs).

The appearance of geophytes are not necessarily restricted to vegetative regeneration, since the recruitment of _Ixia_ _dubia_ was partly from soil-stored seed banks. Presence of both vegetative reproduction and long lived soil-stored seed banks may confer complete immunity to both seasonality and frequency of disturbance. Geophytes without a potential for long distance dispersal are likely to put maximum reproductive effort into the immediate post-dispersal period. This reproductive effort should result in their propagules having longer periods for establishment until dominance by other growth forms occurs. In contrast, geophytes with a potential for long distance dispersal (e.g. *Aristea*) can spread their reproductive effort in time since the propagules are widely dispersed and can colonize newly created disturbances.

Annual plants are largely reliant on persistent soil-stored seed banks ('in situ' resilience) rather than effective long-distance propagule dispersal (resilience 'by migration') (*sensu* Grubb & Hopkins 1986). The pattern of recolonization in annual plants is represented by a series of waves (Figure 10). The species composition within these waves is constant, unlike that found in Chaparral vegetation (Keeley *et al*. 1981). Their post-disturbance presence is smaller, less persistent, but later than for geophytes (*cf*. Kruger & Bigalke 1984). Replenishment of seed banks will, however, probably occur after each annual appearance. Increasing frequencies of disturbance will promote an increase in their dominance through both the availability of soil nutrients and lack of competition for space from perennial plants, but will be restricted to winter and spring months, since summer months are unlikely to provide sufficient moisture for maintaining growth. The development of perennial plants will suppress the recruitment success of both annual plants and geophytes and therefore their maximum reproductive effort will be restricted to short post-disturbance periods. Indigenous, annual plants were comparatively uncommon on both a species and abundance criteria in this study, whereas introduced, herbaceous annual plants were abundant; a situation also found in low altitude Chaparral (Keeley & Sonderstrom 1986).

Perennial graminoids which include sedges (Cyperaceae), grasses (Poaceae) and restioids (Restionaceae) will usually appear latter than geophytes or annuals. If the disturbance occurs during late winter or early spring rather than late summer or autumn, then these plants may appear earlier than either annuals or geophytes, although maximum reproductive effort will still be later and spread over a much longer time. Persistent soil-stored seed banks are commonly associated with these species, and may prevent extinction in the event of repeated frequent disturbances. However, their resilience will be less than either geophytes or annual plants.

Resprouting vertebrate dispersed species generally produced flowers and fruit shortly after fire and thereby exploited the post-burn release of nutrients (van Wilgen & Le Maitre 1981; Brown & Mitchell 1986; Stock & Lewis 1986). Similar re-establishment patterns have been recorded for Chaparral (Keeley & Keeley 1984; Keeley 1986). Unlike Chaparral, local plants are restricted to a single fruit season between fires and their biomass decreases after fruiting (Figure 10). Also, individual sizes of fleshy fruits vary greatly among local species with *Myrica quercifolia* fruits being *ca* 3 mm and an unnamed *Colpoon* sp. (referred to as *Osyris abyssinica* var. *speciosa* by Hill 1915) being *ca* 18 mm in length. Local plants are also variable with respect to patterns of fruit ripening and dispersal agents. Species such as *Protasparagus compactus* (T.M. Salter) Oberm. and *Rhus angustifolia* L. ripen their fruit quickly and are eaten and dispersed by birds. The *Colpoon* sp. also produces ripe fruit within a year, and much fruit is eaten and possibly dispersed by baboons. Initial fruit development in *Euclea polyandra* is also rapid, but final ripening is delayed for many months (18-20). Since these latter fruits are brown in colour, have a noticeable scent and are presented below the branches and about 180 mm above the ground, it is assumed that they are adapted for rodent dispersal (Van der Pijl 1972). Delayed fruit ripening may be synchronized with the re-establishment of the surrounding vegetation which should provide rodents with protection from predators.

As in Chaparral (Keeley 1986), no persistent soil-stored seed banks occurs in these resprouting, vetebrate-dispersed plants, but a few seeds germinate after fruiting. Recruitment of these plants is subject to high mortalities and requires long disturbance free periods for the development of lignotubers (Keeley 1986). These species are resilient to fairly frequent fires (Keeley 1986) but their presence decreases with too frequent fires (see Zelder *et al*. 1983). This is possibly due to stress imposed by the nutrient deficiencies of Mountain Fynbos soils (Kruger 1979; Lambrechts 1979; Campbell 1983). This nutrient imposed stress may explain the absence of reproductive effort following bushcutting (pers. obs).

Reseeding, but non-vertebrate dispersed species, are easily the most abundant in fynbos (Table 2; Richardson & van Wilgen 1986). This suite of species had the greatest variation with respect to vital attributes (Appendix 1). Initial recruitment was primarily from canopy-stored seeds on serotinous plants (e.g. *Protea*), with subsequent recruitment from both soil-stored seed banks (e.g. *Roella incurva*) and from plants with very dispersive seeds (e.g. *Pelargonium* spp.). There is a steady increase in biomass, and due to the variety of plant species, a long period for maximum reproductive effort. Since canopy and soil-stored seed banks exist, resilience to frequent disturbances is variable depending on the plant species. Plants with large seed banks that are not completely exhausted after a disturbance will be the most resilient (*Roella incurva* and *Passerina* spp.) (Pierce 1987) whereas species with canopy stored seed banks will be eliminated if another disturbance occurs before reproductive maturity is achieved. Canopy stored seed banks are locally most common in Proteaceae (Lamont *et al*. 1985; Le Maitre 1987) and appear to be adapted to fire frequencies of *ca* 12 - 15 years (Bond 1980; Kruger 1981). Extended fire-free intervals adversely effect recruitment due to loss of seed viability (Bond 1985). Even within canopy stored Proteaceae, resilience to disturbance is variable and comparatively low for weakly serotinous species such as *Protea repens* (Jordaan 1965; Cowling 1987b) which rapidly lose seed viability with time (Coetzee 1984; Myburg & Rust 1975). Optimal seedling recruitment in *P. repens* only occurs if the disturbance follows directly after the annual seed production (Jordaan 1965, 1982).

The recruitment of bird-dispersed species under potential avian perches was the only evidence for facilitation succession. Although a few seedlings were observed away from perches, few were able to establish themselves naturally. Suitable avian perches are likely to be scarce in fynbos and to be restricted to relatively mature vegetation. However, seedling establishment is likely to be restricted to canopy gaps which are relatively scarce in fynbos. Senescent vegetation may provide gaps suitable for the establishment of these species. Since the seedlings of these species are not resilient to fire, establishment requires comparatively long disturbance free periods. Once maturity is reached their resilience to fire is enhanced since many of the species are then able to resprout.

The general scarcity of trees in fynbos (Moll et al. 1980), particularly pioneers, may severely limit the potential for forest species to colonize fynbos sites. Abandoned orchards in mediterranean France acted as nuclei for the establishment of other bird-dispersed plant species (Debussche et al. 1982). Livingston (1972) showed that stones which are used by birds as perching sites are important in the establishment of junipers. Rocky outcrops in fynbos vegetation frequently support bird-dispersed plants. However, this pattern of occurrence may reflect protection from fire rather than suitability for perching.

Successional processes

Cowling & Pierce (in prep.) report a succession pattern (grassland through fynbos to thicket) that is best described by floristic relays. Bird-dispersed plants are restricted to the later stages of succession (30 - 50 years post-disturbance). Vegetation re-establishment at Fernkloof suggests that succession is best described by the "initial floristic composition" model until senescence in fynbos vegetation facilitates establisment of bird-dispersed plants through the provision of both perching sites and gaps in the canopy. Autosuccession (Hanes 1971) may occur in individual fynbos species, but is not common. Individual species rather than plant communities should be classified with respect to succession models.

Figure 11 summarizes hypothesized relationships between disturbance regimes, soil nutrients and type of succession that may occur in the local vegetation. Succession in the form of "initial floristic composition" should be favoured under fairly frequent disturbance regimes and low soil nutrient status and is typified by the re-establishment of reseeding Protea and Erica spp. in Mountain Fynbos. Soil nutrients released are likely to be quickly exhausted with the first wave of colonizing species. Consequently, continued colonization by plants cannot be maintained. Where availability of soil nutrients is greater autosuccession processes should be more common. This is typified by the continuous re-establishment of Elytropapus rhinocerotis (L.f.) Lees. that occurs in disturbed Renosterveld. Under these circumstances, soil nutrients are available for the establishment of plants during inter-

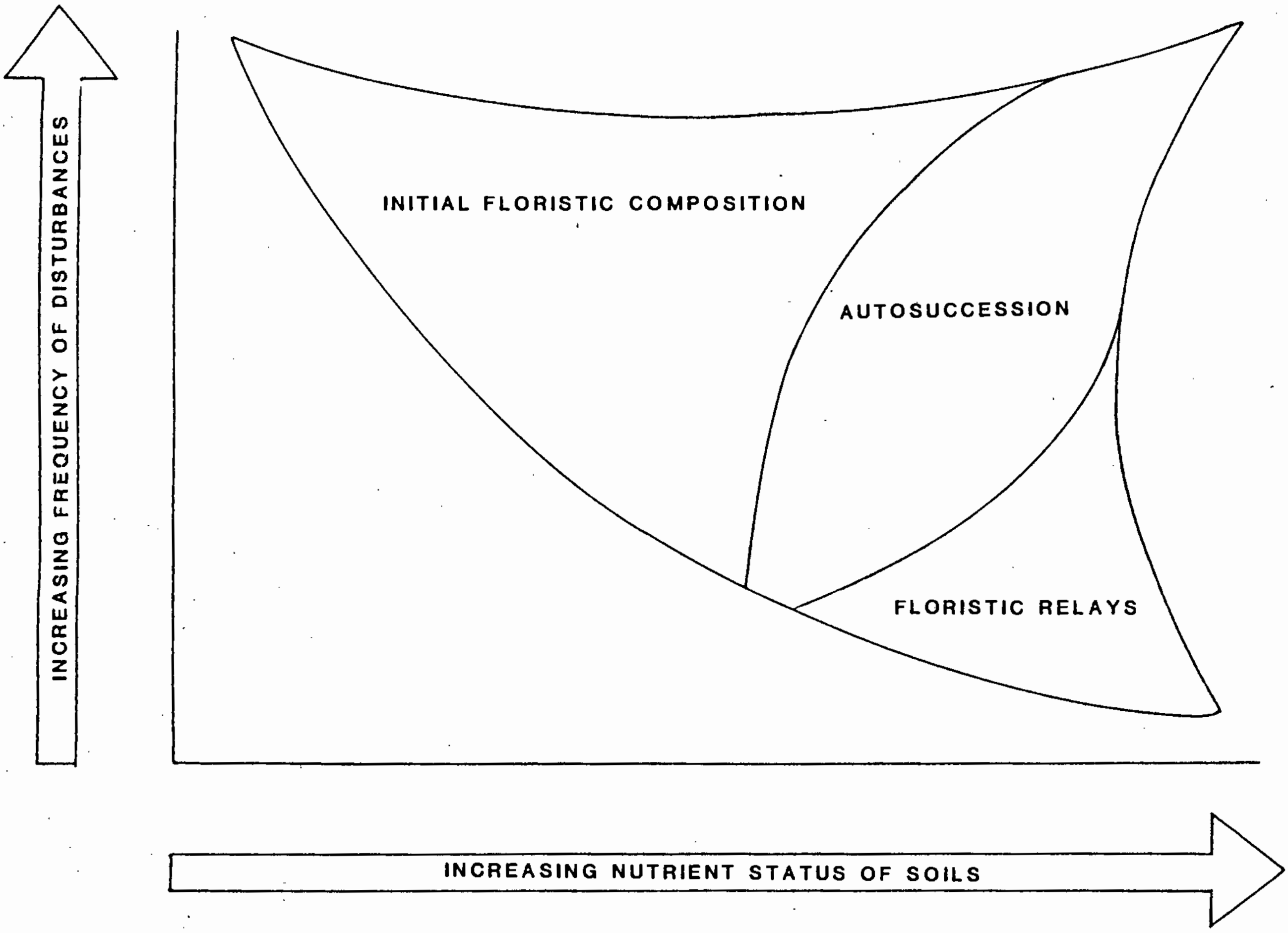


Figure 11 The hypothesized relationships between the succession models 'Initial Floristic Composition', 'Autosuccession' and 'Floristic Relays', and soil nutrients and disturbance regimes.

disturbance periods. Infrequent disturbances, especially if combined with freely available soil nutrients, are most likely to possess a successional pattern characterized by floristic relays. Senescence of some plants accompanied by an availability of soil nutrients should promote temporal changes in plant communities. The accumulation of organic material in soil may facilitate not only growth but even germination of Coastal Thicket species such as *Sideroxylon inerme* L. (R.M. Cowling, pers. comm.).

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Appendix 1 The vital attributes (see Table 1) of all plant species found recolonizing a cleared site at Fernkloof Nature Reserve, Hermanus. A = woody, reseeding and vertebrate dispersed, B = woody, resprouting and vertebrate dispersed, C = woody, reseeding and non-vertebrate dispersed, D = woody, resprouting and non-vertebrate dispersed, E = geophytes, F = herbaceous, annual and perennial plants, G = introduced graminoids, H = indigenous graminoids, I = restiods, J = cyperaceous plants, * = alien plants. Nomenclature follows Bond & Goldblatt (1984).

Bryophyte sp					
Pteridium aquilinum (L.) Kuhn					
Asophodelaceae					
Caesia contorta (L.f.)	F	L_a^s	S_s	V_o	D_o
Trachyandra revoluta (L.) Kunth	E	L_m^s	S_o	V_{aj}	D_o
Trachyandra sp.	F	L_m^s	S_o	V_{aj}	D_o
Cyperaceae					
Cyperaceae sp.	J	L_m^s	S_s	V_a	D_o
Ficinia bulbosa (L.) Nees	J	L_m^s	S_s	V_a	D_o
Ficinia deusta (Bergius) Levyns	J	L_m^s	S_s	V_a	D_o
Ficinia filiformis (Lam.) Schrader	J	L_m^s	S_s	V_a	D_o
Isolepis antarctica Nees	J	L_a^s	S_s	V_o	D_o
Scirpus ecklonii Steudel	J	L_m^s	S_s	V_a	D_o
Tetraria fasciata (Rottb.) C.B. Clarke	J	L_m^m	S_s	V_a	D_o
Eriospermaceae					
Eriospermum nanum Marloth	E	L_m^s	S_o	V_{aj}	D_o
Haemodoraceae					
Lanaria lanata (L.) Durand & Schinz	E?	L_m^s	S_o	V_a	D_a
Wachendorfia paniculata L.	E	L_m^s	S_o	V_{aj}	D_o

Hyacinthaceae					
Albuca juncifolia Baker	E	L_s^s	S_o	V_{aj}	D_o
Lachenalia peersii Marloth ex W. Barker	E	L_s^s	S_o	V_{aj}	D_o
Ornithogalum thyrsoides Jacq.	E	L_m^s	S_o	V_a	D_o
Hypoxidaceae					
Spiloxene curculigoides (Bolus) Garside	E	L_m^s	S_o	V_{aj}	D_o
Iridaceae					
Aristea oligocephala Baker	E	L_m^s	S_o	V_a	D_a
Aristea spiralis (L.f.) Ker Gawler	E	L_m^s	S_o	V_a	D_a
Bobartia longicyma Gillett	E	L_m^s	S_o	V_a	D_o
Geissorhiza aspera Goldbl.	E	L_m^s	S_o	V_a	D_o
Geissorhiza hispidula (Foster) Goldbl.	E	L_m^s	S_o	V_a	D_o
Geissorhiza sp.	E	L_m^s	S_o	V_a	D_o
Ixia dubia Vent.	E	L_m^s	S_o	V_{aj}	D_o
Romulea rosea (L.) Ecklon	E	L_m^s	S_o	V_a	D_o
Watsonia pyramidata (Andrews) Klatt	E	L_m^s	S_s	V_a	D_o
Orchidaceae					
Holothrix mundii Sonder	E	L_m^s	S_s	V_a	D_o
Monadenia sp.	E	L_m^s	S_s	V_a	D_o
Satyrium odorum Sonder	E	L_m^s	S_s	V_a	D_o
Satyrium sp.	E	L_m^s	S_s	V_a	D_o
Poaceae					
*Briza maxima** L.	G	L_a^s	S_s	V_o	D_o
Cymbopogon marginatus (Steudel)	H	L_s^s	S_s	V_a	D_o
Cymbopogon nardus? (L.) Rendle	H	L_s^s	S_s	V_a	D_o
Koeleria capensis (Thunb.) Nees	H	L_s^s	S_s	V_a	D_o
*Lagurus ovatus** L.	G	L_a^s	S_s	V_o	D_a

Panicum maximum Jacq.	H	L^s_m	S_s	V_a	D_o
Pentaschistis malouinensis (Steudel) Clayton	H	L^s_s	S_s	V_a	D_o
Plagiochloa uniolae (L.f.) Adamson & Sprague	H	L^s_m	S_o	V_a	D_o
Restionaceae					
Calopsis vimineus (Rottb.)	I	L^m_m	S_s	V_a	D_o
Elegia filacea Masters	I	L^m_m	S_s	V_a	D_o
Mastersiella digitata (Thunb.) C. Benedict	I	L^m_m	S_s	V_a	D_o
Restionaceae sp.	I	$L^{m?}_{m?}$	$S_{s?}$	V_a	$D_{o?}$
Thamnochortus gracilis Masters	I	L^m_m	S_s	V_a	D_o
Strelitziaceae					
Cyanella hyacinthoides L.	E	L^s_m	S_o	V_a	D_o
Anacardiaceae					
Rhus lucida L.	B	L^m_m	S_o	V_a	D_b
Aizoaceae					
Adenogramma lichtensteiniana (Schultes) Druce	F	L^s_s	S_s	V_o	D_o
Adenogramma sp.	F	L^s_s	S_s	V_o	D_o
Apiaceae					
Centella difformis (Ecklon & Zeyher) Adamson	C	L^s_s	S_s	V_o	D_o
Centella tridentata (L.f.) Drude	C	L^s_s	S_s	V_o	D_o
Centella triloba (Thunb.) Drude	C	L^s_s	S_s	V_o	D_o
Asteraceae					
Arctotis semipapposa (DC.) Beauv.	C	L^s_s	S_s	V_a	D_a
Athanasia parviflora L.	C	L^s_m	S_o	V_o	D_a
Athanasia trifurcata (L.) L.	C	L^s_m	S_o	V_o	D_a
Athanasia sp.	C	L^s_m	S_o	V_o	D_a
Berkeya barbata (L.f.) Hutch.	C	L^s_m	S_s	V_a	D_o
Chrysanthemoides monilifera (L.) Norlindh	A	L^s_m	S_o	V_a	D_b

Corymbium cymosum E. Meyer ex DC.	C	L_s^s	S_s	V_o	D_o
Cotula turbinata L.	F	L_a^s	S_s	V_o	D_a
Disparago lasiocarpa Cass.	C	L_m^s	S_o	V_o	D_a
Disparago laxifolia DC.	C	L_m^s	S_o	V_o	D_a
Edmondia sesamoides (L.) Willd.	C	L_m^s	S_s	V_o	D_a
Gazania pectinata (Thunb.) Sprengel	F	L_s^s	S_s	V_a	D_a
Gazania sp.	F	L_s^s	S_s	V_a	D_a
Helichrysum crispum (L.) D. Don	F	L_a^s	S_o	V_o	D_a
Helichrysum indicum (L.) Grierson	F	L_a^s	S_o	V_o	D_a
Helichrysum sp.	F	L_a^s	S_o	V_o	D_a
Helichrysum vestitum (L.) Schrank	F	L_s^s	S_o	V_o	D_a
Metalasia muricata (L.) D. Don	C	L_s^s	S_o	V_o	D_a
Metalasia seriiphifolia DC.	C	L_s^s	S_o	V_o	D_a
Metalasia sp.	C	L_s^s	$S_{o?}$	V_o	$D_?$
Oedera capensis (L.) Druce	C	L_m^s	S_s	V_o	D_o
Othonna bulbosa L.	D	L_m^m	S_o	V_a	D_o
Othonna parviflora Bergius	C	L_m^m	S_o	V_a	D_o
Othonna quinquedentata Thunb.	C	L_s^s	S_s	V_o	D_o
Phaenocoma prolifera (L.) D. Don	C	L_m^s	S_s	V_o	D_a
Senecio burchellii DC.	C	L_s^s	S_o	V_o	D_a
Senecio pubigerus L.	C	L_s^s	S_o	V_o	D_a
Senecio sp.	C	L_s^s	$S_{o?}$	V_o	$D_?$
Stoebe capitata Bergius	C	L_m^s	S_o	V_o	D_a
Stoebe plumosa (L.) Thunb.	C	L_m^s	S_o	V_o	D_a
Ursinia anthemoides (L.) Poiret	F	L_s^s	S_o	V_o	D_a
Ursinia chrysanthemoides (Lees.) Harvey	F	L_s^s	S_o	V_o	D_a

Bruniaceae					
Berzelia lanuginosa (L.) Brongn.	C	L_m^m	S_s	V_o	D_o
Campanulaceae					
Lobelia coronopifolia L.	F	L_m^s	S_o	V_a	D_o
Lobelia chamaepitys Lam.	F	L_m^s	S_o	V_a	D_o
Lobelia pinifolia L.	F	L_m^s	S_o	V_a	D_o
Prismatocarpus sessilis Ecklon ex A. DC.	F	L_a^s	S_s	V_o	D_o
Roella incurva A.DC.	C	L_a^s	S_s	V_o	D_o
Wahlenbergia cernua (Thunb.) A. DC.	F	L_s^s	S_s	V_o	D_o
Wahlenbergia obovata Brehmer	F	L_a^s	S_s	V_o	D_o
Caryophyllaceae					
Silene gallica L.	F	L_a^s	S_s	V_o	D_o
Crassulaceae					
Crassula capensis (L.) Baillon	F	L_a^s	S_s	V_o	D_o
Crassula fascicularis Lam.	F	L_a^s	S_s	V_o	D_o
Crassula filiformis (Ecklon & Zeyher) Dietr.	F	L_a^s	S_s	V_o	D_o
Droseraceae					
Drosera cistiflora L.	F	L_m^m	S_s	V_a	D_o
Drosera trinervia Sprengel	F	L_m^m	S_s	V_a	D_o
Ebenaceae					
Diospyros glabra (L.) de Winter	A	L_m^m	S_o	V_{aj}	D_b
Euclea polyandra (L.f.) E. Meyer ex Hiern	B	L_m^m	S_o	V_{aj}	D_b
Ericaceae					
Blaeria ericoides L.	C	L_m^s	S_s	V_o	D_o
Erica corifolia L.	C	L_m^s	S_s	V_o	D_o
Erica rhopolantha Dulfer	C	L_m^s	S_s	V_o	D_o
Erica sessiliflora L.f.	D	L_m^s	S_s	V_a	D_o

Erica sp.	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Euphorbiaceae					
Euphorbia silenifolia (Haw.) Sweet	D	L^{m}_{m}	$S_{o?}$	V_{a}	D_{o}
Fabaceae					
*Acacia baileyana** F. Meull.	C	L^{m}_{m}	S_{s}	V_{a}	D_{o}
*Acacia cyclops**A. Cunn. ex G. Don	A	L^{m}_{m}	S_{s}	V_{o}	D_{b}
Acacia longifolia (Andrews) Willd.	C	L^{m}_{m}	S_{s}	V_{a}	D_{o}
Amphithalea ericifolia (L.) Ecklon & Zeyher	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Amphithalea sp.	C	$L^{s}_{m?}$	S_{s}	V_{o}	$D_{o?}$
Aspalathus laricifolia Bergius	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Aspalathus serpens R. Dahlgren	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Hypocalyptus oxalidifolius (Sims) Baillon	F	L^{s}_{s}	S_{s}	V_{o}	D_{o}
Indigofera glomerata E. Meyer	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Podalyria sericea R. Br.	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Rhynchosia capensis (Burm. f.) Schinz.	F	L^{s}_{s}	S_{s}	V_{o}	D_{o}
Virgilia divaricata Adamson	C	L^{s}_{m}	S_{s}	V_{o}	D_{o}
Flacourtiaceae					
Kiggelaria africana L.	A	L^{m}_{m}	S_{o}	V_{a}	D_{b}
Gentianaceae					
Sebaea exacoides (L.) Schinz	F	L^{s}_{a}	S_{s}	V_{o}	D_{o}
Geraniaceae					
Pelargonium capitatum (L.) L'Her.	C	L^{s}_{s}	S_{o}	V_{a}	D_{a}
Pelargonium cucullatum (L.) L'Her.	C	L^{s}_{s}	S_{o}	V_{a}	D_{a}
Pelargonium myrrhifolium (L.) L'Her.	C	L^{s}_{s}	S_{o}	V_{a}	D_{a}
Pelargonium sp.	C	L^{s}_{s}	S_{o}	V_{a}	D_{a}
Lauraceae					
Cassytha ciliolata Nees	C	L^{m}_{m}	S_{o}	V_{o}	D_{b}

Malvaceae					
Hibiscus aethiopicus L.	F	L_m^s	S_s	V_{aj}	D_o
Mesembryanthemaceae					
Carpobrotus edulis (L.) N.E. Br.	C & D	L_m^s	S_s	V_a	D_o
Erepsia anceps (Haw.) L. Bolus	C	L_s^s	S_s	V_o	D_o
Lampranthus bicolor (L.) N.E. Br.	C	L_s^s	S_s	V_o	D_o
Myricaceae					
Myrica quercifolia L.	B	L_m^m	S_s	V_{aj}	D_b
Myrsinaceae					
Myrsine africana L.	B	L_s^m	S_o	V_a	D_b
Myrtaceae					
Eucalyptus sp.	C	L_m^m	S_s	V_a	D_o
Oxalidaceae					
Oxalis caprina L.	E	L_m^s	S_s	V_a	D_o
Oxalis eckloniana Presl	E	L_m^s	S_s	V_a	D_o
Oxalis heterophylla DC.	E	L_m^s	S_s	V_a	D_o
Oxalis luteola Jacq.	E	L_m^s	S_s	V_a	D_o
Oxalis obtusa Jacq.	E	L_m^s	S_s	V_a	D_o
Oxalis pes-caprae L.	E	L_m^s	S_s	V_a	D_o
Oxalis polyphylla Jacq.	E	L_m^s	S_s	V_a	D_o
Oxalis sp.	E	L_m^s	S_s	V_a	D_o
Portulacaceae					
Rumex cordatus Desf.	E	L_m^s	S_s	V_a	D_o
Proteaceae					
Aulax umbellata (Thunb.) R. Br.	C	L_m^m	S_c	V_o	D_o
Leucadendron salignum Bergius	C & E	L_m^m	S_c	V_a	D_o
Leucadendron tinctum I.J. Williams	C	L_m^m	S_c	V_o	D_o

Leucadendron xanthoconus (Kuntze) K. Schum.	C	L^m_m	S_c	V_o	D_o
Protea compacta R. Br.	C	L^m_m	S_c	V_o	D_o
Protea repens (L.) L.	C	L^m_m	S_c	V_o	D_o
Protea scabra R. Br.	D	L^m_m	S_c	V_a	D_o
Protea sp.	C	L^m_m	S_c	V_a	D_o
Rhamnaceae					
Phylica ericoides L.	C	L^m_m	S_s	V_o	D_a
Phylica lasiocarpa Sonder	C	L^m_m	S_s	V_a	D_o
Phylica sp.	C	L^m_m	S_s	V_o	D_o
Rosaceae					
Cliffortia sp.	C	L^s_m	S_s	V_o	D_o
Rubiaceae					
Anthospermum sp.	C	L^s_m	S_s	V_o	D_o
Anthospermum spathulatum Sprengel	C	L^s_m	S_s	V_o	D_o
Rutaceae					
Agathosma imbricata (L.) Willd.	C	L^s_m	S_s	V_a	D_o
Santalaceae					
Thesium commutatum Sonder	C	L^s_m	S_o	V_o	D_o
Thesium sp	C	L^s_m	S_o	V_o	D_o
Scrophulariaceae					
Halleria lucida L.	A	L^m_m	S_o	V_a	D_b
Hemimeris racemosa (Houtt.) Merrill	F	L^s_s	S_s	V_a	D_o
Manulea minor Diels	F	L^s_a	S_s	V_o	D_o
Nemesia barbata (Thunb.) Benth.	F	L^s_a	S_s	V_o	D_o
Nemesia pinnata (L.f.) E. Meyer ex Benth.	F	L^s_a	S_s	V_o	D_o
Polycarena sp.	F	L^s_a	S_s	V_o	D_o
Selago spuria L.	F	L^s_a	S_s	V_o	D_o

Sterculiaceae

Hermannia hyssopifolia L.	F	L_s^s	S_s	V_a	D_o
Hermannia joubertiana Harvey	F	L_s^s	S_s	V_a	D_o
Hermannia rudis N.E. Br.	F	L_s^s	S_s	V_a	D_o
Hermannia sp.	F	L_s^s	S_s	V_a	D_o

Thymelaeaceae

Gnidia pinifolia L.	C	L_m^s	S_s	V_a	D_o
Gnidia sp.	C	L_m^s	S_s	V_a	D_o
Passerina sp.	C	L_m^m	S_s	V_a	D_o
Passerina vulgaris Thoday	C	L_m^m	S_s	V_a	D_o
Struthiola confusa C.H. Wright	C	L_m^s	S_s	V_o	D_o
Struthiola sp.	C	L_m^s	S_s	V_o	D_o

CHAPTER 3

Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Fruit phenology of indigenous and alien plants in the southwestern Cape, South Africa

Contents

Study site

Results

Fruit phenology of indigenous and alien plants in the southwestern Cape, South Africa

Contents /continued

Discussion

Fruit phenology of indigenous and alien plants in the southwestern Cape

Abstract

The fruiting phenology of 58 indigenous and nine alien plant species was studied in Coastal Thicket, ecotonal areas and Afromontane Forest/Thicket vegetation types. Data on the periods from flower to fruit development and the degree of fruiting synchrony in conspecifics were also collected. Fruiting was least seasonal and most predictable in Coastal Thicket vegetation, whereas it was unpredictable, although largely restricted to autumn and spring, in Afromontane Forest. The alien species had more predictable fruiting periods, and also had spring and autumn peaks. Fruiting seasons in the south-western Cape were usually shorter than in the eastern Cape. These results support the results of other studies carried out in similar vegetation types.

To be submitted to *S. Afr. J. Bot.*

Introduction

Birds may constitute important agents for the dispersal of certain plants possessing fleshy fruits. Within the broad Cape Floral Kingdom such plants appear to be particularly common in Strandveld vegetation (Siegfried 1982), Afromontane Forest/Thicket (Phillips 1927; Milewski 1982: Knight in prep. Chapter 1) and Coastal Thicket vegetation types (Liversidge 1972; Pierce 1984; Pierce & Cowling 1984; Knight in prep. Chapter 1). Based on Liversidge (1972) and Pierce & Cowling (1984) the availability of these fruits is not predictable and no distinct fruiting seasonalities occurred. This study, therefore tested to determine if similar patterns occurred in a southwestern Cape Coastal Thicket.

Based on theoretical considerations, I predicted that (1) autumn fruiting would be most advantageous for the majority of plants, since both germination and rapid establishment could take place during the wet winter months (May to September). Garwood (1983) found that 75% of the woody species in a Panamanian forest germinated early in the rainy season.

Cowling (1983) predicted that "high cost, low profit sclerophyll shrubs" that extend into non-seasonal or winter rainfall regions (southwestern Cape) of southern Africa would possess greater phenological flexibility. Consequently I sought to determine if (2) those fruit-bearing species which occupied a winter rainfall region possessed longer and different fruiting seasons to the eastern Cape which receives rain throughout the year.

Finally I sought to determine if (3) there were species which had predictable fruit seasons in the southwestern Cape, and therefore could be exploited by ephemeral populations of frugivores such as Rameron Pigeons Columba arquatrix and Red-faced Mousebirds Colius indicus.

Study site

Vegetation

The fruiting phenology of indigenous and alien plant species possessing fleshy fruits was examined at Hermanus (34° 25′ S; 19° 16′ E). Three separate vegetation types were recognized and studied, a Coastal Thicket vegetation, an Afromontane Forest/Thicket vegetation and an ecotonal vegetation between the Mountain Fynbos and Afromontane Forest. Figure 1 shows the relative positions of these vegetation types, prior to the fires of December 1985 and February 1986, which burnt most of the ecotonal and Afromontane Forest/Thicket vegetation. The Coastal Thicket is situated on calcified sand dunes that are penetrated by highly acidic, organic rich seepage zones. The rest of the vegetation in the area occurs on Table Mountain Sandstone that is penetrated by narrow shale bands. These soils are nutrient poor and acidic.

Coastal Thicket is very dense vegetation and varies in height between 1 and 4,5 m tall. Coastal Thicket occurring in seepage areas is more similar to the Afromontane Forest/Thicket and may be greater than 4,5 m in height. Consequently this vegetation is a complex mosaic of different plant communities. Dominant and widespread plant species include *Rhus lucida* and *R. glauca* (including hybrids between the two species), *Sideroxylon inerme*, *Protasparagus aethiopicus* and *Cassine maritima*. Locally dominant species include *Euclea racemosa*, *Rhus crenata*, *Rapanea melanophloeos* and *Olea exasperata*. Although woody vegetation is easily the most dominant in terms of plant cover, it comprises only about 50 species. Of these 50 species 40 possess fleshy fruits, and represent about 80% of the canopy cover. In contrast, small forbs and geophytes possess a negligible cover (<0,1%) but represent the majority of 900 + coastal plant species collected and held at the Hermanus herbarium.

The ecotone sites included all areas that were at the fringe of the Coastal Thicket vegetation, the Afromontane Forest/Thicket, and the Mountain Fynbos. This vegetation therefore included riparian vegetation, as well as vegetation that occurred on the lower mountain slopes between Coastal Thicket and Mountain Fynbos vegetation. The riparian vegetation was between 3 and 4 m

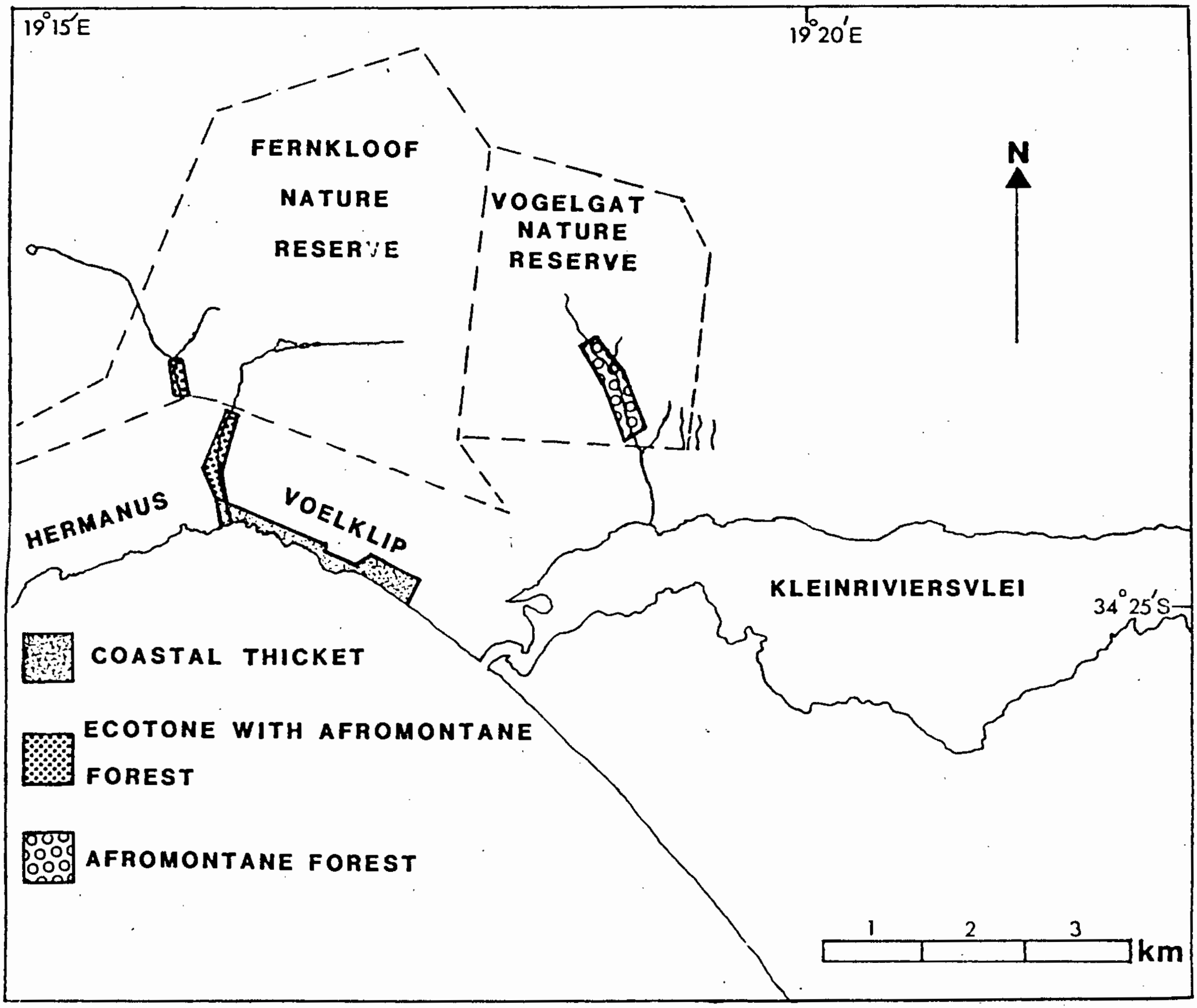


Figure 1 Map of the study sites in the Hermanus district showing the relative positions of the three vegetation types.

tall, whereas other ecotonal areas were less than 1 m. Dominant species in the riparian vegetation included Halleria lucida and Maytenus acuminata. The other ecotonal areas were dominated by Chrysanthemoides monilifera and Euclea polyandra. The parasitic Cassytha ciliolata was abundant throughout the ecotonal areas and smothered much of the vegetation.

The Afromontane Forest/Thicket vegetation had both the fewest number of species possessing fleshy fruits and the lowest cover of such species. Dominant species not possessing fleshy fruits included Cunonia capensis, Laurophyllus capensis and Brachylaena neriifolia. Of the species possessing fleshy fruits the dominants included Olea capensis, Hartogiella schinoides, Rapanea melanophloeos and Cassine peragua. The vegetation was generally 4 to 6 m tall, with emergent Olinia ventosa up to 8 m tall.

The other important natural vegetation type at Hermanus was Mountain Fynbos which covered the mountain slopes. With the exception of Grubbia tomentosa and Grubbia rosmariinifolia there are no other plants possessing fleshy fruits that were restricted to this vegetation. However, after fires resprouting Haemanthus species, Protasparagus compactus, Diospyros glabra, Myrica krausianna, M. quercifolia, Myrsine africana, Euclea polyandra and an unnamed Colpoon sp. bear fruit. Since, these plants appear to produce fruit only after fire, a phenological study could not be undertaken (see Chapter 2).

Climate

Mean annual rainfall recorded at the coast was 595 mm with a coefficient of variation of 18,5% (Magnetic Observatory 1947-1985). Annual rainfall was, however, higher in the mountains with a mean rainfall of 1235 mm for the years 1982 to 1985 (I.J.M. Williams personal communication). From Figure 2 it can be seen that most rainfall (60%) occurred during the autumn and winter months (April to August), a further 17% occurred in spring (September and October). The summer months of December and January were usually the driest. From Figure 2 it can be seen that actual evapotranspiration, calculated from temperature and rainfall and assuming a 200 mm soil moisture retention (Thornthwaite & Mather 1957), was highest in summer, with only the months May to September possessing water surpluses. Actual evapotranspiration does,

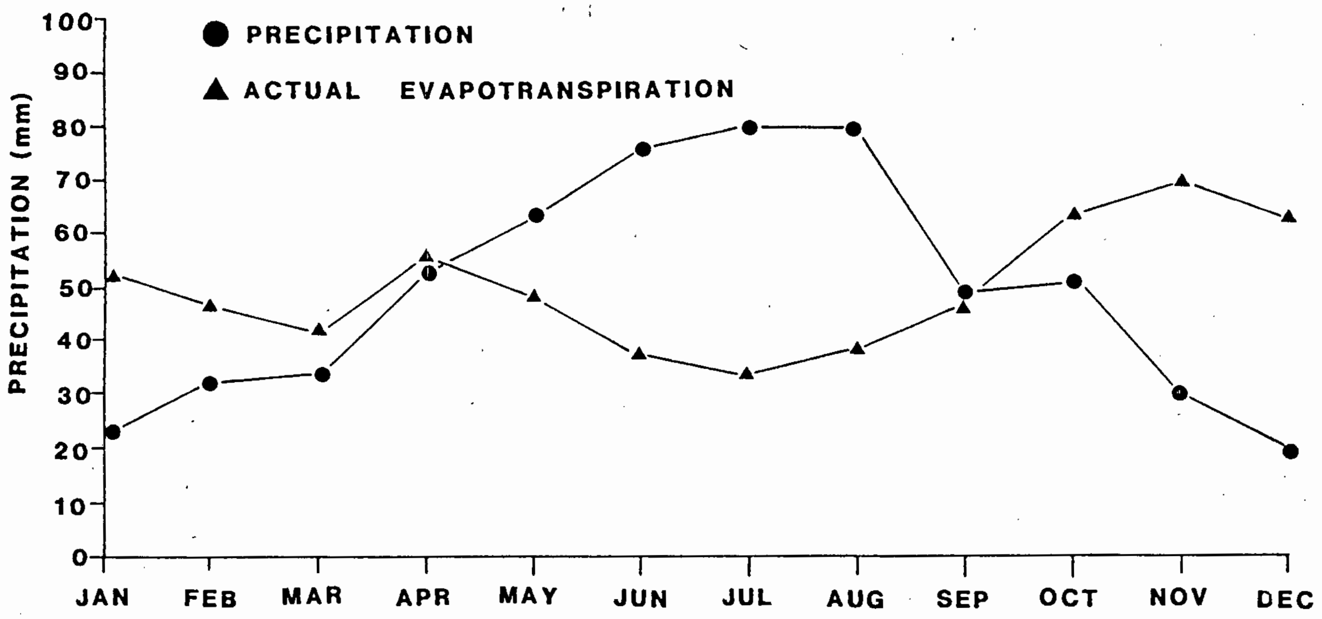


Figure 2 Climate of Hermanus showing average monthly rainfall and actual evapotranspiration calculated from temperature and rainfall (Thornthwaite and Mather 1957).

however, show a bimodal pattern, with peaks in November and April. The warmest month at Hermanus is January (mean temperature 20,7°C) and the coolest is July (13,0°C). Highest and lowest mean maximum and minimum temperatures are 25,4°C (in January) and 8,2°C (July). The absolute maximum and minimum temperatures recorded at the Observatory (1963-1985) are 37,5°C (February 1975) and 1,5°C (July 1982), and consequently frost virtually never occurs. The climate is therefore warm temperate and transitional between Koppen Csa and Csb climates (Specht & Moll 1983).

The rainfall and potential evapotranspiration for the period from 18 months prior to the study up to 6 months post study period (Figure 3) showed that only 1983 had a climate similar to the generalized regime of Figure 2, except for the extremely wet February. The winters of 1982, 1984 and 1985 were rather dry, whereas the summer of 1984/1985 was rather wet. Periods of potential water deficit from 1982 to 1985 could occur in any month of the year. In the cold-stressed versus drought-stressed gradients proposed for mediterranean regions (Mitrakos 1980), Hermanus appears to represent a drought-stressed extreme.

Land use

Hermanus, a popular seaside resort, has been subject to considerable pressures to expand its residential areas, to the detriment of the natural vegetation. Two nature reserves conserve the mountain vegetation (ecotone, Afromontane Forest/Thicket and Mountain Fynbos). These reserves (Fernkloof and Vogelgat) were formerly farms which supported very low populations of sheep. The coastal vegetation is municipal commonage and is maintained as part of Fernkloof. A prescribed burning plan was drawn up for Fernkloof, but never implemented as fires in December 1985 and February 1986 burnt both reserves. The coastal sites prior to their conservation were browsed by cattle until 1957 (I.J.M. Williams pers. comm.).

Alien Vegetation

Alien plants are widespread, and their eradication is the major objective in the management of the two reserves. In the coastal sites the most dominant

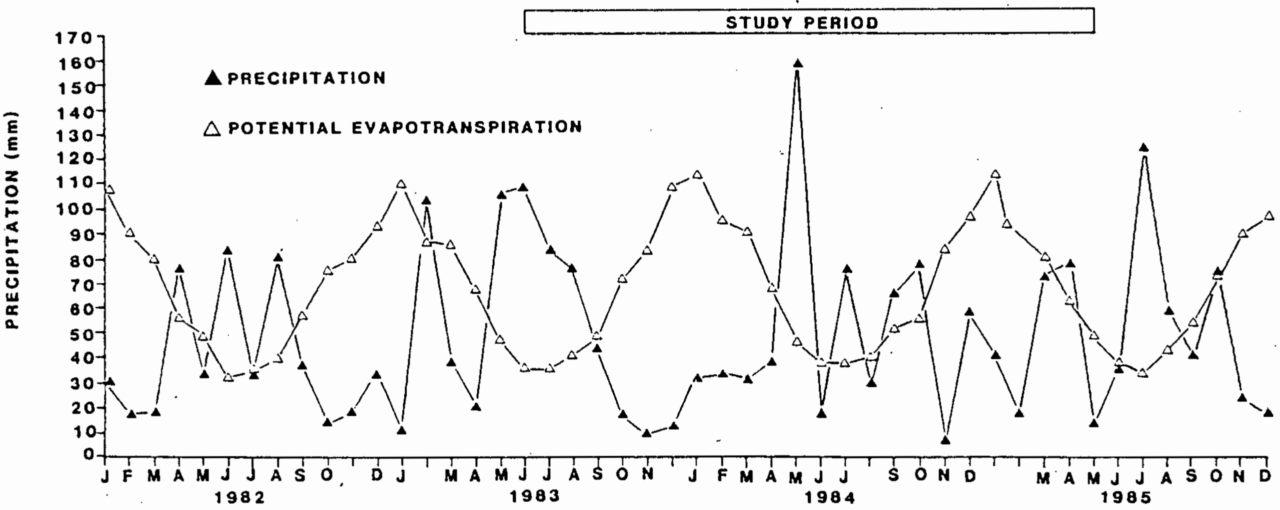


Figure 3 Rainfall and potential evapotranspiration at Hermanus for the period 1982 to 1985.

alien species is Acacia cyclops; others include Myoporum serratum, Metrosideros excelsus (which has a capsulated seed that is not truely fleshy, but is nevertheless eaten and dispersed by frugivores), Phytolacca octandra and Solanum nigrum. In the ecotonal areas (particularly the riparian sites) Pittosporum undulatum, Rubus sp. (fruticosa?), Solanum mauritianum and Lantana camara occur. In the Afromontane Forest/Thicket an occasional Pittosporum undulatum occurs. Of the non-bird-dispersed alien plants, Leptospermum laevigatum occurs in the ecotonal areas, Acacia longifolia in the riparian sites and Hakea sericea, Pinus pinaster and P. radiata in Mountain Fynbos.

Materials and Methods

The fruiting phenology of 58 indigenous and 9 alien plant species possessing fleshy fruits was examined every month during a two-year period (June 1983 to May 1985). Of the 58 indigenous species studied, 42 occurred in the Coastal Thicket vegetation, whereas 17 occurred in the ecotone and 13 in the Afromontane Forest/Thicket. Since a high degree of asynchronous fruiting occurred a species was recorded as fruiting only when five individual plants could be found fruiting within a homogeneous vegetation stand. Homogeneous stands were defined by undertaking a vegetation classification of the study sites using Braun Blanquet cover abundance classes (see Chapter 4). In the Coastal Thicket all woody plants within 34 fixed 10 m diameter plots were tagged (see Chapter 4). On these tagged plants individual branches were tagged, and individual fruits were marked by coloured wool tied around the peduncle. This allowed both the monthly rate of ripening and the availability of newly ripened fruits to be monitored. In addition both intraspecific flowering and fruiting synchrony was estimated by comparing tagged plants within the plots to untagged plants outside the plots.

The monthly presence/absence of fruit for each species was analysed (using a chi-square test) to determine if there were any associations between seasonality and site ($P < 0,05$). A Boolean factor analysis was also applied to each vegetation type. The variables were defined by months, whereas the plant species represented the samples. Boolean factor analysis reduced the 24 variables to a fewer number of factors, allowing me to group months which had a similar composition of species in fruit. Since the arithmetic of a Boolean factor analysis is binary, the relationship of each variable with each factor score is also binary. Variables can also be related to more than one factor. Factor loadings were used to relate samples (species) with each of the factors (groups of months). Factor loadings are also binary, and consequently species may also be represented by more than one factor. This technique allowed me to determine peaks in fruiting, and also to identify those plant species possessing either predictable or extended fruiting.

The overall phenological patterns were compared to similar studies undertaken in the eastern Cape (Liversidge 1972; Pierce & Cowling 1984). The average availability of fruit was calculated for each species (percentage of species fruiting in each month relative to the total number of species which fruited during the study period) and was calculated for each of the vegetation types. For each vegetation type and species, an index of predictability was determined by calculating the number of months in which fruiting co-occurred in the same month for each of the two calendar years. This was then expressed as a percentage of the total number of months in which fruiting occurred during the two-year period. For example, a species which fruited in August and September in the one year and August to October in the following year would have coinciding fruiting in four out of five months and a monthly predictability of 80%. Both monthly fruit availability and ripening for Coastal Thicket plants were correlated (Spearman Rank Correlation r_s; Siegal (1956)) with mean monthly rainfall, monthly mean of maximum and minimum temperatures, mean monthly temperature, potential evapotranspiration and mean monthly rainfall minus potential evapotranspiration.

Results

Coastal Thicket

This vegetation was represented by the greatest number of species possessing fleshy fruits (42). However, *Protasparagus compactus*, *P. rubicundis*, *Maytenus lucida* and *M. procumbens* did not present any fruit displays during the two-year study period. The phenology of each of the 38 species which fruited is summarized in Appendix 1a. On average, slightly more than 25% of the species fruited during each month. However, the monthly predictability of

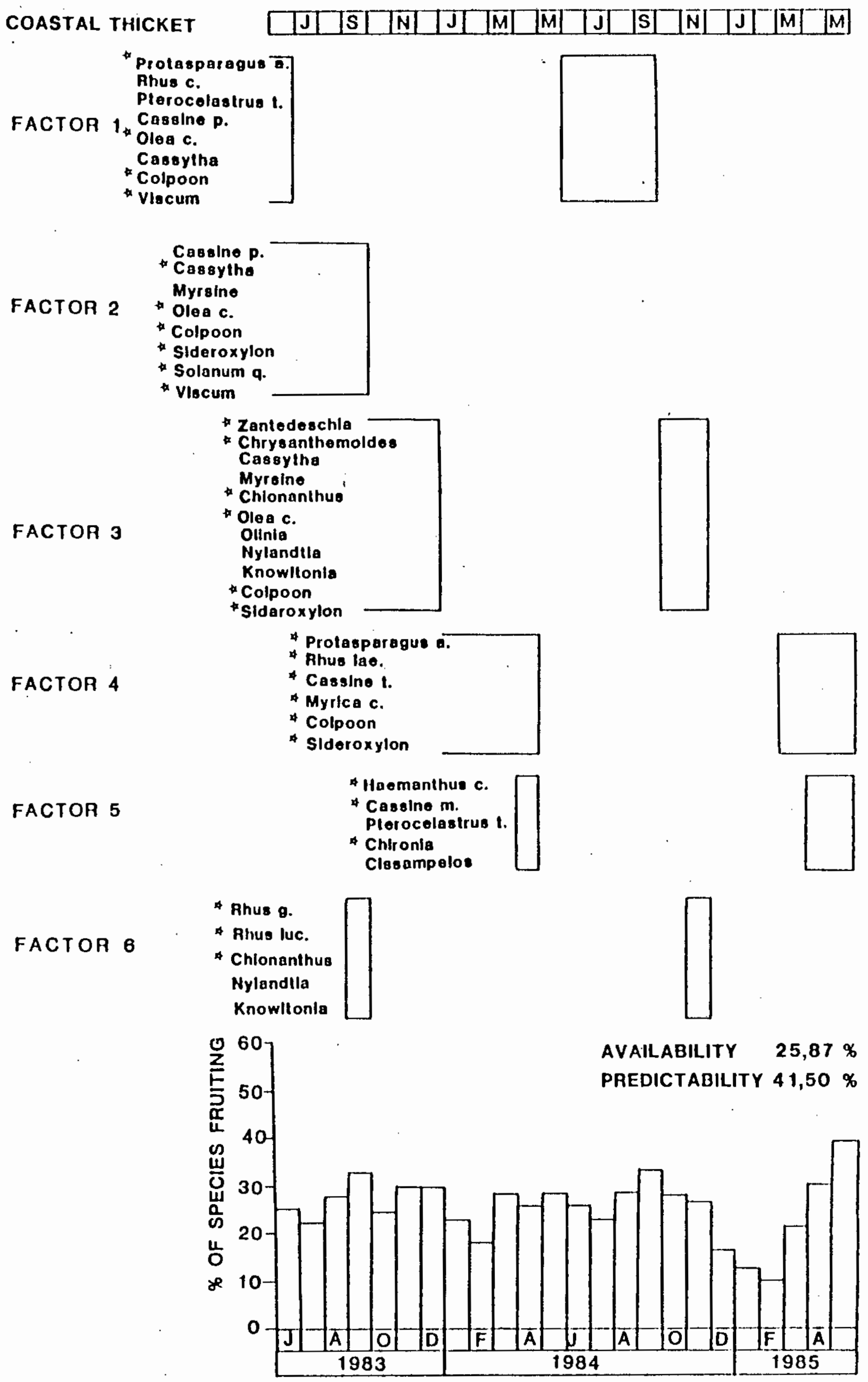


Figure 4 The number of species fruiting in each month of the study period and the results of the Boolean factor analysis for the coastal thicket vegetation. Each factor is represented by one or more blocks which clusters those months possessing similar species in fruit. Each species that has a positive correlation with the factor is listed at the side of the block.

fruiting was a fairly low 41,5% (Figure 4), and indeed would have been lower still, if it were not for species such as Colpoon compressum which fruited throughout the year. During the two-year period, very minor peaks in fruiting occurred in spring and autumn, whereas February had the fewest species in fruit. The first factor in the Boolean factor analysis grouped the winter months of June 1983 with June to September 1984. With the exception of Rhus crenata, the species associated with this factor appeared to be regular winter fruiting species. Factor 2 was defined by spring fruiting months of 1983. A large number of species was represented in both factors 1 and 2 and indicated longer fruiting during 1983. Some species such as Myrsine africana and Solanum quadrangulare appeared to fruit only during this period, and therefore were likely to be fairly irregular fruiters. Factor 3 was described by spring-summer months of 1983 and 1984, and consequently species associated with this factor possessed more regular summer fruiting. Since species such as Cassytha ciliolata, Olea capensis and Colpoon compressum are associated with all three of the first factors, these species are considered to possess long fruiting seasons. The fourth factor grouped the late summer and autumn months of 1983 and 1984. Included in this factor are Protasparagus aethiopicus, Rhus laevigata and Myrica cordifolia. These species all had fairly long three to four month fruiting seasons. Factor 5 also included autumn fruiting in 1983 and 1984, but represented the short duration fruiting species Haemanthus coccineus, Chironia baccifera and Cassine maritima. The last factor (6) described short-season spring fruiting species such as Rhus glauca, R. lucida, Chionanthus foveolata, Nylandtia spinosa and Knowltonia capensis. Overall the number of species that fruited for each month did not vary greatly except for early 1985, when very few species fruited.

Ecotone areas

This vegetation was represented by 17 species, all of which fruited during the study period. The phenology of each species is summarized in Appendix 1b. On average 34% of the species fruited during each month. However, the monthly predictability of fruiting was the same as that in the Coastal Thicket (41%). The first factor (Figure 5) accounted for summer (December 1983 to January 1984) fruiting and included Euclea polyandra and Hartogiella schinoides. Factor 2 described autumn fruiting species (Kiggelaria africana, Rapanea

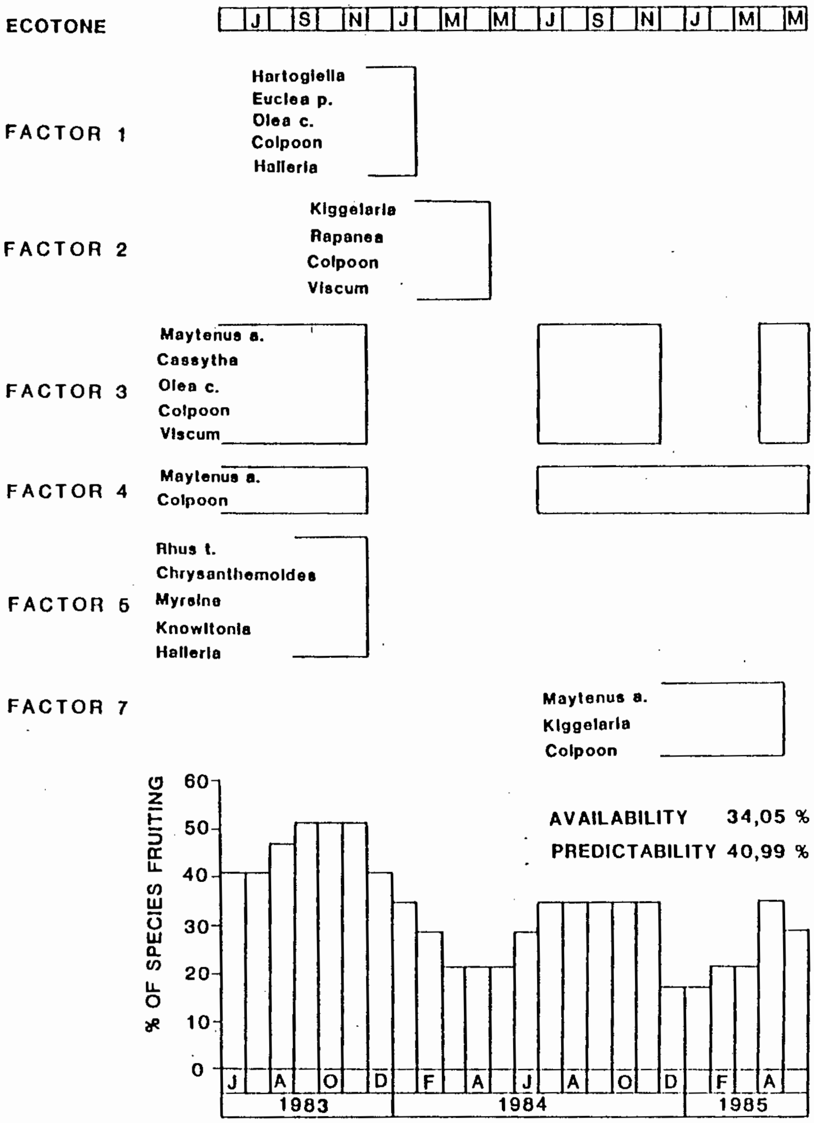


Figure 5 The number of species fruiting in each month of the study period and the results of the Boolean factor analysis for the ecotone vegetation. Each factor is represented by one or more blocks which clusters those months possessing similar species in fruit. Each species that has a positive correlation with the factor is listed at the side of the block.

melanophloeos and *Viscum capense*). In both factors 1 and 2, only months within a single year were described, and species such as *Rapanea melanophloeos*, *Euclea polyandra*, *Halleria lucida* and *Hartogiella schinoides* had irregular fruiting. In factor 3, the following months clustered together, June to November 1983, July to November 1984 and April to May 1985. This factor described the long fruiting species, *Maytenus acuminata*, *Cassytha ciliolata*, *Olea capensis*, *Colpoon compressum* and *Viscum capense*. Factor 4 again accounted for the two species with the longest fruiting seasons, *Colpoon compressum* (24 months) and *Maytenus acuminata* (17 months). The clustering of these months largely reflected the phenology of *Maytenus acuminata*. Factor 5 accounted for spring fruiting in 1983, whereas factor 7 accounted for autumn 1985 fruiting. As in the Coastal Thicket, those species that fruit most regularly also fruited during spring and autumn.

Afromontane Forest/Thicket

This vegetation was represented by the fewest number of plant species (13) which fruited during the two-year period. The only species in which fruit displays were not recorded was *Curtisia dentata*. The phenology of each species is summarized in Appendix 1c. On average slightly more than 20% of the species fruited during each month, and the monthly predictability of fruiting was very low (16%; Figure 6). The most notable fruiting species in this vegetation type was *Halleria lucida* which fruited for the first eleven months of the two-year study period, and was the only species associated with the first factor (Figure 6). Factor 2 accounted for *Pterocelastrus rostratus*, the other species that possessed prolonged fruiting. Although both *Pterocelastrus rostratus* and *Halleria lucida* fruited during many months of the study, neither species possessed seasonally predictable fruiting. The third factor was described by 1983 and 1984 spring fruiting species, with *Chrysanthemoides monilifera* and *Knowltonia capensis* having predictable seasonal fruiting. Both factors 4 and 5 were related to fruit flushes in the midsummer of 1983-1984 and autumn 1985, respectively. *Hartogiella schinoides* was associated with both of the last factors.

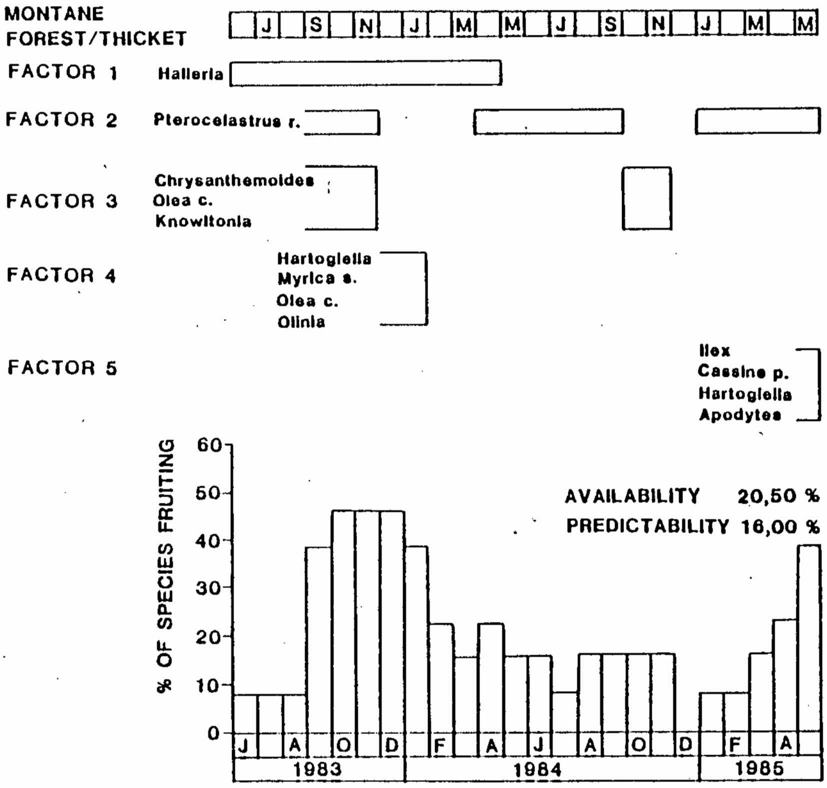


Figure 6 The number of species fruiting in each month of the study period and the results of the Boolean factor analysis for the Afromontane Forest/Thicket vegetation. Each factor is represented by one or more blocks which clusters those months possessing similar species in fruit. Each species that has a positive correlation with the factor is listed at the side of the block.

Alien species

The fruiting phenology of the nine alien species that occurred in Hermanus are summarized in Appendix 1d. The availability and predictability of fruiting does not differ greatly from that occurring in the Coastal Thicket (*cf.* Figures 1 and 7). However, this group of species possessed the most pronounced 1984 autumn and spring peaks in fruiting that occurred in any of the suites of species. Further, the period of June to August (1984) was without any alien species in fruit. Figure 7 summarizes the results of the Boolean factor analysis. The first factor included the long fruiting of *Solanum mauritianum*. The second factor included the fairly predictable autumn fruiting of *Solanum nigrum* and *Lantana camara*, whereas the third factor included the spring fruiting *Phytolacca octandra* and *Rubus* sp; the latter also fruiting in autumn 1984. Factors 4, 5 and 6 appeared to cluster late summer/autumn, mid-summer and spring seasons, respectively. *Pittosporum undulatum* appeared to have a long fruiting season that stretched across all three of these factors.

In all three vegetation types, and in the suite of alien species, fruiting peaks occurred in either spring or autumn. However, the alien plants appeared to have fruiting seasons that are partly out of phase with the indigenous plants. The indigenous plants possessed a double spring peak, followed by an autumn peak, whereas the alien plants possessed a single autumn peak followed by a double spring peak.

Relationships between fruit ripening and availability and climate

Monthly availability of fruit was only related to mean monthly minimum temperature ($\underline{r}_{s22}$ = -0,37; $\underline{P}$ < 0,05: Table 1), whereas the monthly ripening of fruit was both positively related to mean monthly rainfall ($\underline{r}_{s22}$ = 0,43; $\underline{P}$ < 0,05) and mean annual rainfall minus potential evapotranspiration ($\underline{r}_{s22}$ = 0,62; $\underline{P}$ < 0,01) and negatively related to potential evapotranspiration ($\underline{r}_{s22}$ = -0,60; $\underline{P}$ < 0,01), mean monthly temperature ($\underline{r}_{s22}$ = -0,56; $\underline{P}$ < 0,01), mean monthly maximum temperature ($\underline{r}_{s22}$ = -0,53; $\underline{P}$ < 0,01) and mean monthly minimum temperature ($\underline{r}_{s22}$ = -0,51; $\underline{P}$ < 0,01). These results appear to reflect the autumn and spring peaks in fruiting, and correspond with moderately high

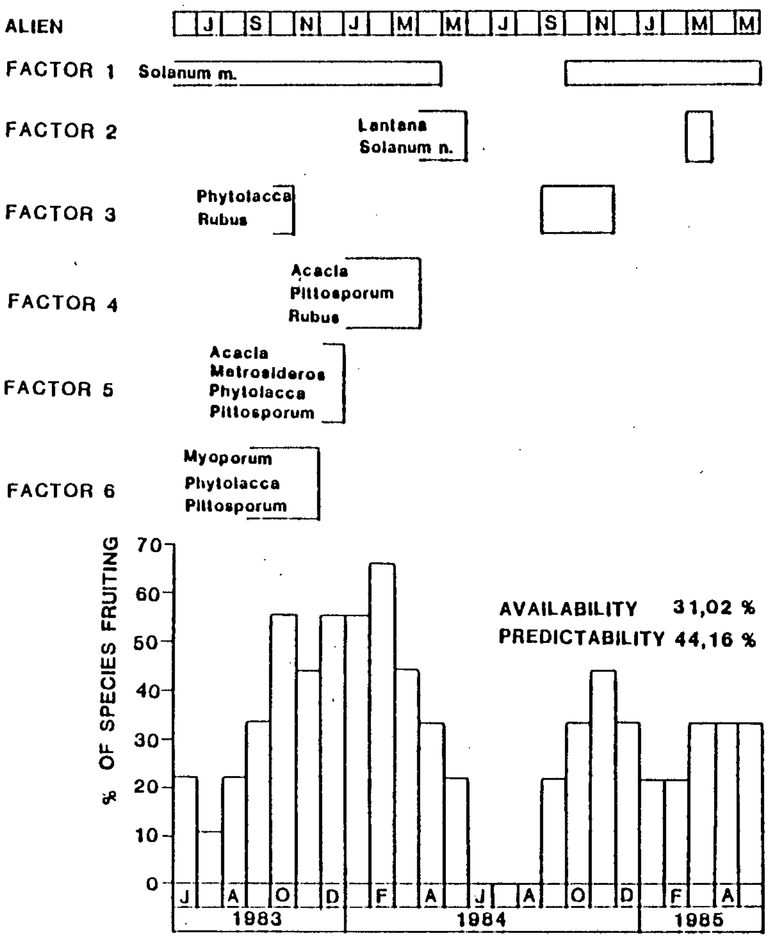


Figure 7 The number of species fruiting in each month of the study period and the results of the Boolean factor analysis for the alien vegetation. Each factor is represented by one or more blocks which clusters those months possessing similar species in fruit. Each species that has a positive correlation with the factor is listed at the side of the block.

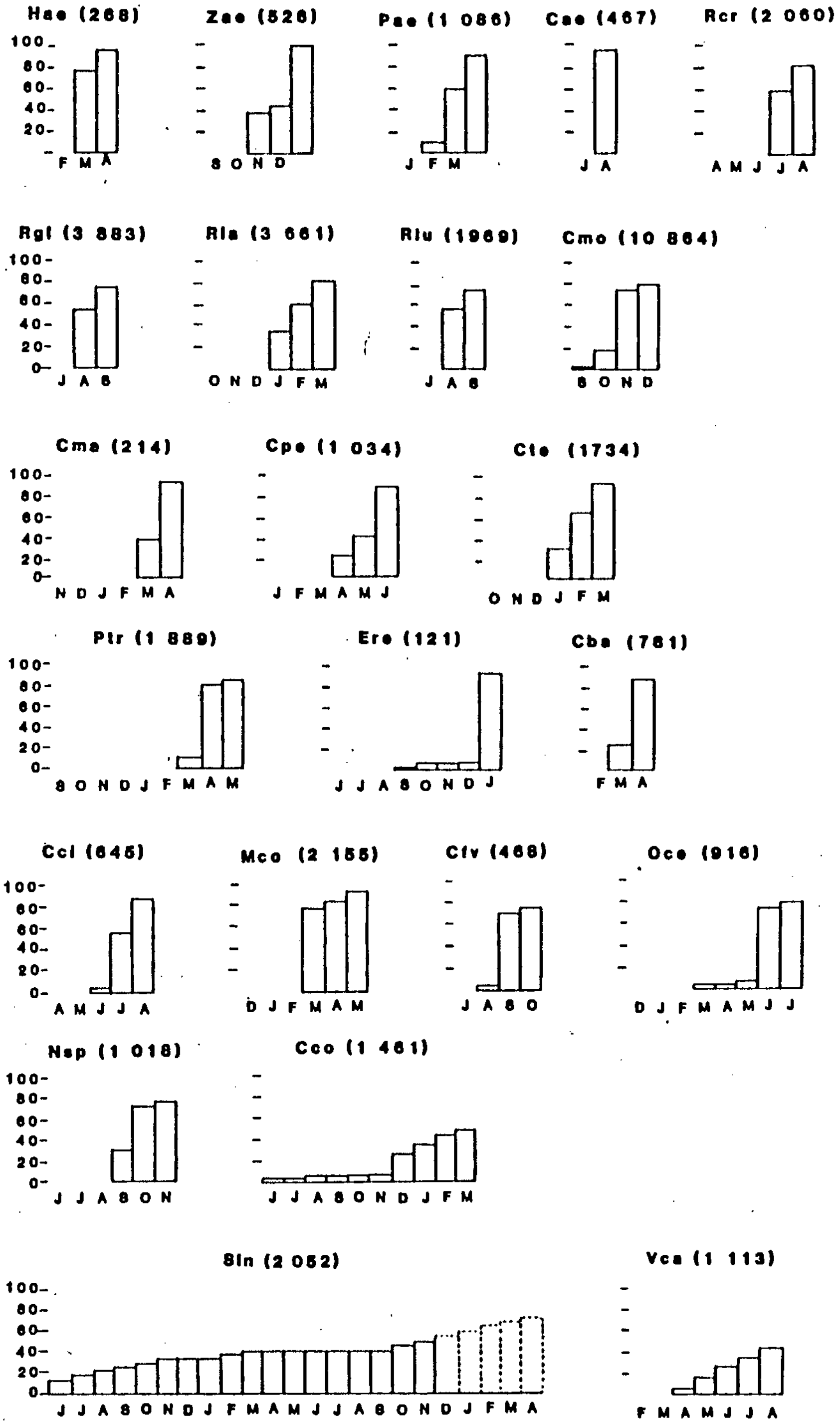
Table 1 Spearman Rank Correlations between monthly availability of fruit and active ripening of fruit with six environmental variables.

Environmental variables	Fruit availability $\underline{n}=22$	Fruit ripening $\underline{n}=22$
Mean monthly rainfall	-0,08	+0,43*
Mean monthly maximum temperature	-0,26	-0,53**
Mean monthly minimum temperature	-0,37	-0,51**
Mean monthly temperature	-0,34	-0,56**
Potential evapotranspiration	-0,28	-0,60**
Mean monthly rainfall minus potential evapotranspiration	+0,21	+0,62**

* $\underline{P} < 0,05$

** $\underline{P} < 0,01$

Figure 8 The rates of ripening from full-sized, but unripe to fully ripe fruits for Coastal Thicket species. The first month on the horizontal axis indicates when sampling was initiated, whereas the vertical axis indicates the monthly proportion of species initially marked that have ripened. Values in parentheses represent the number of fruits sampled. Hae = Haemanthus spp., Zae = Zantedeschia aethiopica, Pae = Protasparagus aethiopicus, Cae = Chasmanthe aethiopica, Rcr = Rhus crenata, Rgl = Rhus glauca, Rla = Rhus laevigata, Rlu = Rhus lucida, Cmo = Chrysanthemoides monilifera, Cma = Cassine maritima, Cpe = Cassine peragua, Cte = Cassine tetragona, Ptr = Pterocelastrus tricuspidatus, Erm = Euclea racemosa, Cba = Chironia baccifera, Cci = Cassytha ciliolata, Mco = Myrica cordifolia, Cfv = Chionanthus foveolata, Oca = Olea capensis, Nsp = Nylandtia spinosa, Cco = Colpoon compressum, Sin = Sideroxylon inerme, Vca = Viscum capense.


Hae (268)
100
80
60
40
20
F M A
Zae (526)
S O N D
Pae (1 086)
J F M
Cae (467)
J A
Rcr (2 060)
A M J J A
Rgl (3 883)
100
80
60
40
20
0
J A S
Rla (3 661)
O N D J F M
Rlu (1969)
J A S
Cmo (10 864)
S O N D
Cma (214)
100
80
60
40
20
0
N D J F M A
Cpe (1 034)
J F M A M J
Cle (1734)
O N D J F M
Ptr (1 889)
100
80
60
40
20
0
S O N D J F M A M
Ere (121)
J J A S O N D J
Cba (761)
F M A
Ccl (645)
100
80
60
40
20
0
A M J J A
Mco (2 155)
D J F M A M
Cfv (468)
J A S O
Oce (916)
D J F M A M J J
Nsp (1 018)
100
80
60
40
20
0
J J A S O N
Cco (1 461)
J J A S O N D J F M
Sin (2 052)
100
80
60
40
20
0
J J A S O N D J F M A M J J A S O N D J F M A
Vca (1 113)
F M A M J J A

temperatures and availability of water resources.

Fruiting synchrony and flower to fruit development

In Appendix 2 the estimated degree of intraspecific synchrony in coastal thicket fruit crops is summarized. It should, however, be borne in mind that species such as *Colpoon compressum* and *Sideroxylon inerme* possess staggered fruiting (Figure 8). It is consequently difficult to separate intraspecific and intra-individual (between branches of the same plant) asynchrony in fruiting. A high degree of intra-individual asynchrony in a population of conspecifics could result in an apparent prolonged intraspecific synchrony in fruiting. In Appendix 3 the approximate flower to fruit development period is catalogued. Unfortunately in species that have asynchronous flowering or fruiting, such as *Chrysanthemoides monilifera* and *Rapanea melanophloeos* respectively, it is difficult to place the species in any of the three categories. For example, June flowering in *Chrysanthemoides monilifera* produced fruit only a month earlier than October flowering.

Ripening rates

The rates of ripening from full-sized but unripe fruits to fully ripe fruits varied considerably between the Coastal Thicket plant species (Figure 8). *Sideroxylon inerme* takes up to 18 months to ripening, whereas other species may ripen within a month (*Chasmanthe aethiopicus*). The synchrony in fruiting of similarly mature fruits also varies considerably between plants. *Colpoon compressum*, *Euclea racemosa* and *Olea capensis* all have asynchronous fruiting, this may promote a lengthening in fruit season.

Discussion

Comparison with the eastern Cape

In the eastern Cape (Liversidge 1970, Pierce & Cowling 1984) it appears that *Rhus glauca*, *Rhus lucida*, *Colpoon compressum*, *Sideroxylon inerme* and *Viscum capense* all have a similar seasonal availability of fruits to those of the southwestern Cape (Table 2). However, more species (*Rhus crenata*,

Table 1 The comparison between the monthly fruiting recorded in this study with that of the two eastern Cape studies, Liversidge (1970) Pierce and Cowling (1984).*

	Months of the year											
	J	F	M	A	M	J	J	A	S	O	N	D
<u>Rhus</u> <u>crenata</u> Thunb.						X	X	X	X	X	X	
	0		0	0	0	0	0		0	0	0	0
<u>Rhus</u> <u>glauca</u> Thunb.								X	X	X	X	
						0	0	0	0	0		
<u>Rhus</u> <u>laevigata</u> L.	X	X	X	X	X							
	#	#	#	#	#	#	#					
<u>Chrysanthemoides</u> <u>monilifera</u> L.(Nor)								X	X	X	X	X
	0	0	0	0		0	0	0	0	0		
<u>Cassine</u> <u>maritima</u> (Bolus) L.Bolus								X	X	X	X	X
	0	0	0	0		0	0	0	0	0		
<u>Cassine</u> <u>tetragona</u> (L.f.) Loes	X	X	X	X	X	X			X	X	X	
	0	0	0	0		0			0			
	#	#										#
<u>Maytenus</u> <u>acuminata</u> (L.f.) Loes	X	X	X	X	X	X	X	X	X	X	X	X
					#	#						
<u>Pterocelastrus</u> <u>tricuspidatus</u> (Lam.) Sonder				X	X	X	X	X	X			
	#	#	#									
<u>Euclea</u> <u>racemosa</u> Murray	X	X	X									
	0	0	0	0	0	0				0	0	0
										#	#	#
<u>Chironia</u> <u>baccifera</u> L.		X	X	X								
		0	0	0	0	0			0			
<u>Myrica</u> <u>cordifolia</u> L.			X	X	X	X						
			0	0	0				0	0	0	0
<u>Olea</u> <u>exasperata</u> Jacq.									X	X		
	0		0	0	0		0					0
				#								
<u>Colpoon</u> <u>compressum</u> Bergius	X	X	X	X	X	X	X	X	X	X	X	X
	0	0	0	0	0	0	0	0	0	0	0	0
<u>Sideroxylon</u> <u>inerme</u> L.	X	X	X	X	X	X	X	X	X	X	X	X
	0	0	0	0	0		0	0	0	0	0	0
	#	#	#									#
<u>Solanum</u> <u>quadrangulare</u> Thunb. ex L.f.					X	X	X	X				X
								0				
<u>Passerina</u> <u>rigida</u> Wikstrom												X
	0	0								0	0	0
<u>Viscum</u> <u>capense</u> L.f.				X	X	X	X	X	X			
			0	0	0	0	0	0	0	0		

*X This study, 0 Liveridge, # Pierce and Cowling 1984.

Chrysanthemoides monilifera, *Cassine maritima*, *Euclea racemosa*, *Chironia baccifera*, *Myrica cordifolia*, *Olea exasperata* and *Passerina rigida* have a longer seasonal availability of fruits in the eastern Cape than in the southwestern Cape (Table 1). From the two studies cited and the present one it appears that only *Cassine tetragona*, *Maytenus acuminata*, *Pterocelastrus tricuspidatus*, and *Solanum quadrangulare* have a longer seasonal availability of fruits in the southwestern Cape (Table 1).

The first hypothesis stated that fruiting in autumn followed by seedling establishment during the moist winters may be advantageous if the plant is to escape post-dispersal seed-predation. Since the association between fruiting seasonality and site was non-significant (X^2 = 8,60; *df* = 22), and maximum species fruiting occurred in spring and autumn (Figures 4-7) an autumnal fruiting is unlikely to be an essential adaptation for mediterranean-type plants. However, periods of moderately high temperatures and availability of water had the most number of species in fruit.

The second hypothesis stated that the tropically derived species that have penetrated winter rainfall areas of the southwestern Cape should have a longer fruiting season. From inspection of Table 1 it is evident that the same plant species in the eastern Cape tend to have longer fruiting seasons. Consequently the second hypothesis that Coastal Thicket plant species in the species depauperate southwestern Cape would have lengthened fruit seasons is rejected.

The third hypothesis was to determine if any species possessed predictable fruiting and could therefore be used by itinerant frugivores. In the coastal sites, both *Colpoon compressum* and *Sideroxylon inerme* were able to fruit in any month of the year. Fairly predictable spring fruiting species included *Chrysanthemoides monilifera*, *Knowltonia capensis*, *Rhus glauca*, *R. lucida*, *Cassytha ciliolata* and *Nylandtia spinosa* (factors 3 and 6; Figure 2). Predictable autumn fruiting species included *Haemanthus coccineus*, *Cassine maritima*, *Chironia baccifera* and *Myrica cordifolia* (factors 4 and 5; Figure 4). In the ecotone areas relatively predictable fruiting species included *Maytenus acuminata* (factor 4; Figure 5) and *Viscum capense* (factor 3; Figure 5) and also *Kiggelaria africana* (factors 2 and 7; Figure 5). Other species that appeared to have fairly predictable fruiting, but were not characterized by the Boolean factor analysis included Chrysanthemoides monilifera and Knowltonia capensis (Appendix 1b). In the Afromontane Forest/Thicket vegetation, Chrysanthemoides monilifera and Knowltonia capensis appeared to be the only predictable fruiting species (factor 3; Figure 6). With regard to the alien plants, Lantana camara and Solanum nigrum had predictable autumn fruiting and Phytolacca octandra and Rubus sp. had predictable spring fruiting (factor 3; Figure 7). These species may support locally itinerant populations of frugivores, thereby confirming the third hypothesis.

Timing of fruiting

The seasonal ripening and presentation of fruit is dependent on a large number of events prior to fruiting. These include the predictability of the environment at both flowering and fruiting, and the presence of both pollinator and disperser vectors at the appropriate times. Since the majority of species in Appendices 1a-d are insect or bird pollinated (Chasmanthe aethiopica and Halleria lucida) the presence of the appropriate pollinator is important for fruit to be set and be dispersed. Avian seed-dispersers such as the Sombre Bulbul (Andropadus importunus) and Cape Bulbul (Pycnonotus capensis) are present all year round, and therefore, unlike in northern temperate areas, there is no need to co-ordinate fruit production with seasonal utilization of fruit by migrant frugivores (Thompson & Willson 1979; Stiles 1980; Herrera 1982a,1982b; Stapanian 1982).

The presentation of both flowers and fruits can be seasonally synchronized or prolonged. Synchronized flowering can be accompanied by an asynchronous fruiting season as occurs in Myrsine africana, Rapanea melanophloeos, Olea capensis and Sideroxylon inerme. In contrast, Chrysanthemoides monilifera possessed asynchronous flowering followed by synchronized fruiting. Halleria lucida and Colpoon compressum possessed asynchronous flowering and fruiting, but Kiggelaria africana, Myrica cordifolia and Knowltonia capensis had synchronized flowering and fruiting.

Fruiting also needs to be coordinated with germination, especially if species propagules are subject to either a high degree of seed predation

(Chrysanthemoides monilifera) or seedling predation. By preventing germination until conditions are suitable, a more successful seedling establishment may result (Rathcke & Lacey 1985). This strategy is only effective if seed predation is low. High seed predation may have promoted the evolution of mast fruiting (Ilex mitis, Myrica serrata, Rapanea melanophloeos and Olinia ventosa), and is a strategy that results in predator satiation. Smith (1970), Sork & Boucher (1977) and Sork (1983) showed that those species possessing mast fruiting had successful seedling establishment only after a period of mast fruiting. In the southern Cape, a massive seedling recruitment of R. melanophloeos occurred following a mast fruiting (C. Geldenhuys, personal communication). Massive fruiting of R. melanophloeos at Hermanus in May 1987 also preceded massive seedling recruitments (pers. obs). In experimental studies it has been shown that asynchronous fruiting in the tropical shrub Hybanthus prunifolius resulted in higher seed predation than that occurring in individuals that fruited synchronously (Augspurger 1981). However, in the case of Rapanea melanophloeos at Hermanus, neither the mast fruiting that occurred in the forest (Appendix 1c) nor the meagre asynchronous fruiting that occurred in the Coastal Thicket produced any seedling recruitment. It was also noted that in both Rapanea melanophloeos and Olea exasperata massive synchronized flowering in anticipated preparation for mast fruiting (November 1983) resulted in total fruit abortion. The fruiting recorded for these two species (Appendix 1 a) was at a very low intensity and only among a few individual plants. It therefore appears that asynchronous timing in reproductive effort produced ripe and viable fruits. It is not known whether mast crops also produce viable seeds. Other factors influencing the timing of fruiting in some plants include later ripening in larger fruit crops of the blueberry Vaccinium (Lyrene 1943), and earlier fruiting in blueberry plants that produced many-seeded berries as opposed to those individuals producing fewer seeded berries (Aalders and Hall 1961). Similar aspects in the fruiting in Chrysanthemoides monilifera were examined but such results were not confirmed. It has also been suggested that carbohydrate investments in the meristem may promote the development of flower buds and thereby inhibit vegetative growth (Borchert 1983). However, simultaneous vegetative growth and fruiting has been described (Jurik 1983) and shoot initiation was observed during fruiting in Myrica cordifolia and Sideroxylon inerme (pers. obs). Simultaneous shoot elongation, flowering and fruiting occurs in *Colpoon compressum* and in this regard is similar to its relative *Osyris quadripartita* found in southern Spain (Herrera 1984).

Peaks and regularity in fruiting

Autumn fruiting

One of the aims of this study was to identify species possessing predictable seasonal fruiting. Unfortunately, the results obtained relate to only two fruiting seasons. Long-term predictabilities would probably be much lower than suggested by these results. It does appear that there are slight peaks in the number of species fruiting in autumn and spring. It is conceivable that such peaks are the products of either seed predation and or resource utilization. If fruit is to be produced in autumn, the fruit development leading to maturation would need to occur during summer when evapotranspiration levels are highest (Figures 2 and 3). The development of fruit during the dry period may result in a high degree of inviable or aborted fruits. This appears to have been the case for the Panamanian shrub *Hybanthus prunifolius* (Augspurger 1980). Consequently tropical areas possessing a seasonal rainfall have peak species fruiting during the rainy season (Janzen 1967; Karr 1976; Lieberman 1982). Some of the species that fruit at the beginning of the wet winter season at Hermanus (*Kiggelaria africana*, *Myrica cordifolia*, *Chironia baccifera*) appear to have seedling recruitments just after the first extended rains (May)(see Chapter 2). In experimental sowing of *Rapanea melanophloeos* at Hermanus the seedlings also emerged during May, but only a year after sowing. From experimental studies it appears that both *Kiggelaria africana* and *Myrica cordifolia* possess either a short-term dormancy or no dormancy. The midsummer fruiting of the alien *Acacia cyclops* appears to be followed by an indeterminate but probably innate dormancy period. Dormancy appears to be broken only after fire, but maximum seedling establishment appears to occur during winter (pers. obs).

Spring fruiting

Spring fruiting would allow the development of fleshy fruits during periods of peak moisture availability. Fleshy fruits in seasonal tropical forests are normally produced during the wet months (Lieberman 1982). If fruit production is sufficiently large or seed mortality sufficiently low, fleshy fruits could be produced in spring, taking advantage of development during moist periods, but the ensuing germination could occur in autumn allowing seedling establishment during the wet season. The large fruit production in Chrysanthemoides monilifera appears to have permitted this strategy (pers. obs) and a similar pattern may also be true for Chionanthus foveolata (pers. obs). However, in both of these species a large fruit production is offset by high seed mortality.

Evaluation of techniques

The use of presence/absence data on fruiting may appear crude, but such a technique overcame the considerable conspecific and intra-individual variations in fruiting that occurred. Such variations inhibit the quantification of phenological studies (Pierce & Cowling 1984). The field techniques used allowed gross fruiting within an assemblage of plants to be described and related to environmental variables.

To birds the important aspect of fruiting phenology is not whether the total pattern is random or not, but whether within the total pattern there are any plants with predictable fruiting. Random models are difficult to interpret, since different assumptions in the modelling will yield different results (Rathcke 1983). For example the apparent staggered fruiting in Miconia spp. (Snow 1965) has been shown to be indistinguishable from random (Gleeson 1981). I consider that the use of any of these techniques is only worthwhile in a data set collected over many seasons. Both the field and numerical techniques used in this paper are basically descriptive and, therefore, the results should be used as a framework for addressing future research.

Conclusion

1) In the Coastal Thicket there is never any month without ripe fruits. In ecotone areas and, in particular the Afromontane Forest/Thicket and alien plants, a greater fruiting seasonality exists.

2) The irregular fruiting in most species, together with variable flower to fruit development periods, and an asynchronous fruit production in conspecifics, confirms that phenological flexibilities exist for these plants. This is further confirmed by species that are able to produce vegetative growth throughout the year (*Myrica cordifolia*, *Colpoon compressum* and *Sideroxylon inerme*).

3) A small suite of species possesses seasonally regular fruiting, and are most dominant in the Coastal Thicket. These species may be important for maintaining the locally itinerant populations of frugivores.

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Appendix 1a The fruiting phenology of 38 indigenous plant species occurring in the coastal thicket vegetation at Hermanus, south-western Cape.

	Months from 1983 to 1985																						
	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Coastal thicket species.				1983										1984								1985		
Amaryllidaceae																								
Haemanthus coccineus L.											X	X										X	X	
Haemanthus sanguineus Jacq.										X											X	X		
Araceae																								
Zantedeschia aethiopica L. Sprengel						X	X	X										X	X	X				
Asparagaceae																								
Myrsiphyllum declinatum (L.) Oberm.														X	X	X								
Protasparagus aethiopicus (L.) Oberm.	X								X	X	X	X	X	X	X								X	X
Protasparagus capensis (L.) Oberm.								X														X		
Iradaceae																								
Chasmanthe aethiopica (L.)N.E. Br.			X												X	X								
Anacardiaceae																								
Rhus crenata Thunb.													X	X	X	X	X							X
Rhus glauca Thunb.			X	X												X	X	X						
Rhus laevigata L.								X	X	X	X	X								X	X	X	X	X
Rhus lucida L.			X	X														X	X	X				
Asteraceae																								
Chrysanthemoides monilifera (L.) Nor					X	X	X								X	X	X	X						
Celastraceae																								
Cassine maritima (Bolus) L.Bolus										X	X												X	X
Cassine peragua L.	X	X	X	X								X	X	X	X	X								X
Cassine tetragona (L.f.) Loes								X	X	X	X	X	X			X	X	X						X
Maytenus heterophylla (Ecklon & Zeyher)N.Robson																			X					
Pterocelastrus tricuspidatus (Lam.)Sonder	X	X									X	X	X	X	X	X							X	X
Cucurbitaceae																								
Kedrostis nana (Lam.)Cogn.				X						X												X		
Ebenaceae																								
Euclea racemosa Murray								X	X	X														
Gentianaceae																								
Chironia baccifera L.										X	X												X	X

Lauraceae																								
<u>Cassytha</u> <u>ciliolata</u> Nees	X	X	X	X	X	X	X							X	X	X	X							
Menispermaceae																								
<u>Cissampelos</u> <u>capensis</u> L.f.																						X	X	X
Myricaceae																								
<u>Myrica</u> <u>cordifolia</u> L.										X	X	X	X									X	X	X
Myrsinaceae																								
<u>Myrsine</u> <u>africana</u> L.	X	X	X	X	X	X	X																	
<u>Rapanea</u> <u>melanophloeos</u> (L.) Mez													X											
Oleaceae																								
<u>Chionanthus</u> <u>foveolata</u> (E.Meyer)Stearn				X	X	X	X																	X
<u>Olea</u> <u>capensis</u> (L.)	X	X	X	X	X	X	X	X					X	X	X	X	X	X				X	X	X
<u>Olea</u> <u>exasperata</u> Jacq.																X	X							
Oliniaceae																								
<u>Olinia</u> <u>ventosa</u> (L.) Cuf.					X	X	X																	
Polygalaceae																								
<u>Nylandtia</u> <u>spinosa</u> (L.)Dumort.				X	X	X	X	X	X								X	X						
Ranunculaceae																								
<u>Knowltonia</u> <u>capensis</u> (L.) Huth				X	X	X											X	X						
Santalaceae																								
<u>Colpoon</u> <u>compressum</u> Bergius	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Sapotaceae																								
<u>Sideroxylon</u> <u>inerme</u> L.	X	X	X	X	X	X	X	X	X	X	X	X					X	X	X	X	X	X	X	X
Solanaceae																								
<u>Lycium</u> <u>afrum</u> L.						X																		
<u>Solanum</u> <u>quadrangulare</u> Thunb. ex L.f.	X	X	X									X							X					
Thymelaeaceae																								
<u>Passerina</u> <u>ericoides</u> L.							X																	
<u>Passerina</u> <u>rigida</u> Wikstrom							X																	
Viscaceae																								
<u>Viscum</u> <u>capense</u> L.f.	X	X	X	X								X	X	X	X	X							X	X

Appendix 1b The fruiting phenology of 17 indigenous plant species occurring in the ecotone vegetation at Hermanus.

	Months from 1983 to 1985																							
Ecotone vegetation	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Anacardiaceae																								
Rhus lucida L.			X	X														X	X	X				
Rhus rosmarinifolia Vahl												X	X	X										
Rhus tomentosa L.					X	X																		
Asteraceae																								
Chrysanthemoides monilifera (L.) Nor					X	X	X								X	X	X	X						
Celastraceae																								
Hartogiella schinoides (Sprengel) Codd							X	X															X	X
Maytenus acuminata (L.f.) Loes.	X	X	X	X	X	X								X	X	X	X	X	X	X	X	X	X	X
Ebenaceae																								
Diospyros glabra (L.) de Winter								X	X												X			
Euclea polyandra (L.f.) E. Meyer ex Hiem							X	X																
Flacourtiaceae																								
Kiggelaria africana L.										X	X	X									X	X	X	
Lauraceae																								
Cassytha ciliolata Nees	X	X	X	X	X	X	X							X	X	X	X							
Myrsinaceae																								
Myrsine africana L.	X	X	X	X	X	X																		
Rapanea melanophloeos (L.) Mez									X	X	X	X	X											
Oleaceae																								
Olea capensis (L.)	X	X	X	X	X	X	X	X					X	X	X	X	X	X				X	X	X
Ranunculaceae																								
Knowltonia capensis (L.) Huth				X	X	X											X	X						
Santalaceae																								
Colpoon compressum Bergius	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Scrophulariaceae																								
Halleria lucida L.	X	X	X	X	X	X	X	X	X	X	X													
Viscaceae																								
Viscum capense L.f.	X	X	X	X								X	X	X	X	X							X	X

Appendix 1c The fruiting phenology of 13 indigenous plant species occurring in the mountain forest/thicket vegetation at Hermanus.

Mountain forest/thicket vegetation	Months from 1983 to 1985																							
	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Aquifoliaceae																								
Ilex mitis (L.) Radlk.																						X	X	X
Asteraceae																								
Chrysanthemoides monilifera (L.) Nor				X	X	X									X	X	X	X						
Celastraceae																								
Cassine peragua L.																								X
Hartogiella schinoides (Sprengel) Codd							X	X															X	X
Pterocelastrus rostratus (Thunb.) Walp.				X	X	X					X	X	X	X	X	X				X	X	X	X	X
Icacinaceae																								
Apodytes sp.																								X
Myricaceae																								
Myrica serrata Lam.							X	X	x															
Myrsinaceae																								
Rapanea melanophloeos (L.) Mez									X	X	X	X	X											
Oleaceae																								
Chionanthus foveolata (E. Meyer) Stearn							X																	
Olea capensis (L.)				X	X	X	X	X																
Oliniaceae																								
Olinia ventosa (L.) Cuf.					X	X	X	X																
Ranunculaceae																								
Knowltonia capensis (L.) Huth				X	X	X											X	X						
Scrophulariaceae																								
Halleria lucida L.	X	X	X	X	X	X	X	X	X	X	X													

Appendix 1d The fruiting phenology of nine alien plant species occurring in all vegetation types at Hermanus.

	Months from 1983 to 1985																							
Alien vegetation	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Fabaceae																								
Acacia cyclops A. Cunn. ex G. Don							X	X	X	X								X	X	X				
Myoporaceae																								
Myoporum serratum R. Br.					X	X			X															
Myrtaceae																								
Metrosideros excelsus Soland. ex Gaertn.							X	X											X					
Phytolaccaceae																								
Phytolacca octandra L.				X	X	X	X									X	X	X						
Pittosporaceae																								
Pittosporum undulatum Vent.			X	X	X	X	X	X	X														X	X
Rosaceae																								
Rubus sp. (*fruticosus* L. ?)					X			X	X	X						X	X	X						
Solanaceae																								
Solanum mauritianum Scop.		X	X	X	X	X	X	X	X	X	X						X	X	X	X	X	X	X	X
Solanum nigrum L. Complex		X									X	X									X	X		
Verbenaceae																								
Lantana camara L. Complex									X	X	X	X										X	X	X

Appendix 2 The degree of synchrony in fruiting that occurred in the Coastal Thicket vegetation at Hermanus during June 1983 to May 1985.

Species with less than 20 % synchrony at peak fruiting

Myrsiphyllum declinatum, *Protasparagus capensis*, *Cassine maritima*, *Cassine peragua*, *Maytenus heterophylla*, *Kedrostis nana*, *Euclea racemosa*, *Cissampelos capensis*, *Rapanea melanophloeos*, *Olea exasperata*, *Olinia ventosa*, *Lycium afrum*, *Solanum quadrangulare*

Species with between 20 and 40 % synchrony at peak fruiting

Zantedeschia aethiopica, *Pterocelastrus tricuspidatus*, *Cassytha ciliolata*, *Myrsine africana*, *Olea capensis*, *Nylandtia spinosa*, *Passerina ericoides*, *Passerina rigida*

Species with greater than 40 % synchrony at peak fruiting

Haemanthus coccineus, *Haemanthus sanguineus*, *Protasparagus aethiopicus*, *Chasmanthe aethiopica*, *Rhus crenata*, *Rhus glauca*, *Rhus laevigata*, *Rhus lucida*, *Chrysanthemoides monilifera*, *Cassine tetragona*, *Chironia baccifera*, *Myrica cordifolia*, *Chionanthus foveolata*, *Knowltonia capensis*, *Colpoon compressum*, *Sideroxylon inerme*, *Viscum capense*

Appendix 3 Approximate flower to fruit development period in the Coastal Thicket vegetation at Hermanus during June 1983 to May 1985.

Normal flower to fruit development less than 3 months

Haemanthus coccineus, *Haemanthus sanguineus*, *Zantedeschia aethiopica*, *Chasmanthe aethiopica*, *Chrysanthemoides monilifera*, *Knowltonia capensis*

Normal flower to fruit development taking from 3 to 6 months

Myrsiphyllum declinatum, *Protasparagus aethiopicus*, *Protasparagus capensis*, *Rhus crenata*, *Rhus glauca*, *Rhus laevigata*, *Rhus lucida*, *Cassine maritima*, *Cassine peragua*, *Cassine tetragona*, *Maytenus heterophylla*, *Kedrostis nana*, *Chironia baccifera*, *Cassytha ciliolata*, *Nylandtia spinosa*, *Colpoon compressum*, *Solanum quadrangulare*, *Passerina ericoides*, *Passerina rigida*, *Viscum capense*

Normal flower to fruit development taking more than 6 months

Pterocelastrus tricuspidatus, *Euclea racemosa*, *Myrica cordifolia*, *Myrsine africana*, *Rapanea melanophloeos*, *Chionanthus foveolata*, *Olea capensis*

Normal flower to fruit development not determined

Cissampelos capensis, *Olea exasperata*, *Olinia ventosa*, *Lycium afrum*

CHAPTER 4

Fruits in the south-western Cape and their...

Biogeography

Reproduction & Re-establishment

Phenology

▶ Avian Utilization

Competition (Alien vs Indigenous)

Presentation

Opportunistic Dispersal

Dispersal Efficiency

Relationship with Episodic events

Seed predators

Avian frugivory and aggression in relation to fruit availability in a South African Coastal Thicket

Contents

Avian frugivory and aggression in relation to fruit availability in a South African Coastal Thicket

Contents /continued

Avian frugivory and aggression in relation to fruit availability in a South African Coastal Thicket.

Abstract

The use of fleshy fruits of 22 plant species by avian frugivores was studied from June 1983 to May 1984 at Hermanus, southwestern Cape Province, South Africa. Aggressive interactions between birds at fruit crops were also recorded. Contrary to predictions of coevolutionary models, the overall use of fleshy fruits by each avian species was in direct proportion to the availability of fruits. A limited preference existed among frugivores for species bearing fleshy fruits that were either available continuously or were seasonally predictable. For the majority of plant species, frugivory was restricted to, or dominated by a single avian species. Also contrary to expectation, reduced availability of fleshy fruits did not promote increased aggressive interactions among avian frugivores. Instead such interactions were most frequent during periods of fruit abundance, due to increased use of fruits by predominantly insectivorous birds.

To be submitted to Ibis

Introduction

Attributes of fleshy fruits, such as size, nutritional value and seed investment have been used to predict patterns of fruit use by birds (Snow 1971; McKey 1975; Howe & Estabrook 1977). Attempts to test such predictions (e.g. Frost 1980) have failed to quantify overall temporal and spatial fruit availability.

Lack (1954) argued that food is the major regulator of avian populations, with the consequence that competition for food may be expected. Moore (1978) and Snow & Snow (1984) quantified aggressive avian interactions which occurred during the defence of limited, winter fruit resources. However, none of these studies quantified the availability of fruit.

In this study of fruit-frugivore interactions in a South African Coastal Thicket an attempt was made to relate fruit availability with avian use and aggression. Observed avian use of fruit was compared to fruit availability using the null hypothesis that birds use fruit (observed frugivory) in direct proportion to its availability (expected frugivory). A second hypothesis based on Leck (1972) predicted that frugivore aggression should be most frequent during relative fruit scarcity, and least frequent during fruit abundance.

Materials & Methods

Study area

This study was undertaken in Coastal Thicket vegetation, referred to as South Coast Strandveld by Moll *et al*. (1984), at Hermanus (34° 25′ S; 19° 16′ E), Cape Province, South Africa. The vegetation is a complex mosaic of different plant assemblages. Dominant and widespread plant species bearing fleshy fruits include *Rhus lucida*, *R. glauca*, *Rhus* hybrids, *Sideroxylon inerme*, *Protasparagus aethiopicus* and *Cassine maritima*. Locally dominant species include *Euclea racemosa*, *Rhus crenata*, *Rapanea melanophloeos* and *Olea exasperata*. Plant nomenclature follows Bond & Goldblatt (1984). Although woody vegetation is dominant in terms of plant cover, it is represented by only 50 species, whereas small forbs and geophytes which contribute a negligible cover (< 0,01%) represent the majority of the 900 + coastal plant species collected locally and held at the Hermanus herbarium.

Field techniques

In order to achieve equal sampling throughout the 16 ha study site major plant assemblages were identified using a floristic classification based on percentage canopy cover within 40 100 m^2 releves. Nine plant species assemblages were recognized (Figure 1), and within each assemblage four permanent circular plots (10 m in diameter) were demarcated. Sampling for avian frugivory was therefore directed at the species within the habitat, rather than at individual plants (cf. Kantak 1979; Frost 1980; Stapanian 1982; Pratt & Stiles 1985).

Monthly occurrence of fruiting for each plant species was recorded, and all reproductively mature plants were individually labelled. Intraspecific synchrony in fruiting was determined by comparing labelled plants with unlabbelled plants up to 10 m away from the plot and was scored on a scale of 1 to 3 (< 20%, 20-40%, >40% fruiting individuals). Fruit crop sizes were estimated by sampling branches, and were scored on a scale of 1 to 6 (1-10, 11-100, 101-1 000, 1 001-10 000, 10 001-100 000, > 100 000 fruits per plant). The abundance of each plant species was calculated using the data collected from the releves. Data were corrected for the different areas occupied by the nine plant assemblages and abundance of plants was expressed as a percentage of total area. Fruit quality (Table 1) was subjectively assessed according to nutritional value, seed size and persistence on the plant (Stiles 1980). The nutritional value of fruit was based on pericarp texture and appearance. Pericarp that was oily and dry in feel was considered to be lipid-rich, whereas watery and sugary fruit was considered to be low in lipids. The 1 - 8 ordinal scale (Table 1) assumes that investment in the pericarp constitute a greater reward for frugivores than if resources had been invested in the seed.

Use of fruit by birds was recorded during 15 minute observation periods in each permanent, circular plot and was replicated four times each month (June 1983 to May 1984). Sequence of sampling at the plots was randomized. All

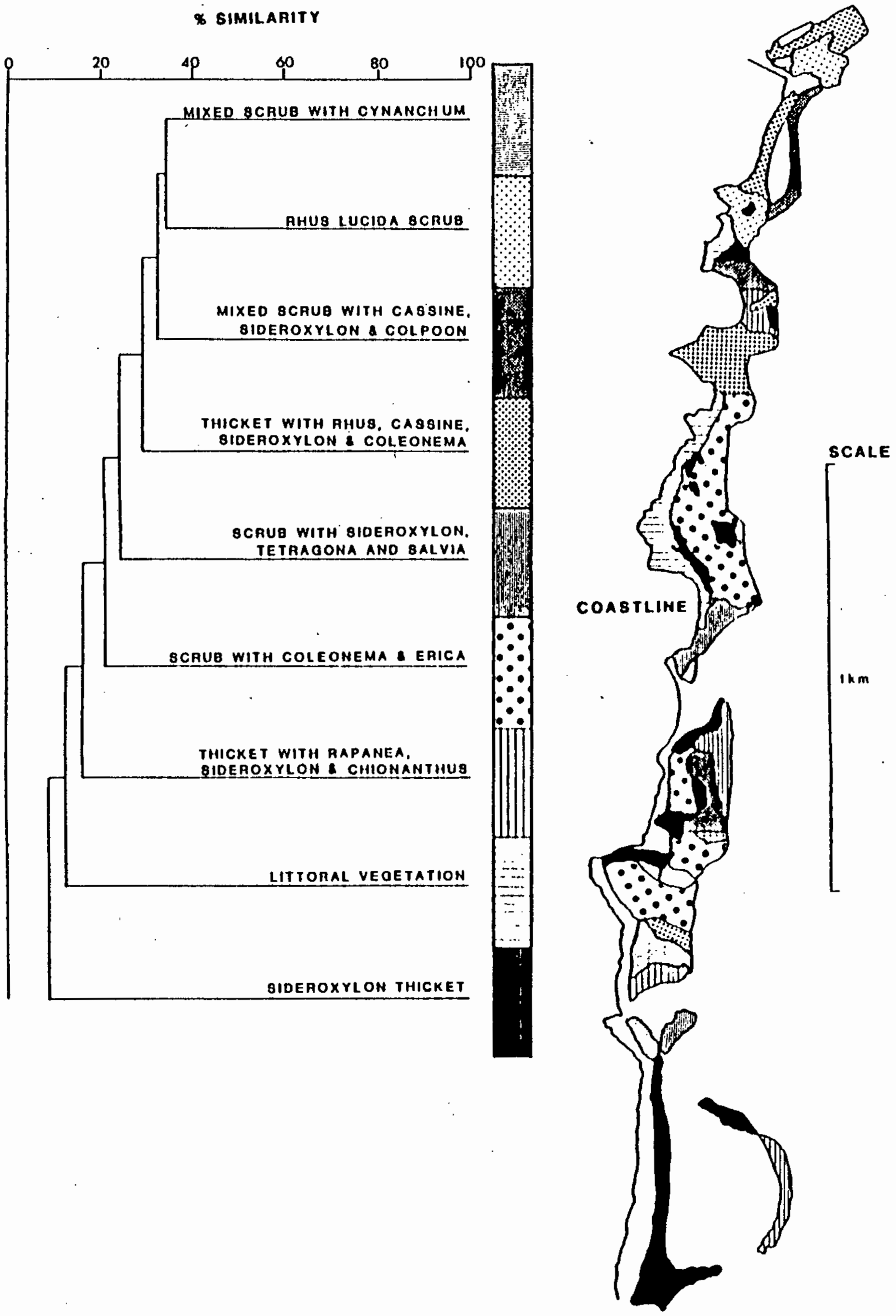


Figure 1 Map showing the nine plant species assemblages recognized in the Coastal Thickets at Hermanus. Blank areas represent either dunes or areas devoid of natural vegetation.

Table 1 Three parameters used to classify plants occurring in a southern African Coastal Thicket on a one to eight ordinal scale of increasing fruit quality.

Ordinal scale of fruit quality	Parameters		
	Seed investment	Pericarp quality	Retention on plant
1	Low	Low	Short
2	High	Low	Short
3	Low	Low	Long
4	Low	High	Short
5	High	Low	Long
6	High	High	Short
7	Low	High	Long
8	High	High	Long

observed avian frugivory accumulated for each species was ranked with respect to other species. All cases of aggressive avian interaction were noted during these 15 minute observation periods, even if they occurred outside the circular plots. A frugivorous bird approaching and attempting to drive off any other bird was considered to represent an aggressive interaction, irrespective of whether the attack was successful.

Numerical techniques

The floristic composition of the 40 releves was classified using a Bray & Curtis (1957) measure of similarity, and pictorially represented as a dendrogram.

The fruit characteristics of plants with fruits used and not used by birds were compared by means of Mann-Whitney U tests (Siegel 1956). Fruit characteristics were also related to avian frugivory using Spearman Rank Correlations (Siegel 1956).

For each plant species fruit ripening synchrony, crop size and seasonal availability together with average plant abundance were integrated into a single index representing total fruit availability. This index was derived using a procedure whereby each plant species was ranked with respect to all other plant species and for each of the four variables. The four sets of ranks (representing each variable) were totalled for each species. The accumulated scores were, in turn, ranked among species. These rankings represented expected frugivory and were compared to observed frugivory using a Spearman Rank Correlation. Correspondence analysis (Greenacre 1984; Underhill & Peisach 1985) was used to describe individual plant-bird relationships by means of an ordination plot. The relationship between frugivore size (based on mass data from Maclean (1985)) and fruit size (mean length) was determined using a Spearman Rank Correlation.

Table 2 Fruit quality, quantity and availability of 22 plant species in Coastal Thicket vegetation in relation to their use by frugivorous birds.

Plant species	Plants bearing fleshy fruit					Frugivorous birds		
	*Fruit type	No. of months in which ripe fruit is available	@Fruit crop size	+Fruit ripening synchrony with conspecifics	Overall plant cover (%)	Overall no. of frugivores feeding at each plant species	Overall no. of species feeding at each plant	No. of months with fruit-eating records for each plant species
Haemanthus sp.	2	2	2	3	0,2	2	1	1
Zantedeschia aethiopica	2	3	2	2	0,1	1	1	1
Protasparagus aethiopicus	2	5	4	3	5,1	5	1	1
Rhus glauca	5	2	5	3	4,2	224	5	2
Rhus laevigata	5	5	5	3	2,2	73	2	2
Rhus lucida	5	2	5	3	12,2	273	6	2
Chrysanthemoides monilifera	2	3	5	3	0,8	153	4	1
Cassine maritima	1	2	3	1	3,7	1	1	1
Cassine tetragona	1	5	4	3	1,4	17	3	1
Euclea racemosa	5	3	2	1	3,3	1	1	1
Chironia baccifera	1	2	4	3	0,6	62	2	1
Cassytha ciliolata	1	7	3	2	1,7	17	4	2
Myrica cordifolia	8	3	4	3	0,5	1	1	1
Chionanthus foveolata	8	4	4	3	2,2	44	5	3
Olea capensis	8	8	4	2	0,3	41	3	1
Colpoon compressum	5	12	1	3	2,1	147	5	9
Sideroxylon inerme	5	12	6	3	27,9	541	8	12
Solanum quadrangulare	1	4	3	1	0,3	1	1	1
Viscum capense	1	5	3	3	0,1	37	2	1
Acacia cyclops	8	4	5	3	0,1	41	4	2
Myoporum serratum	2	3	4	1	< 0,1	27	2	1
Phytolacca octandra	1	4	2	1	< 0,1	1	1	1

*Fruit type

1 = Fruit with low seed investment, low quality pericarp and short retention period on the plant

2 = Fruit with high seed investment, low quality pericarp and short retention period on the plant

5 = Fruit with high seed investment, low quality pericarp and long retention period on the plant

8 = Fruit with high seed investment, high quality pericarp and long retention period on the plant

@Fruit crop size

1 = 1 - 10 ripe fruit per plant

2 = 11 - 100 ripe fruit per plant

3 = 101 - 1000 ripe fruit per plant

4 = 1001 - 10000 ripe fruit per plant

5 = 10001 - 100000 ripe fruit per plant

6 = >100000 ripe fruit per plant

+Fruit ripening synchrony

1 = <20% simultaneous fruiting

2 = 20 - 40% simultaneous fruiting

3 = >40% simultaneous fruiting

Table 3 Fruit quality, quantity and availability of 13 plant species in Coastal Thicket which produced fleshy fruits that were not used by frugivorous birds.

Plant species	Fruit type	No. of Months in which ripe fruit was available	Fruit crop size	Fruit ripening synchrony with conspecifics	Overall plant cover
Protasparagus aethiopicus	5	1	2	1	0,05
Chasmanthe aethiopica	2	1	2	3	0,28
Cassine peragua	1	5	3	1	0,32
Pterocelastrus tricuspidatus	8	4	4	2	0,61
Kedrostris nana	2	2	1	1	0,03
Myrsine africana	5	7	4	2	0,81
Olinia ventosa	5	3	4	1	0,01
Nylandtia spinosa	2	6	4	2	0,01
Knowltonia capensis	2	3	3	3	0,06
Lycium afrum	1	1	3	1	0,02
Passerina ericoides	1	1	4	2	0,01
Passerina rigida	1	1	5	2	1,02
Solanum nigrum	1	3	1	1	0,01

Results

Vegetation classification

Nine plant assemblages were recognized at the study site, and each was assumed to be relatively homogeneous. Due to the floristic complexity of the vegetation, cut-off points for defining vegetation similarities were low. Moreover, the resulting dendrogram showed almost perfect chaining, indicating a poor overall classification for the vegetation. The nine plant assemblages are most clearly discriminated with regard to height and plant cover, rather than floristics alone. The mixed scrub community is distinct from the *Rhus lucida* scrub in being taller (> 2m) and possessing a high cover of the creeper *Cynanchum obtusifolium*. The other mixed scrub plant assemblage is taller still and possessed both *Cassine tetragona* and *Sideroxylon inerme*. Given no disturbance this plant assemblage is likely to develop into 4 to 5 m high thicket dominated by *Sideroxylon inerme*, *Chionanthus foveolata* and where sufficiently damp *Rapanea melanophloeos*. The scrub vegetation dominated by *Tetragona fruticosa* and *Salvia africana-lutea* is lower (1 to 1,5 m) and occurs in the more wind-exposed sites. Dwarfed species of *Sideroxylon inerme* are still to be found in this vegetation, but were not recorded in the littoral vegetation which is dominated by *Myrica cordifolia*, *Passerina rigida*, and mesembryanthemums (particularly *Ruschia macowaniii*). The assemblage dominated by *Erica plukenetti* and *Coleonema alba* is structurally the most distinctive, and is similar to Campbell's (1985) Ericaceous Fynbos, excepting for an absence of restioids. The most widespread plant assemblage is the tall (> 4 m), almost pure stand of *Sideroxylon inerme*.

Fruit availability

Thirty-five species fruited during the period June 1983 to May 1984. Fruits of 22 species were used by birds. Birds concentrated their feeding on the common fruiting species (Mann Whitney U test = 230,5; $P < 0,01$)(Tables 2 and 3). Of the 13 plant species not used by frugivores all except *Passerina rigida* had less than 1% cover and, indeed, 62% of these species had less than 0,1% cover. Species used by birds possessed more synchronized fruiting with conspecifics than species not used by birds (U = 208,5; $P < 0,05$) and had a higher than expected frugivory (U = 224,5; P < 0,01).

Of the 22 species used by frugivorous birds (Table 2), seasonal availability of fruit varied between two months (*Haemanthus* spp., *Rhus glauca*, *R. lucida*, *Cassine maritima* and *Chironia baccifera*) and continuous availability (*Colpoon compressum* and *Sideroxylon inerme*). Standing fruit crops varied from 10 fruits per plant (*Colpoon compressum*) to greater than 100 000 fruits per plant (*S. inerme*). In the 22 species used by birds many possessed either over 40% synchrony in fruiting or little synchrony (Table 2). The overall abundance of these plants varied from the rare (alien plants *Myoporum serratum* and *Phytolacca octandra*) to the most common species (*S. inerme*) which covered over a quarter of the area. All of the above fruit characteristics were assumed to be independent of each other except fruit crop size and fruit synchrony ($r_{s\ 20}$ = 0,44; P < 0,05), since intercorrelations were non-significant.

Avian use of fleshy fruits

Seasonal availability of fruit crops was not significantly related to avian frugivory, whereas fruit quality was only related to the number of months in which avian frugivory was observed (Table 4). Size of fruit crop was related to the number of frugivorous bird species, their abundance but not to the number of months in which frugivory was observed (Table 4). Synchrony of fruiting was related to the number of frugivorous bird species, their abundance and the number of months in which avian frugivory was observed (Table 4). Overall plant cover of species was only related to the number of months in which frugivory occurred (Table 4).

Expected and observed frugivory

Expected frugivory based on fruit production and seasonal availability was correlated with number of frugivorous bird species (Figure 2) and their abundance (Figure 3). This suggests that birds' overall use of fruit was in direct proportion to overall fruit availability.

Table 4 Spearman rank correlations between fruit characteristics and their use by avian frugivores in a South African Coastal Thicket.

Fruit character	Overall no. of frugivores feeding at each plant	Overall no. of species feeding at each plant	No. of months with fruit-eating records for each plant species
Fruit quality	0,26	0,29	0,41*
No. of months in which ripe fruit was available	0,14	0,24	0,29
Fruit crop size	0,59**	0,51**	0,34
Fruit ripening synchrony with conspecifics	0,53**	0,44*	0,39*
Overall plant cover (%)	0,34	0,35	0,41*

* $\underline{P} < 0,05$
** $\underline{P} < 0,01$

Table 5 The percentage avian utilization of 22 indigenous and alien plants occurring in Coastal Thicket vegetation at Hermanus during June 1983 to May 1984. Figures in parentheses represent total number of fruit-eating visits by bird species.

Plant species	Bird species										Total No. of fruit-eating visits by all birds at each plant species
	Columba arquatrix (302)	*Colius striatus* (504)	*Colius indicus* (169)	*Pycnonotus capensis* (23)	*Andropadus importunis* (84)	*Cossypha caffra* (22)	*Apalis thoracica* (1)	*Tchagra tchagra* (6)	*Zosterops pallidus* (598)	*Ploceus capensis* (1)	
Haemanthus Sp.	0	0	0	100,0	0	0	0	0	0	0	2
Zantedeschia aethiopica	0	0	0	100,0	0	0	0	0	0	0	1
Protasparagus aethiopicus	0	0	0	0	100,0	0	0	0	0	0	5
Rhus glauca	0	0	11,6	0,9	0,9	0,9	0	.0	85,7	0	224
Rhus laevigata	0	0	0	0	0	1,4	0	0	98,6	0	73
Rhus lucida	0	25,6	0	1,8	1,5	0	0,4	0	70,3	0,4	273
Chrysanthemoides monilifera	98,0	0	0	0,7	0,7	0,7	0	0	0	0	153
Cassine maritima	0	0	0	0	100,0	0	0	0	0	0	1
Cassine tetragona	0	82,4	0	0	11,8	5,9	0	0	0	0	17
Euclea racemosa	0	0	0	0	100,0	0	0	0	0	0	1
Chironia baccifera	96,8	0	0	3,2	0	0	0	0	0	0	62
Cassytha ciliolata	0	82,4	0	5,9	5,9	5,9	0	0	0	0	17
Myrica cordifolia	0	0	0	100,0	0	0	0	0	0	0	1
Chionanthus foveolata	0	63,6	29,6	2,3	2,3	0	0	2,3	0	0	44
Olea capensis	0	68,3	0	0	2,4	0	0	0	29,3	0	41
Colpoon compressum	0	57,1	35,4	0,7	6,1	0	0	0,7	0	0	147
Sideroxylon inerme	16,6	44,0	9,6	0,9	10,4	2,2	0	0,7	15,5	0	541
Solanum quadrangulare	0	0	0	100,0	0	0	0	0	0	0	1
Viscum capense	0	0	0	0	0	2,7	0	0	97,3	0	37
Acacia cyclops	0	34,2	31,7	0	0	4,9	0	0	29,3	0	41
Myoporum serratum	0	51,8	48,2	0	0	0	0	0	0	0	27
Phytolacca octandra	0	0	0	0	0	100,0					

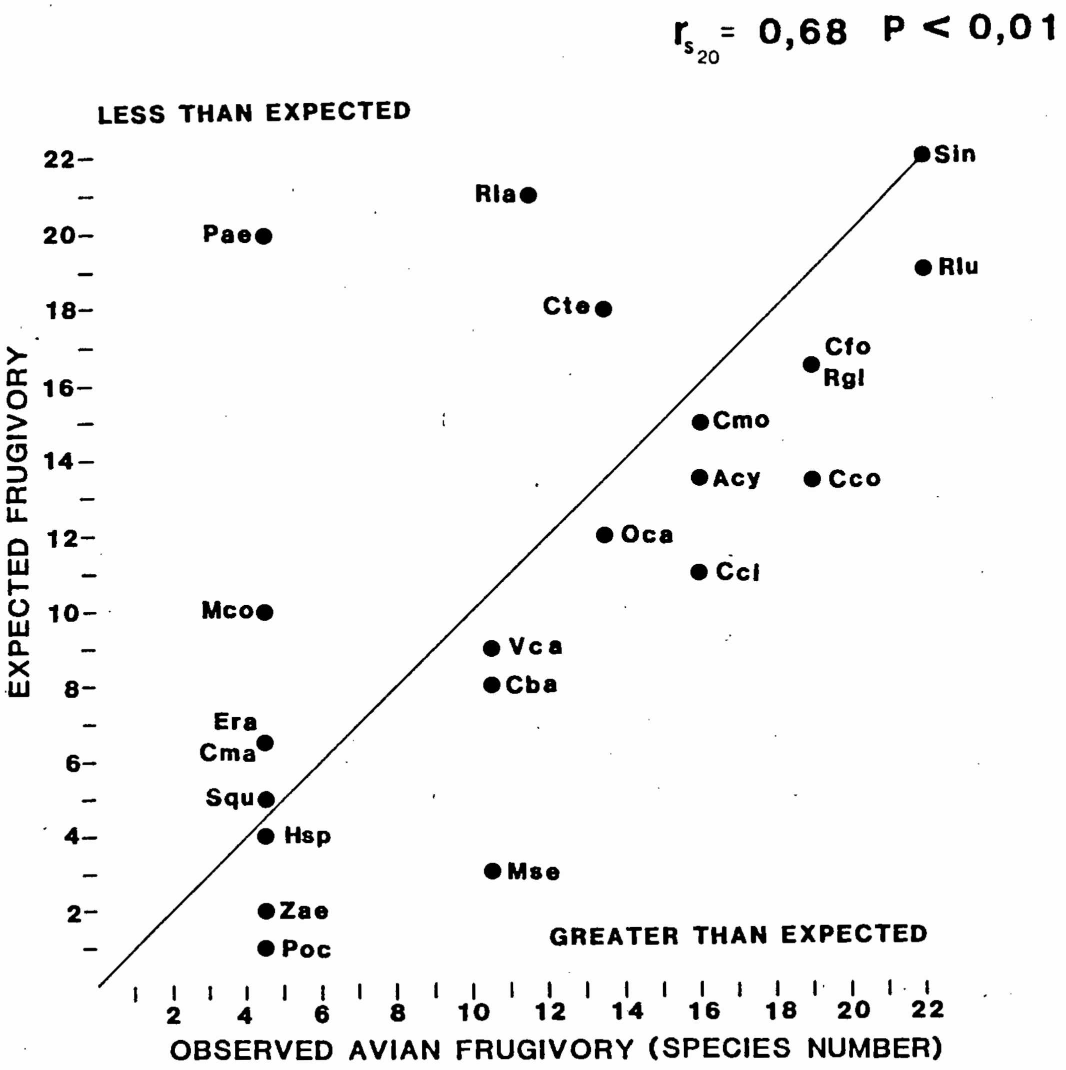


Figure 2 The ranked relationships between the expected number of bird species (derived from fruit production and long-term seasonal availability) and the observed number of bird species feeding on fruit of 22 plant species. Plant species are: Hsp = Haemanthus species, Zae = Zantedeschia aethiopica, Pae = Protasparagus aethiopicus, Rgl = Rhus glauca, Rla = R. laevigata, Rlu = R. lucida, Cmo = Chrysanthemoides monilifera, Cma = Cassine maritima, Cte = Cassine tetragona, Era = Euclea racemosa, Cba = Chironia baccifera, Cci = Cassytha ciliolata, Mco = Myrica cordifolia, Cfo = Chionanthus foveolata, Oca = Olea capensis, Cco = Colpoon compressum, Sin = Sideroxylon inerme, Squ = Solanum quadrangulare, Vca = Viscum capense, Acy = Acacia cyclops, Mse = Myoporum serratum, Poc = Phytolacca octandra.

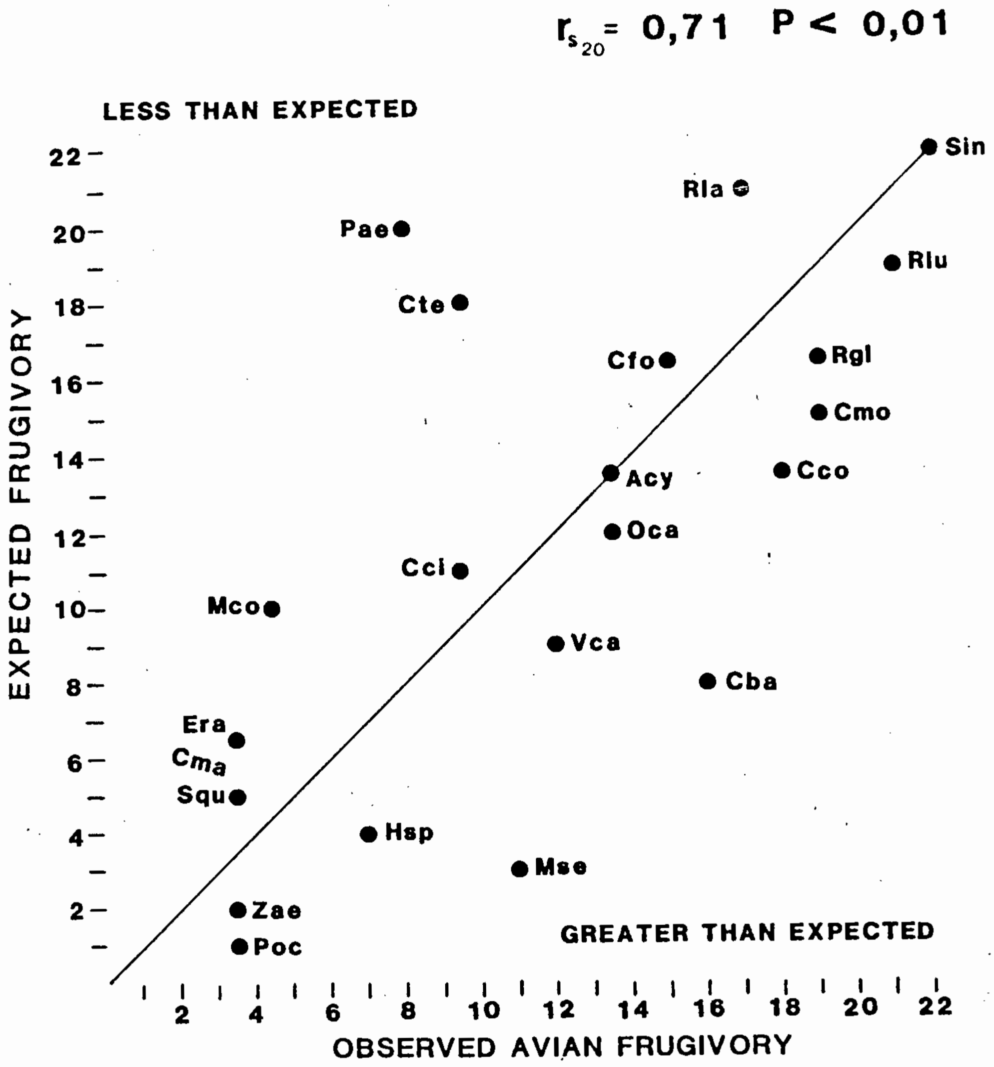


Figure 3 The ranked relationships between the expected number of individual birds (derived from fruit production and long-term seasonal availability) and the observed number of individual birds feeding on fruit of 22 plant species. Plant species are: Hsp = Haemanthus species, Zae = Zantedeschia aethiopica, Pae = Protasparagus aethiopicus, Rgl = Rhus glauca, Rla = R. laevigata, Rlu = R. lucida, Cmo = Chrysanthemoides monilifera, Cma = Cassine maritima, Cte = Cassine tetragona, Era = Euclea racemosa, Cba = Chironia baccifera, Cci = Cassytha ciliolata, Mco = Myrica cordifolia, Cfo = Chionanthus foveolata, Oca = Olea capensis, Cco = Colpoon compressum, Sin = Sideroxylon inerme, Squ = Solanum quadrangulare, Vca = Viscum capense, Acy = Acacia cyclops, Mse = Myoporum serratum, Poc = Phytolacca octandra.

On the basis of standardized observations 10 frugivorous bird species were found to use the fruits of 22 plant species during June 1983 and May 1984. Resident Sombre Bulbuls *Andropadus importunus* and Cape Bulbuls *Pycnonotus capensis* each consumed the fruits of 12 species (Table 5). In contrast, the itinerant Rameron Pigeons *Columba arquatrix* accounted for 302 feeding records but consumed the fruits of only 3 species (*Chrysanthemoides monilifera*, *Chironia baccifera* and *S. inerme*). At least 60% of fruit-eating visits at each plant species were represented by a single bird species (Table 5). *Colpoon compressum*, *S. inerme*, *Acacia cyclops* and *M. serratum* are the exceptions to this generalization.

Some of the specificity in fruit use by frugivores may be attributed to fruit size. The largest frugivores, Rameron Pigeons, ate intermediate-sized fruits, whereas the next largest frugivores, the Red-faced and Speckled Mousebirds (*Colius indicus* and *C. striatus* respectively) ate large (*Colpoon compressum* and *Chionanthus foveolata*) and intermediate-sized fruits (Figure 4). The smallest frugivores (Cape White-eyes *Zosterops pallidus*) ate mostly the small *Rhus* fruits (Figure 4). Since intermediate-sized *S. inerme* fruits were eaten by 80% of the frugivore species it was not appropriate to group *S. inerme* in any cluster. However, frugivory by Cape White-eyes on *S. inerme* fruits did not result in seed-dispersal since only the pericarp was eaten. Similarly, foraging by mousebirds on *Chionanthus foveolata* often did not result in seed-dispersal. Overall fruit size was positively correlated with the average mass of frugivores using the fruit ($r_{s\ 20} = 0{,}56$; $P < 0{,}01$).

Frugivore aggression

August, September and December 1983 and March to May 1984 were identified as the six months of fruit abundance with estimated fruit availability varying between 80 and 130 ripe fruit m^2, whereas fruit availability in the other six months varied between 12 and 70 ripe fruit m^2 (Figure 5). The most conspicuous fruit displays during periods of abundance were those of *Rhus glauca*, *R. laevigata*, *R. lucida*, *Chironia baccifera* and *Chrysanthemoides monilifera*. A total of 52 aggressive avian interactions was recorded, 49 of which occurred during the six months in which fruit was abundant (Table 6). If corrected for the number of frugivore observations a 22 fold increase in

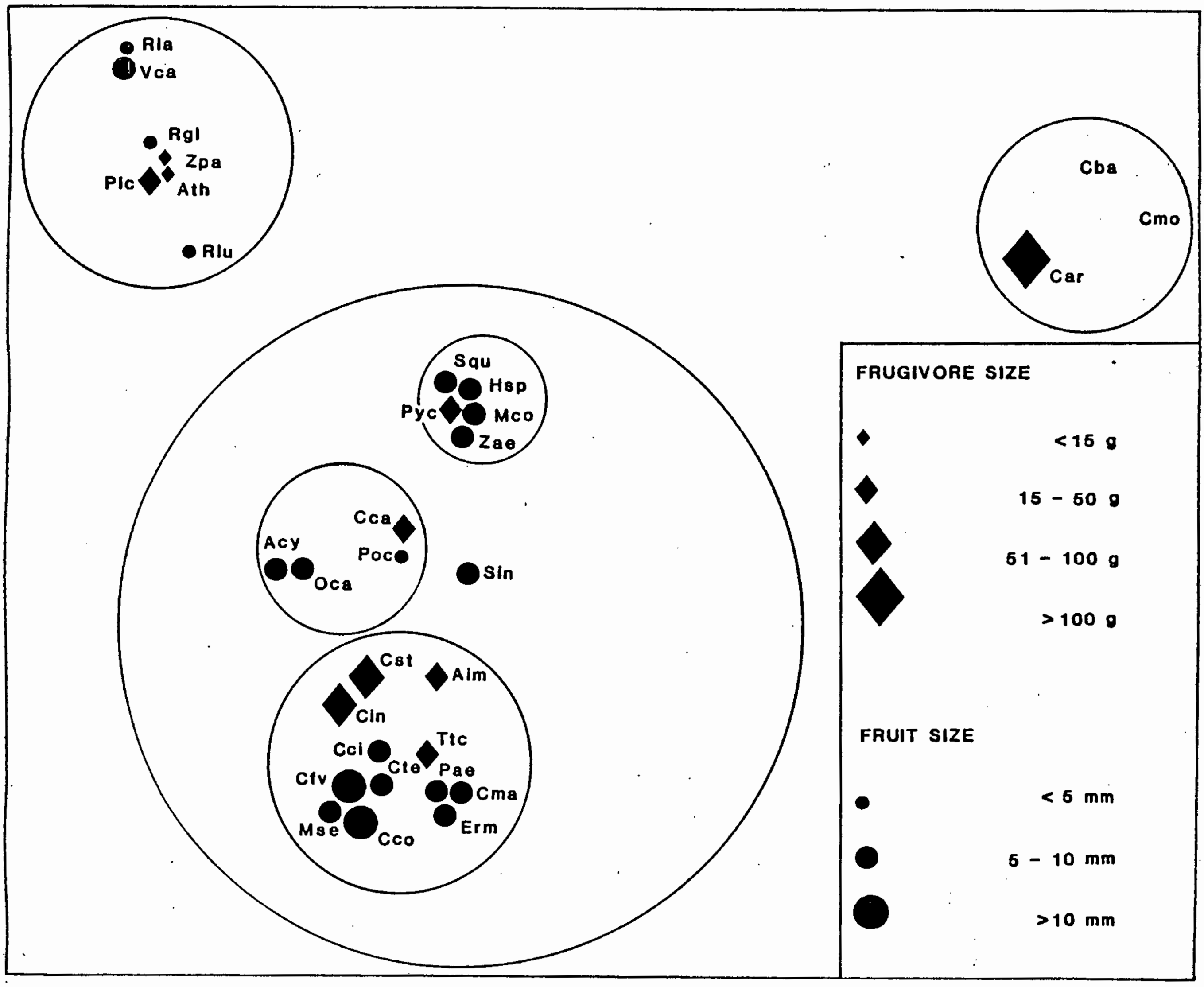


Figure 4 A correspondence analysis ordination plot representing fruit-eating by 10 avian species (diamonds) at 22 plant species (dots) at Hermanus. Bird species are: Car = *Columba arquatrix*, Cst = *Colius striatus*, Cin = *Colius indicus*, Pyc = *Pycnonotus capensis*, Aim = *Andropadus importunus*, Cca = *Cossypha caffra*, Ath = *Apalis thoracica*, Ttc = *Tchagra tchagra*, Zpa = *Zosterops pallidus*, Plc = *Ploceus capensis*. Plant species are: Hsp = *Haemanthus* species, Zae = *Zantedeschia aethiopica*, Pae = *Protasparagus aethiopicus*, Rgl = *Rhus glauca*, Rla = *R. laevigata*, Rlu = *R. lucida*, Cmo = *Chrysanthemoides monilifera*, Cma = *Cassine maritima*, Cte = *Cassine tetragona*, Era = *Euclea racemosa*, Cba = *Chironia baccifera*, Cci = *Cassytha ciliolata*, Mco = *Myrica cordifolia*, Cfo = *Chionanthus foveolata*, Oca = *Olea capensis*, Cco = *Colpoon compressum*, Sin = *Sideroxylon inerme*, Squ = *Solanum quadrangulare*, Vca = *Viscum capense*, Acy = *Acacia cyclops*, Mse = *Myoporum serratum*, Poc = *Phytolacca octandra*. The first two axes explain 72% of the variation in the data.

avian aggressiveness resulted during fruit abundance. These interactions were not necessarily related to territorial defence. Aggressive interactions occurred at *Rhus* spp (27), *Chrysanthemoides monilifera* (7), *Chironia baccifera* (6), *Viscum capense* (5) and *Sideroxylon inerme* (3). The Fiscal Shrike *Lanius collaris* initiated the greatest number of aggressive encounters (Table 6) while defending territories dominated by fruiting *Rhus* plants. However, based on casual observations Fiscal Shrikes ate few *Rhus* fruits but made greater use of fruits of the mistletoe *V. capense*, a parasite of *R. glauca* and *R. lucida*. On several occasions Fiscal Shrikes were unsuccessful in their attempts to defend territories against flocks of Rameron Pigeons. On one occasion a Rameron Pigeon was noted to peck at and drive off a Fiscal Shrike that had earlier attempted to defend its territory. In contrast to Rameron Pigeons, flocks of mousebirds were never observed to displace other birds (Table 6). Few aggressive avian interactions occurred during periods of fruit scarcity, and were restricted to birds feeding at *S. inerme* fruits. On two occasions Sombre Bulbuls chased Cape Bulbuls away from fruit crops, and on one occasion a flock of Rameron Pigeons displaced a single Cape Bulbul which had attempted to defend a small patch of *Colpoon compressum* fruits adjacent to a plentiful supply of *S. inerme* fruits. Paradoxically, the Rameron Pigeons ignored the *C. compressum* fruits which, being presented terminally (Knight in press; Chapter 6), may have been unavailable to these large birds. Overall, intraspecific interactions were less frequent than interspecific interactions and were restricted to three species on six occasions (Table 6). These results conflict with the hypothesis that aggressive avian frugivore interactions should be related to fruit shortage.

Discussion

Sampling biases

In collecting these data, sampling biases are bound to occur (see Wheelwright *et al*. 1984). Observations of avian frugivory were excluded from analysis if they occurred outside the fixed plots. This may result in an under-representation of itinerant frugivores which may be seasonally important but rarely encountered. Secondly, common plants were sampled at greater intensities than rare plants. However, in contrast to Wheelwright *et al.*

(1984) there was little correlation between frugivore use and cover abundance of the plant species (Table 4). Using solely visual observations of frugivory may bias towards a greater representation of the more conspicuous birds. The only frugivores (Table 5) that could be considered cryptic were the Sombre Bulbuls, which were more frequently encountered than the other frugivorous species. In larger suites of avian frugivores, particularly if encountered in tall vegetation, biases implicit in visual observations on frugivore activity may become considerable. Observations on the rate of fruit-eating by the different bird species would have been a better measurement of observed frugivory, but the density of vegetation prevented such data from being collected.

Frugivore use of fleshy fruits

All of the 35 plant species which produced fleshy fruits, except Kedrostis nana, fitted the general syndrome of bird-dispersal (small 4 - 10 mm, often brightly-coloured but odourless fruits)(Van der Pijl 1972). Thirteen of these plant species, including Kedrostis nana, were not used by avian frugivores. All of these plants are uncommon to the area and/or possessed small fruit crops with many of the fruits < 4 mm in length. Wheelwright et al. (1984) also found that the rarer plants were seldom important in the diet of frugivorous birds, though they did not examine fruit availability. The non-use of Cassine peragua fruits was possibly the most surprising, since the fruits are conspicuous (bright red and 8 mm in length) and freely available (ca 900 fruits plant^{-1}) over long periods (5 months yr^{-1}). It is speculated that the dense vegetation frequently surrounding these fruits inhibits their use by birds (see Knight in press; chapter 6).

This study suggests that frugivore use of fleshy fruits is likely to be a product of overall fruit availability rather than the physical or chemical characteristics of the fruits per se (McKey 1975). Since most studies, except Herrera (1984), have not examined all aspects of fruit availability per unit area in relation to avian fruit use, it is difficult to establish which plants are preferred by avian frugivores (see Petrides 1975). The technique of calculating a ranked expected frugivory based on fruit production criteria and then relating it to ranked observed frugivory may be the easiest way of identifying preferred foods. *Myoporum serratum*, *Chironia baccifera*, *Colpoon compressum* and *Chrysanthemoides monilifera* experienced greater frugivory than expected and may represent preferred foods (Figure 3). The greater than expected use of *M. serratum* may have been a sampling artifact arising from a rare plant producing few fruit (i.e. having a low expected frugivory) being used by two frugivorous bird species. *Chironia baccifera* fruits are both seasonally predictable (Knight in prep.; chapter 3) and conspicuous with bright orange fruits. The conspicuousness of *C. baccifera* fruit displays is enhanced by their occurrence in the low (< 0,3 m) and less dense littoral vegetation (pers. obs). Foraging at these plants may have influenced the normally arboreal Rameron Pigeons (Rowan 1983) to feed from the ground. *Chrysanthemoides monilifera* produced fruits that are predictably available during the austral spring and attracting the same frugivores as *Chironia baccifera*. *Colpoon compressum* and *Sideroxylon inerme* fruits were available throughout the year. Consequently, it is thought that a species possessing either temporally predictable or continuous fruiting may be preferred by frugivores such as the Rameron Pigeon. Oatley (1984) reports a similar situation for Rameron Pigeons in Natal. It appears that most of their diet there consists of the continuously available *Solanum mauritianum* fruits. However, during October and early November large flocks make long diurnal trips (*ca* 20 km each way) to feed on the seasonally predictable fruit crops of *Morus nigra* (mulberry)(Oatley 1984).

The positive correlation between fruit and frugivore size suggests that there is a degree of partitioning in fruit resources. Diamond (1975) found in New Guinea that increasing fruit size was accompanied by an increasing size of fruit pigeons (N = eight species) which used the fruit resources. However, Crome (1975) found no relationship between size of seven pigeon species and fruit selection in a Queensland tropical forest. Rameron Pigeons eat fruits varying considerably in size (e.g. *Celtis africana* *ca* 4 mm in length to 16 mm *Chionanthus foveolata*), but have not been observed to eat fruit as large (20 - 30 mm) as those eaten by the similarly sized New Guinean pigeon *Ptilinopus nanus* (Diamond 1975). It seems that there is little chance of predicting the size of fruit eaten from the size of frugivore.

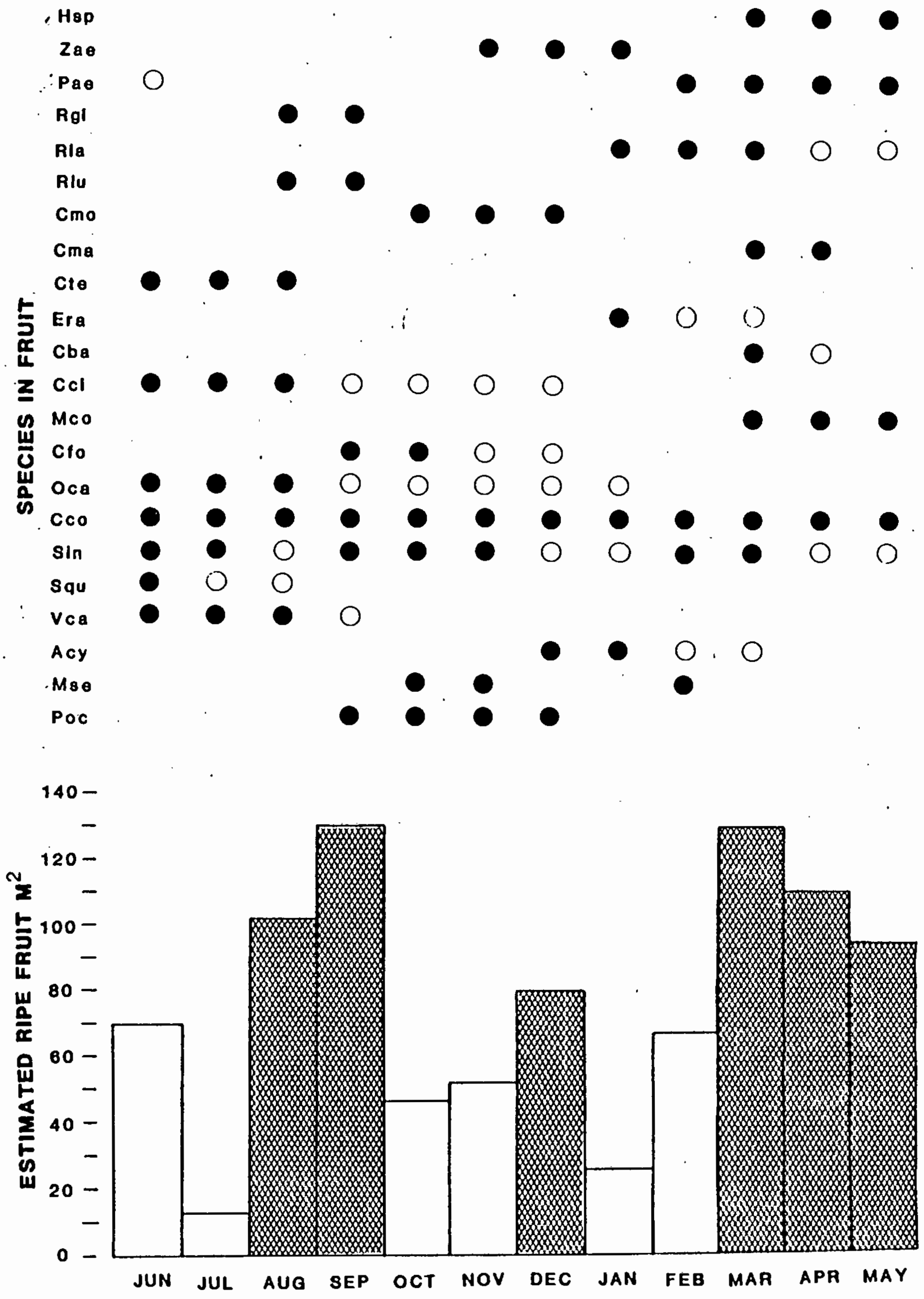
Fruit-frugivore specificity

The predominance of a single species of frugivore at most plant species (Table 5) has not been reported for any other plant assemblage (e.g. Kantak 1979; Frost 1980; Herrera 1984; Wheelwright *et al*. 1984). Dispersal carried out by a small suite of avian species was predicted (Snow 1971; McKey 1975; Howe & Estabrook 1977) to occur only in species producing high-reward, nutritious fruits (fruit type 8; Table 7). Since, in this study fruit quality and other characteristics were largely independent of avian fruit use (Table 4; Figures 2 & 3) such processes are unlikely to occur (see Frost 1980; Herrera & Jordano 1981; Herrera 1984). Alternatively, species-specific dispersal (Table 5) may appear as a result of insufficient sampling. In particular, itinerant frugivores removed large quantities of fruit, but were infrequently encountered (e.g. 10 Rameron Pigeon flocks and 13 Red-faced Mousebird flocks recorded in 408 hours). Resident frugivores such as the solitary Cape Bulbul and the gregarious Cape White-eye were more frequently encountered (50 and 23 encounters respectively). However, the number of plant species used by these two bird species varied greatly (12 and 7 respectively). It is possible that itinerant and gregarious frugivores (e.g. Rameron Pigeon) genuinely use fewer plant species than resident solitary birds (e.g. Cape Bulbuls). Species-poor plant-frugivore assemblages such as occur at Hermanus, may have a greater probability of possessing species-specific reciprocal dependence (see Herrera 1984). Extreme depauperacy and specialization of fruit-frugivore assemblages may have accounted for the alleged dependence of *Calvaria major* (related to *S. inerme*, formerly *C. inerme*) on the Dodo *Raphus cucullatus* for the dispersal of its seeds (Temple 1977). Strong inter-dependence may exist in a few cases, even if the overall plant-frugivore community shows little species specificity (see Herrera 1984 on *Pistacia lenticus*/*Sylvia atricapilla* and *Viburnum tinus*/*Erithacus rubecula* relationships).

Aggressive avian interactions

Avian frugivore interactions were most frequent during periods of fruit abundance (Table 6). Therefore the hypothesis that fruit scarcity should promote avian aggression is rejected. Low levels of aggressive avian interactions at fruit crops (Table 6) have been recorded previously (Terborgh

Figure 5 Monthly fruit production and phenology for Coastal Thicket plants occurring at Hermanus. Shaded bars indicate periods when fruit was considered abundant. Dots above the bars indicate the occurrence of active fruit ripening for each plant species. Circles indicate that fruit was available but not actively ripening. Plant species are: Hsp = *Haemanthus* species, Zae = *Zantedeschia aethiopica*, Pae = *Protasparagus aethiopicus*, Rgl = *Rhus glauca*, Rla = *R. laevigata*, Rlu = *R. lucida*, Cmo = *Chrysanthemoides monilifera*, Cma = *Cassine maritima*, Cte = *Cassine tetragona*, Era = *Euclea racemosa*, Cba = *Chironia baccifera*, Cci = *Cassytha ciliolata*, Mco = *Myrica cordifolia*, Cfo = *Chionanthus foveolata*, Oca = *Olea capensis*, Cco = *Colpoon compressum*, Sin = *Sideroxylon inerme*, Squ = *Solanum quadrangulare*, Vca = *Viscum capense*, Acy = *Acacia cyclops*, Mse = *Myoporum serratum*, Poc = *Phytolacca octandra*.



SPECIES IN FRUIT
Hsp
Zae
Pae
Rgl
Rla
Rlu
Cmo
Cma
Cte
Era
Cba
Ccl
Mco
Cfo
Oca
Cco
Sin
Squ
Vca
Acy
Mse
Poc
ESTIMATED RIPE FRUIT M^2
140
120
100
80
60
40
20
0
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

& Diamond 1970; Cruz 1974; Foster 1977; McDiarmid *et al.* 1977) and Willis (1966) suggested that competitive exclusion prevented aggressive interactions at fruiting plants. Such interactions are more frequently associated with flowers which provide nectar resources (Pratt 1984). This may be due to nectar resources being both renewable and therefore spatially more predictable, and by providing a greater concentration of food energy (*cf.* Baker 1975 & Wheelwright *et al.* 1984). A fruit resource worth defending by birds should have either a high energy content and long retention period on the plant (e.g. *Ilex aquifolium* and *Hedera helix* (Snow & Snow 1984)), or provide staggered fruit availability over long periods when other fruits are less available (e.g. *Ficus aurea* (Merritt 1980)). Fruit defence is usually more common when fruit and other food become scarce, as often occurs during the winter months in northern Europe and America (Moore 1978; Merritt 1980; Snow & Snow 1984), but may also occur under tropical conditions (e.g. in toucans *Ramphastos swainsonii* and *R. sulfuratus* (Howe 1977)). Unlike temperate regions, many instances of frugivore aggression in the tropics were unrelated to maintenance of feeding territories (Leck 1972; Bourne 1974; Howe 1977).

The occurrence of aggressive avian interactions during periods of fruit abundance (Table 6) has not been reported elsewhere. Such interactions are due to the increased number of birds (20 spp.) using fruits when they become abundant. Half of these species are primarily insectivorous and their use of fruit is casual. Nevertheless, seeds regurgitated by casual frugivores are almost always intact (pers. obs). Casual frugivores (particularly shrikes) and gregarious frugivores (particularly European Starlings *Sturnus vulgaris*) are intolerant of other birds and contribute to the majority of interactions. Fiscal Shrikes, in particular, aggressively defend their territories, even though such defence is unlikely to be related to the protection of fruit resources *per se*. Much of the aggression of these casual frugivores is thought to be a behavioural carryover from the active, predatory behaviour required to secure invertebrates. The intraspecific aggression found in foraging Red-winged Starlings *Onychognathus morio* and European Starlings are exceptions and are thought to be related to establishment of dominance hierarchies (Feare 1984). The rarity of aggressive interactions during periods when fruit was less abundant was mostly due to fewer birds feeding at

Table 6 Matrix of all aggressive avian interaction accumulated over one year for periods of fruit abundance (top and bold) and fruit scarcity (bottom). A '/' indicates a bird species that was not observed eating fruits during periods of fruit scarcity.

Species	Car	Sse	Sca	Cst	Cin	Pyc	Aim	Tol	Mru	Cca	Ath	Lco	Lfe	Ttc	Tze	Svu	Omo	Sbi	Zpa	Plc
Columba arquatrix	0																			
(Car)	/																			
Streptopelia semitorquata	0	0																		
(Sse)	/	/																		
Streptopelia capicola	0	0	0																	
(Sca)	/	/	/																	
Colius striatus	0	0	0	0																
(Cst)	0	/	/	0																
Colius indicus	0	0	0	0	0															
(Cin)	0	/	/	0	0															
Pycnonotus capensis	0	0	0	0	0	0														
(Pyc)	1	/	/	0	0	0														
Andropadus importunus	0	0	0	0	0	1	0													
(Aim)	0	/	/	0	0	2	0													
Turdus olivaceus	0	0	0	0	0	0	0	0												
(Tol)	0	/	/	0	0	0	0	0												
Monticola rupestris	0	0	0	0	0	0	0	0	0											
(Mru)	0	/	/	0	0	0	0	0	0											
Cossypha caffra	0	0	0	0	0	0	0	0	0	0										
(Cca)	0	/	/	0	0	0	0	0	0	0										
Apalis thoracica	0	0	0	0	0	0	0	0	0	0	0									
(Ath)	/	/	/	/	/	/	/	/	/	/	/									
Lanius collaris	7	3	2	1	0	4	0	3	3	3	0	0								
(Lco)	/	/	/	/	/	/	/	/	/	/	/	/								
Laniarius ferrugineus	1	0	0	0	0	0	0	0	0	0	0	0	0							
(Lfe)	/	/	/	/	/	/	/	/	/	/	/	/	/							
Tchagra tchagra	0	0	0	0	0	0	0	0	0	0	0	0	0	0						
(Ttc)	/	/	/	/	/	/	/	/	/	/	/	/	/	/						
Telophoros zeylonus	1	1	0	0	0	2	0	0	1	2	0	0	0	0	1					
(Tze)	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/					

Table 6 continued/

Species	Car	Sse	Sca	Cst	Cin	Pyc	Aim	Tol	Mru	Cca	Ath	Lco	Lfe	Ttc	Tze	Svu	Omo	Sbi	Zpa	Plc
Sturnus vulgaris (Svu)	1 /	0 /	0 /	0 /	0 /	1 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	1 /	3 /				
Onychognathus morio (Omo)	1 0	0 /	0 /	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 /	0 /	0 /	0 /	0 /	0 /	2 0			
Spreo bicolor (Sbi)	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /		
Zosterops pallidus (Zpa)	0 0	0 /	0 /	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 /	1 /	0 /	0 /	1 /	1 /	1 0	0 /	0 0	
Ploceus capensis (Plc)	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /	0 /

the fruit crops (10 spp.). It is likely that fruit resources never became critically low during the study period, and frugivore segregation at fruit crops could be maintained.

In conclusion, it is difficult to demonstrate preferred use of fleshy fruits of particular plant species by avian frugivores. Identifying preferred fruits cannot be undertaken without information on total fruit availability in the environment. Relationships suggesting segregation of fruit selection by suites of avian frugivores needs more data before conclusions can be drawn. Aggressive avian interactions at fruit crops are comparatively rare (cf. Pratt 1984) and are usually initiated by casually frugivorous bird species during periods of fruit abundance. Lack of critical fruit shortages may prevent avian competition for fruit and reduce the probability for aggressive avian interactions from that cause.

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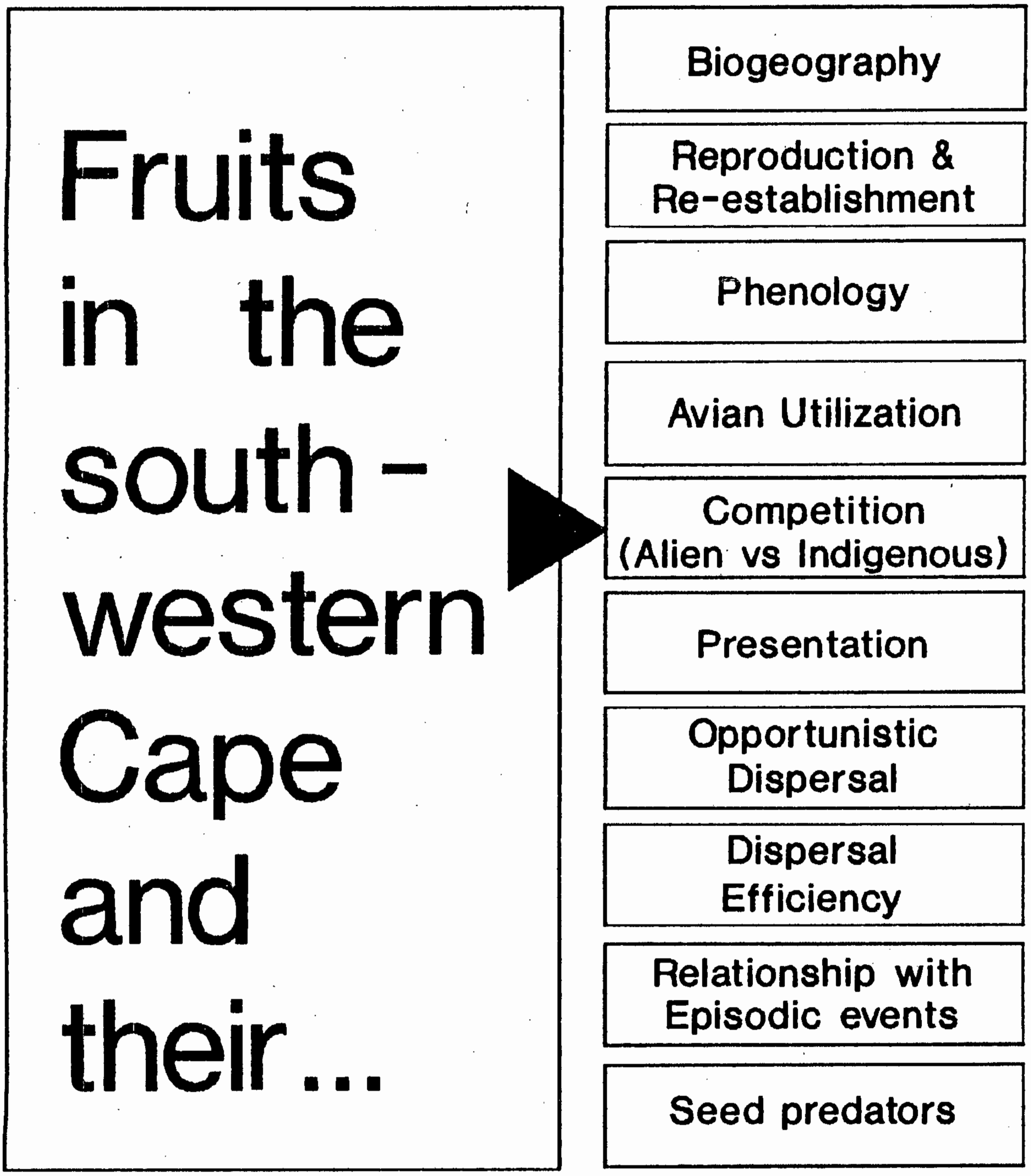
CHAPTER 5



Fruits in the south-western Cape and their...

Biogeography

Reproduction & Re-establishment

Phenology

Avian Utilization

Competition (Alien vs Indigenous)

Presentation

Opportunistic Dispersal

Dispersal Efficiency

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Fruit displays of indigenous and alien plants in the southwestern Cape, South Africa

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Fruit displays of indigenous and invasive alien plants in the southwestern Cape, South Africa

Abstract

Two models are introduced which describe different strategies for presenting fleshy fruits of indigenous and alien plant species. Each model describes a gradient between two end points. In the first model the one end point is occupied by plant species with large, synchronized and conspicuous, but seasonally short, fruit displays. The other end point of this gradient is occupied by species with less conspicuous fruit displays, but presented over a longer fruit season. In the second model, the one end point is occupied by species which maximize all aspects of fruit displays, though presented without regard for seasons. The contrasting end point of this gradient is occupied by species which minimize their investments in regularly presented fruit displays. It was hypothesized that alien species would possess an intensive, and or maximized fruit display, whereas indigenous plants would possess all types of fruit displays. The fruit displays of eight indigenous and six alien woody species are characterized relative to these models. The data was consistent with that of the hypothesis, with alien species favouring a seasonally short but intense fruit presentation, whereas many indigenous species have prolonged fruit presentations. Minimized fruit displays were only recorded for indigenous species, whereas maximized fruit displays were recorded for indigenous and alien plants.

_S_. _Afr_. _J_. _Bot_. 1986, 52: 249-255.

Introduction

Woody alien plants represent a considerable threat to the indigenous vegetation of the southwestern Cape (Stirton 1978). Bird-dispersal of these species is prominent, but has only been studied in detail for Acacia cyclops (Glyphis, Milton & Siegfried 1981). Bird-dispersal is often related to attributes of fleshy fruit displays (McKey 1975; Howe & Estabrook 1977; Stiles 1982). In this paper two fruit display models (Figure 1) are presented which may contribute to explaining the relative success of some of these alien species. Each model represents a gradient but differs with respect to the amount and nature of resources invested in a fruit display. The first model assumes that fruiting seasons are seasonally regular and that resources for an individual fruit display are limited. The end points of this gradient are defined by plant species which produce large, synchronized, conspicuous but seasonally short fruit displays (intensive) and other plant species which have fruit displays that are less conspicuous but are available for longer periods (prolonged). The second model assumes that the maximum number of resources invested in an individual and includes fruit displays that are either infrequent, allowing considerable resource investment to accumulate during non-fruiting periods, or are the product of a constant allocation of resources throughout the season for the production of fruit displays. This represents the one end-point (maximized) of the second model. The other end-point defines species which invest relatively few resources in their fruit displays. The first model, therefore, investigates the efficiency of resources used in producing a fruit display, whereas the second model examines the gross investment of resources. Since resource limitations in plants are difficult if not impossible to determine, only indirect measures of resources could be deduced, therefore, ensuing results will represent trends rather than quantified predictions.

Using the above two models it is hypothesized that indigenous plant species will include all types of fruit displays (both ends of both gradient models), whereas the suite of alien plant species are likely to possess intensive or maximized fruit displays which utilize the services of frugivores possessing large foraging ranges and which facilitate the widespread distribution of seeds. Since the fleshy fruits of all these species examined here have no

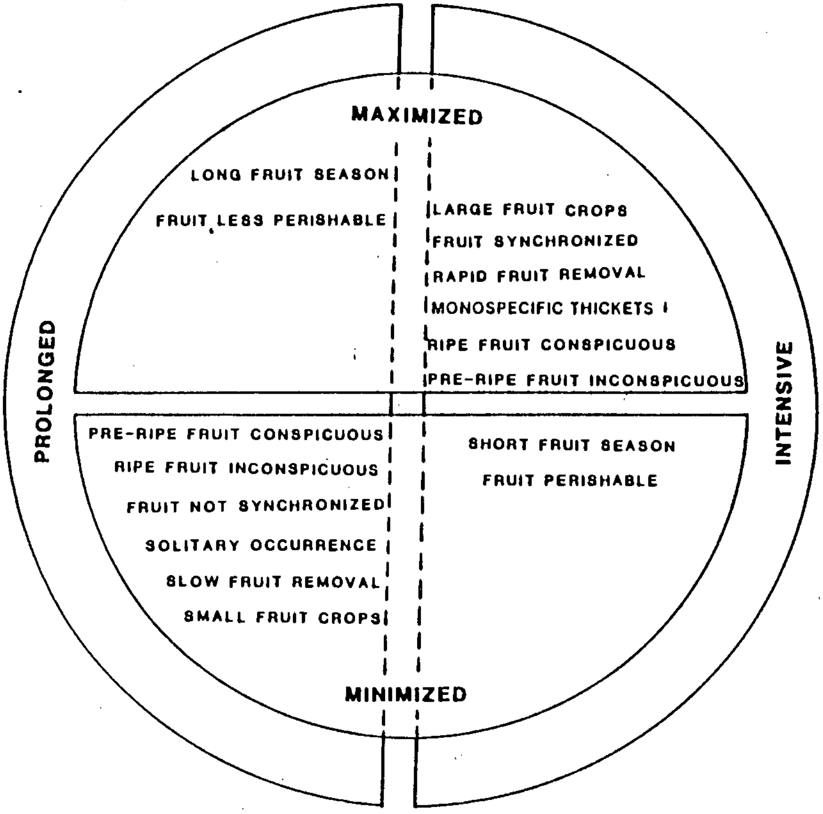

Figure 1 Represents the characteristics of both the intensive – prolonged and maximized – minimized models. The characteristics associated with Model 1 (intensive – prolonged) are represented in right and left hand semicircles, whereas the characteristics associated with Model 2 (Maximized – Minimized) are represented in top and bottom semicircles respectively.

Table 1 Sampling sites, sampling sizes and species used to identify differences in fruit displays between indigenous and alien plants within the south-western Cape

	Chrysanthemoides monilifera (L.) Nor	*Colpoon compressum* Bergius	*Euclea racemosa* Murray	*Myrica cordifolia* L.	*Maytenus acuminata* (L.f.) Loes	*Myrsine africana* L.	*Rapanea melanophloeos* (L.) Mez	*Sideroxylon inerme* L.	*Acacia cyclops* A. Cunn. ex G. Don	*Lantana camara* L. complex	*Myoporum serratum* R. Br.	*Pittosporum undulatum* Vent.	*Rubus* sp. (*fruticosus* L.?)	*Solanum mauritianum* Scop.
Hangklip 1981 – 1983	3	4		3					3					
Betty's Bay 1982 – 1983					3	4	4							
Hermanus 1983	5	5	5	5	5	5	5	5	4	3	3	3	3	3
Milnerton 1981 – 1983	3		3					3	4	3	3			
Orange Kloof 1983					3	3								

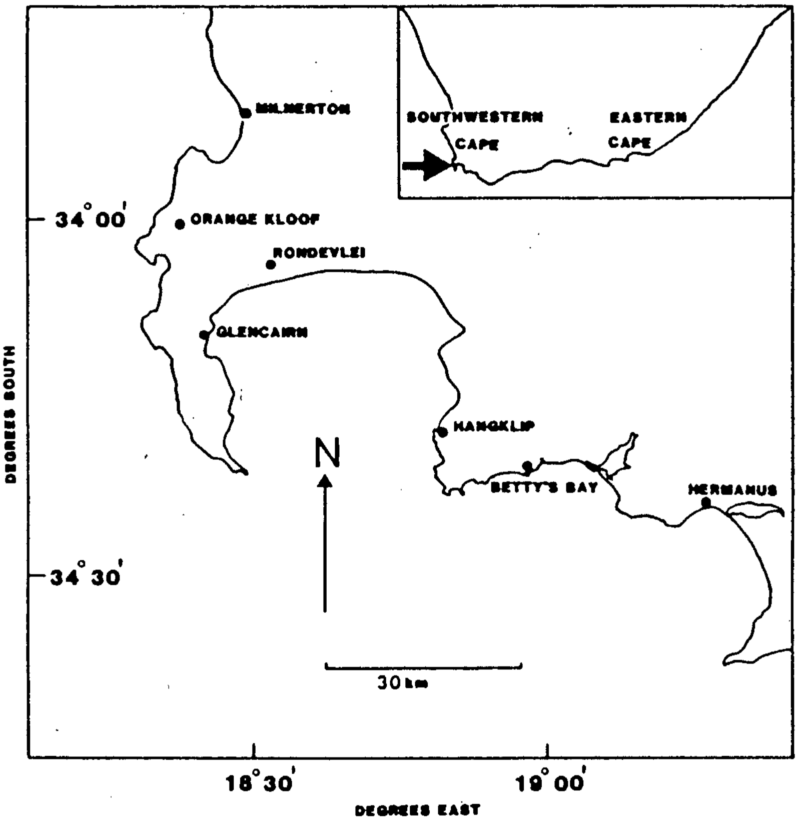

Figure 2 Location of mentioned study sites and place names that occur in the south-western Cape.

Table 2 The delimitation of fruit display variables into four ordinal classes used to analyse differences in fruit displays between indigenous and alien plants within the south-western Cape

	Score			
Variable	1	2	3	4
Size	< 1000	1000 – 5000	5000 – 10000	> 10000
Season length	< 3 months	3 – 6 months	6 – 9 months	> 9 months
Synchrony	< 20%	20 – 40%	40 – 60%	> 60%
Occurrence	solitary	solitary – thickets	thickets	monospecific stands
Pre-ripe	no colour change	slight change	colour change	conspicuous change
Ripe	inconspicuous	visible	conspicuous	highly conspicuous
Removal (per week)	< 1 fruit	1 – 5 fruit	6 – 10 fruit	> 10 fruit
Rotting time	< 1 week	1 – 5 weeks	1 – 3 months	> 3 months

odour and are relatively small (< 15 mm) they are considered to have evolved for avian rather than mammalian dispersal (Van der Pijl 1969). Although fruit of some plant species examined are consumed by baboons (*Papio ursinus*), the seeds recovered from baboon faeces have not germinated under test conditions. This paper, therefore, concentrates on the avian consumption of fruits.

Materials and Methods

The two gradient models (Figure 1) are used to test my hypothesis that indigenous species will have all types of fruit displays, whereas alien species will possess either intensive or maximized fruit displays. Sampling of fruit displays amongst the 14 plant species (*Chrysanthemoides monilifera*, *Colpoon compressum*, *Euclea racemosa*, *Myrica cordifolia*, *Maytenus acuminata*, *Myrsine africana*, *Rapanea melanophloeos*, *Sideroxylon inerme*, *Acacia cyclops*, *Lantana camara*, *Myoporum serratum*, *Pittosporum undulatum*, *Rubus* sp. (*fruticosus* ?) and *Solanum mauritianum*) was undertaken from 1981 to 1983, depending on the site. The number of samples at each site are presented in Table 1. The sample sizes are small, but this was unavoidable due to the labour intensive nature of data capture. The following characteristics of eight indigenous and six alien plant species were recorded at five sites (Table 2, Figure 2):

(1) Fruit crop size (estimated size of standing crop at peak season): fruit was counted on individual branches and extrapolated for the entire plant. Since fruit sizes vary greatly, even on the same plant, fruit sizes were not recorded in the field. The fruits of all species analysed in this study varied between 5 and 12 mm in length

(2) Fruit season length: determined from accumulated observations made on three marked branches per plant since 1981. The cutoff points for defining season length were selected to include approximately 95% of yearly fruit production.

(3) Fruit synchronization: fruiting on marked plants was compared with five adjacent conspecifics and expressed as a percentage.

(4) Plant occurrence: the spatial aggregation of species was ranked from solitary to monospecific thicket stands.

(5) Pre-ripe colour/conspicuousness: monitored during pre-ripening. The existence of a pre-ripe colour phase is considered to enhance the utilization of fruit presented over long periods (Stiles 1982).

(6) Ripe colour/conspicuousness: monitored during ripening.

(7) Fruit removal: estimated by comparing three 'marked' with three 'bagged' branches bearing ripe fruits per plant and calculated on a weekly basis.

(8) Fruit decay: ripe fruit were picked, placed in three bags, and then tied back onto the plant. The fruit in these bags was assessed for signs of fruit decay daily and monthly.

In order to relate these characteristics with regard to the models each of the above characteristics was scored on a 1-4 ordinal scale (Table 2). A model data set (**INTENSIVE**) which best represents an 'intensive' fruit display (Figure 1 and Tables 3) was used to define one end-point of the intensive-prolonged gradient. The characteristics of a prolonged fruit display are also presented in Figure 1. A second model data set (**MAXIMIZED**) that best represents a maximized strategy was used to define the end-point of the maximized-minimized gradient (Table 3). Since this model assumes that all aspects of a fruit display are maximized they were given an ordinal score of 4, except for pre-ripe phase which is probably unnecessary (Table 4). Contrasting this strategy is a minimized fruit display which would possess a conspicuous pre-ripe fruit phase (score 4), whereas all other aspects of the fruit displays will possess a score of 1 (Table 3).

The interrelationships of the eight fruit display variables were analysed with a Spearman rank correlation, while similarity between each of the 14 species and the two models was determined using similarity distances from a cluster analysis of cases (BMDP P2M: Engelman 1985).

Table 3 The ordinal scores for each fruit display variable and 14 south-western Cape plant species together with scores for fruit display models INTENSIVE and MAXIMIZED

	Species															
Variable	INTENSIVE	MAXIMIZED	*Chrysanthemoides monilifera*	*Colpoon compressum*	*Euclea racemosa*	*Myrica cordifolia*	*Maytenus acuminata*	*Myrsine africana*	*Rapanea melanophloeos*	*Sideroxylon inerme*	*Acacia cyclops*	*Lantana camara*	*Myoporum serratum*	*Pittosporum undulatum*	*Rubus* sp.	*Solanum mauritianum*
Crop size	4	4	4	1	3	3	1	2	4	4	4	3	3	3	3	2
Season length	1	4	1	4	2	2	4	2	2	3	2	2	1	2	4	2
Synchronization	4	4	4	1	2	4	1	1	3	2	4	3	4	4	3	3
Occurrence	4	4	3	2	3	3	2	3	3	3	4	3	1	4	3	3
Pre-ripe	1	1	2	4	3	1	1	3	3	1	2	1	1	3	2	2
Ripe	4	4	4	4	2	2	1	2	3	3	4	3	3	3	3	3
Removal	4	4	4	1	2	4	1	1	1	2	4	2	3	3	3	3
Rotting time	1	4	1	3	2	4	4	3	3	2	3	2	2	2	1	2

Results

The basic data for each species is presented in Table 3. The Spearman Rank Correlation analysis (Table 5) indicated that plants with a fast fruit removal also exhibit a high degree of fruiting synchronization with conspecifics ($r_{s\,12} = 0,87$; $P < 0,01$); high degree of fruit synchronization is usually accompanied by short fruiting seasons ($r_{s\,12} = -0,79$; $P < 0,01$). A short fruiting season length is associated with large fruit crops ($r_{s\,12} = -0;66$, $P < 0,01$). Further, large fruit crops exhibit greater fruiting synchronization amongst conspecifics ($r_{s\,12} = -0,57$; $P < 0,01$) and closer spatial associations ($r_{s\,12} = -0,51$; $P < 0,01$). Since large fruit displays are conspicuous but maintained for short periods the characteristics of the intensive-prolonged gradient listed in Figure 1 are confirmed. This implies that many species (indigenous and alien) appear to be limited with regard to resource investments in fruit displays.

Table 5 presents the similarity distances between all 14 plant species and the models **INTENSIVE** and **MAXIMIZED**. These similarity distances are plotted along an intensive-prolonged and a maximized-minimized gradient in a scatter diagram (Figure 3). The indigenous species *Chrysanthemoides monilifera* is most representative of an intensive fruit display and the alien species *Acacia cyclops* the next most similar. The following alien plant species may also be considered to have intensive fruit displays:- *Rubus* sp., *Myoporum serratum* and *Lantana camara*, while the indigenous species *Myrica cordifolia* and *Sideroxylon inerme* also have intensive fruit displays (Figure 3). The alien species *Solanum mauritianum* and *Pittosporum undulatum* favour neither an intensive nor prolonged fruit display strategies, whereas the rest of the species represent the prolonged strategy (Figure 3) and may be important for maintaining resident, avian frugivore populations in the southwestern Cape. The introduced *Acacia cyclops* is the plant species most closely approaching the maximized strategy (Figure 3). Since no alien species possessed a prolonged or minimized fruit display the hypothesis that the suite of indigenous species should include all types of fruit displays, whereas the successful alien plants should possess intensive or even maximized fruit displays is fully confirmed.

Table 4 Spearman rank correlation coefficient matrix for eight fruit display variables based on eight indigenous and six alien plant species occurring in the south-western Cape

	Rotting time	Removal	Ripe	Pre-ripe	Occurrence	Synchrony	Season length
Removal	−0,23						
Ripe	−0,36	0,34					
Pre-ripe	−0,03	−0,32	0,23				
Occurrence	−0,14	0,44	0,19	0,23			
Synchrony	−0,25	0,87	0,38	−0,26	0,42		
Season length	0,25	−0,61	−0,30	0,21	−0,16	−0,79	
Size	−0,25	0,45	0,41	−0,14	0,51	0,57	−0,66

Critical values of Spearman Rank Correlation for significance levels are: r_s = 0,46; P = 0,05; r_s = 0,64; P = 0,01.

Table 5 Matrix of similarity distances for eight indigenous and six alien species occurring in the south-western Cape and the two fruit display models INTENSIVE and MAXIMIZED

	Chrysanthemoides monilifera	*Colpoon compressum*	*Euclea racemosa*	*Myrica cordifolia*	*Maytenus acuminata*	*Myrsine africana*	*Rapanea melanophloeos*	*Sideroxylon inerme*	*Acacia cyclops*	*Lantana camara*	*Myoporum serratum*	*Pittosporum undulatum*	*Rubus* sp.	*Solanum mauritianum*	INTENSIVE	MAXIMIZED
	CCM	CCO	ERM	MCF	MAC	MAF	RMP	SIN	ACY	LCM	MIN	PUN	RSP	SMT	INT	MAX
CCO	15,6															
ERM	9,3	10,7														
MCF	7,8	16,1	7,2													
MAC	18,9	7,3	11,5	11,0												
MAF	14,6	5,4	5,3	10,7	6,3											
RMP	8,2	9,7	4,7	8,3	12,7	6,5										
SIN	8,1	11,7	5,0	8,1	10,7	8,5	5,5									
ACY	3,9	14,1	9,7	6,3	17,4	13,2	6,7	8,5								
LCM	7,4	12,5	4,0	5,5	11,5	9,3	4,7	2,7	7,7							
MIN	7,3	15,0	9,0	7,1	14,0	14,3	9,7	7,7	9,4	5,0						
PUN	6,9	13,4	4,9	7,0	16,4	10,2	5,6	7,6	4,8	4,9	6,5					
RSP	7,3	10,5	7,4	9,2	11,5	7,3	8,2	6,4	9,5	5,5	8,8	6,7				
SMT	7,4	12,3	5,6	3,8	11,5	9,1	4,6	6,3	5,9	3,7	7,0	4,9	5,4			
INT	2,2	17,8	11,6	8,0	19,1	16,9	10,4	8,3	3,7	7,6	7,5	6,7	9,6	9,6		
MAX	7,6	14,3	13,4	6,2	13,7	13,4	10,3	8,4	3,7	9,4	11,0	8,5	9,7	7,7	5,3	

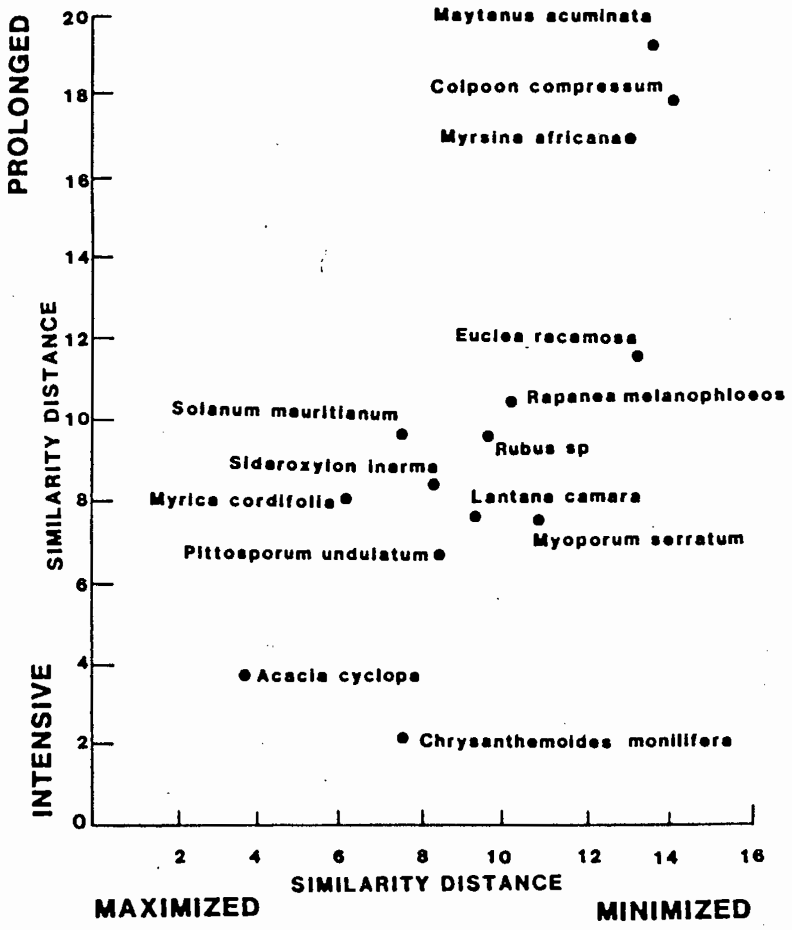

Figure 3 The positions of indigenous and alien species relative to each other and to the intensive – prolonged gradient (Model 1), represented by the vertical axis, and the maximized – minimized gradient (Model 2) represented by the horizontal axis.

Discussion

Advertising cues

In presenting a fruit display plants are required to make compromises in the allocation of resources to their various parts (McKey 1975). Since seeds require sufficient resource reserves to promote competitive germination (Snow 1971), an expensive advertising investment in the disposable pericarp/aril imposes a double drain on resources. Within North America Stiles (1982) hypothesized that fleshy fruit displays in late summer and autumn are enhanced by a conspicuous leaf colour change termed foliar fruit flags. The use of foliar fruit flags during fall is inexpensive in resources since the leaves are to be discarded before winter. This fruiting period also coincides with large scale avian migrations and frequent visitation to fruiting plants by frugivorous birds (Thompson & Willson 1979). Since the forest/scrub within the southwestern Cape is evergreen (Kruger 1979) and there are no large scale migration of birds (Winterbottom 1971) foliar fruit flags do not occur. This study indicates that evergreen plants may, however, enhance the conspicuousness of their fruit displays by the spatial aggregation of conspecifics and the synchronization of fruiting. In this respect both foliar fruit flags and the intensive fruit display maximize the visual impact of their displays without requiring additional resources.

Pre-advertizing cues

Stiles (1982) presented a second hypothesis in favour of a preripe fruit colour phase increasing the probability of seed-dispersal through a suite of resident frugivores which may 'trapline' for ripe fruits. My 'prolonged' endpoint of the first hypothesis is identical with Stiles (1982) hypothesis. A conspicuous unripe fruit phase creates a more persistent stimulant for attracting frugivores. The regular checking of fruit by frugivores would result in faster fruit removal rates, which in combination with limited simultaneous ripening of fruits may result in less fruit being wasted through rotting and non- dispersal. This process would tend to promote longer fruiting seasons which in turn promotes the year-round supply of fruits and the maintenance of a resident frugivorous population. Stiles (1982) indicated that conspicuous preripe fruit colours are particularly common to tropical environments and may occur in temperate fruits that ripen in summer. Although the southwestern Cape is extratropical its fleshy-fruited flora possesses many examples of conspicuous preripe fruit colours which are presented throughout the year. This is primarily due to this part of the flora being derived from the subtropical floras (Milewski 1982; Knight 1984).

Fruit displays colonization and invasion

Indigenous species which are associated with early colonization of disturbances or sand dunes such as Chrysanthemoides monilifera and Myrica cordifolia (Heydorn 1975) exhibit intensive fruit displays (Table 6). In areas of disturbance such as road verges and electricity pylons monospecific stands of colonizing C. monilifera frequently occur (pers. obs). Further, Acacia cyclops which is the most invasive of the six alien species occupies similar coastal habitats and exhibits both maximized and intensive fruit displays (Figure 3). Out of six alien species four can be considered to exhibit either an intensive or a maximized fruit display (Acacia cyclops, Myoporum serratum, Pittosporum undulatum and Rubus sp.). All four of these species under certain circumstances exhibit high potential for colonization, even in the presence of little or no apparent disturbance. Myoporum serratum is invasive in wetland areas of the southern Cape Peninsula (pers. obs). Pittosporum undulatum appears to be invasive into tall scrub and riparian forest (D.M. Richardson & Brink 1985), even where little disturbance has occurred (pers. obs). This species is even invasive into open undisturbed eucalypt forests within its own native Australia (Gleadow 1982). The introduced European Blackbird (Turdus merula) has been identified as the most important avian disperser of these species in Australia (Gleadow 1982). It is therefore possible that either intensive or maximized fruit displays may help promote the invasive ability of introduced plant species.

Chrysanthemoides monilifera

Within the southwestern Cape this species fruits from the end of July to early summer, with particularly large fruit crops being associated with relatively wet winters (pers. obs). Fruits develop quickly after flowering (approximately two months), with plants frequently possessing flowers, unripe and ripe fruits simultaneously. Branch deciduousness (Givnish 1978) usually follows heavy fruiting. First year branches bear few or no fruits, while the second year branches thicken considerably and produce a very large fruit crop, and thereafter usually die back or produce a small number of fruits the following year. This deciduousness may be associated with inadequate resources (particularly water) for maintaining the branch during summer drought-stress. By possessing seasonally disposable branches more resources may be allocated to a rapid and large fruit production soon after wet winter months. Further, ripe fruits that remain on the branch for longer than forty-eight hours abscise. The rapid post winter fruiting of C. monilifera therefore suffers little competition for dispersal agents from other plant species possessing intensive fruit displays.

Myrica cordifolia

In contrast to the rapid fruit development of C. monilifera, fruiting in the indigenous Myrica cordifolia occurs about nine months after the May-July flowering season. There appears to be a continuous development of the fruits throughout the moist winter and spring and a large fruit crop is presented that closely represents a maximized strategy (Figure 3). Final ripening of fruit is slow but continuous throughout the dry summer. Myrica cordifolia could exhibit fruit displays even closer to the maximized strategy (Figure 3) if the fruit removal by avian frugivores was slower. 'Bagged' fruit which are inaccessible to avian frugivores remained on branches for many months after all the other fruit had been removed. A single plant at Hangklip had almost all of its estimated 20 000 fruits removed within three days (9-12 March 1983).

Sideroxylon inerme

The population of indigenous Sideroxylon inerme trees maintain a large fruit crop (+/- 50 000) almost continuously and therefore exhibits a maximized strategy (Figure 3). In the southwestern Cape S. inerme is generally associated with dune vegetation where it is not a pioneer but a climax species. The flowering of S. inerme appears to be highly synchronized and usually occurs in February, with the first ripe fruit available eight months later. However, the ripening of fruits on individual plants and even individual branches may be displaced for anything up to fifteen months (see Chapter 3). Therefore a rationing of fruits promotes a very long fruiting season. Subsequent to a large fruiting display little or no fruit are produced for the next year or two. Since not all plants are synchronized to the same year, fruit is almost always available. This species is probably the most important plant for maintaining avian frugivore populations in the southwestern Cape (pers. obs).

Acacia cyclops

The introduced *Acacia cyclops* is the most widespread of Australian wattles in the Cape Province (Boucher & Stirton 1978) and exhibits a fruit display that most closely represents a maximized strategy (Figure 3). The large and conspicuous fruit display (Glyphis, Milton & Siegfried 1981) together with an ability to form large monospecific stands may promote large avian visitations to fruiting *A. cyclops* trees. *Acacia cyclops* is similar to *M. cordifolia* in that fruit matures slowly taking a full year to develop (Milton & Moll 1982). Unlike *M. cordifolia* ripe fruit is only made available when the pods containing the arillate seeds split. This rationing of fruit maintains a long five month fruit season (pers. obs).

Other alien species

Pittosporum undulatum, *Lantana camara* and *Rubus* sp. all have the ability to produce intensive fruit displays within the southwestern Cape. These fruit displays tend to be far less predictable than those of *A. cyclops* and have few avian visitations (pers. obs). However, their fruit displays may still contribute to the observed encroachment of these species into lower mountain slopes, valleys and along stream banks (Taylor 1978; Marais 1979), and both *Rubus* and *Solanum* species have been recorded in regeneration studies after clearing at Kirstenbosch (Esterhuysen 1936) and are frequently dispersed by the highly mobile Rameron Pigeon (*Columba arquatrix*). *Myoporum serratum* produces large, but irregularly presented fruit displays that are visited by smaller avian frugivores. The fruit display of *M. serratum* tends to present an intensive rather than a maximized strategy. In general this species is not recognized as being invasive, although it appears to be invasive in wetlands (pers. obs). Recently M. serratum saplings have been sighted in indigenous vegetation and A. cyclops thickets at Hermanus, Glencairn (pers. obs) and Rondevlei (H. Langley, pers. comm.). At Rondevlei it is becoming very numerous, especially around mixed alien acacia stands (pers. obs).

Prolonged fruit displays

Rapanea melanophloeos, Myrsine africana and Euclea racemosa exhibit prolonged strategies. Each of these species possess smaller than expected fruit displays, and since the fruit are infrequently consumed by avian frugivores their fruits remained unconsumed. During 1984 R. melanophloeos fruited more heavily than preceding years, but ripe fruit remained on the branches for many months, and were only utilized by avian and mammalian frugivores when virtually no other fleshy fruit were available (July). Colpoon compressum produces few fruits, but ripe fruits are rapidly consumed by avian frugivores, and are very difficult to find (pers. obs). However, all four species possess very conspicuous preripe fruit colour phases, with C. compressum and E. racemosa having red preripe and black ripe phases, while R. melanophloeos and M. africana possess white preripe and purple ripe phases and are therefore all consistent with a prolonged strategy. A prolonged display may rather be considered a strategy whereby fruit availability is maintained during periods when prolific fruit plants have no fruit crops.

Pivotal species and maintenance of resident frugivores

Howe (1984) suggested that not all plant species within a tropical forest are equal, and that local extinction of different species could have ecological consequences for the community at large. Plant species which fruit during periods of fruit scarcity, and supply much of the diet of frugivores during these periods were considered to be 'pivotal' in maintaining the fruit-frugivore community. The local extinction of such pivotal species would result in compounded local extinction of frugivores feeding on them, and in turn a reduction in dispersal and germination success of other plant species possessing fleshy fruits. Howe (1984) cites the Casearia corymbosa occurring at Finca La Selva, eastern Costa Rica as the best example of pivotal species. The aseasonal fruiting of *Ficus* spp. at Aldabra Atoll may also be considered pivotal in the maintenance of obligate frugivores Comoro Blue Pigeon (*Alectroenas sganzini*) and the Seychelles Fruit Bat (*Pteropus seychensis*) (Prys-Jones & Diamond 1984). Since the southwestern Cape possesses only a few plants with regular annual fruiting, the seasonal prediction of fruiting scarcity is impossible to determine, and consequently pivotal species are difficult to identify. However, during July and August 1984 very few fleshy fruits were available for the resident frugivore populations of Sombre Bulbul (*Andropadus importunus*) and Cape Bulbul (*Pycnonotus capensis*). There were, however, an exceptionally large number of *Rapanea melanophloeos* fruits in July and *Rhus crenata* fruits in August. The display of *R. melanophloeos* fruits had been presented since April, but were only consumed during July. Within three weeks all *R. melanophloeos* fruits had been consumed, but in the meantime a large display of *Rhus crenata* fruits had ripened. The supply of *Rhus crenata* fruits lasted until *Chrysanthemoides monilifera* fruits became available. Therefore both *Rapanea melanophloeos* and *Rhus crenata* could be considered pivotal during this fruit shortage. A fruit shortage during this time of year is not an annual event and did not occur during 1983. The population of *Sideroxylon inerme* trees at Hermanus could also be considered as a pivotal fruiting species. This species maintains the frugivore population with its regular source of fruit throughout much of the year. A break in the continued availability of these fruits precipitated the fruit scarcity occurring in July and August 1984. The local extinction of this species would fragment the seasonal availability of fruit provided by all the other species, and probably result in a far smaller frugivore population. I therefore suggest that two types of pivotal species could occur at Hermanus. A short term pivotal species (*R. melanophloeos* and *Rhus crenata*) which overcome short term fruit scarcities, and a long term pivotal species (*S. inerme*) which forms the backbone to the fruit-frugivore community.

Fruit displays:- genetically labile

The fruit displays presented in this study reflect only those patterns that exist within the southwestern Cape. Since *S. inerme*, *R. melanophloeos*, *M. africana* and *M. acuminata* are all at the southern limits of their geographical distribution, their fruiting displays and phenology may not be representative of those characteristic of these species elsewhere. Further, an impoverishment of evergreen broad-leafed shrubs and trees within the southwestern Cape may have promoted the lengthening of fruiting seasons. For example, the fruit display of S. inerme within the southwestern Cape is large and almost continuous throughout the year, whereas in the eastern Cape it appears to be smaller and less freely available (Liversidge 1972). However, Pierce & Cowling (1984) recorded a continuous supply of unripe S. inerme fruits in an Eastern Cape thicket growing on dune sands, whereas ripe fruit were only recorded from November to March. No S. inerme fruits were recorded on plants growing in loam. These results confirm the irregular fruiting of individuals within the moist subtropical thicket scrub occurring under coastal conditions (Liversidge 1972; Pierce & Cowling 1984). A further complication is that most of these species are more commonly associated with year-round or summer rainfall regimes, while within the southwestern Cape a winter rainfall regime exists. Since water availability is particularly critical for some species such as C. monilifera (Weiss 1983), fruiting of this species occurs at the end of winter in the southwestern Cape, whereas in the eastern Cape it occurs in autumn (Liversidge 1972). However C. monilifera possesses six distinct subspecies (Coates Palgrave 1977) with differing fruit morphologies e.g. southwestern Cape C.m. monilifera possesses an orange/brown spherical fruit with pale spherical seeds, while southern Cape C.m. pisifera possesses smaller black ovate fruit and smaller, dark elongated seeds (pers. obs). The fruit displays of Colpoon compressum (syn. Osyris abyssinica) and a sympatric variety Osyris abyssinica var. speciosa (A.W. Hill 1915, Fl. Cap. 5(2,2):209) differ considerably, in that speciosa (which is not considered in this analysis) possesses very large and conspicuous fruit displays, with fruits of far greater individual size and possessing only a red ripe phase (see Chapter 2). Further, it seems that fruit displays are irregular and are produced only after recent fires (I.J.M. Williams, pers. comm.; pers. obs). For these reasons as well as habit, the nature of inflorescence and low height (< 1 m) it is proposed that the taxonomic status of var. speciosa be reviewed.

Alien fruit displays and perturbations of ecosystems

From this analysis it appears that plant species with intensive or maximized fruit displays are usually pioneer species. Indeed Chrysanthemoides monilifera, which was introduced into Australia around 1908, has become an aggressive invader into Acacia longifolia stands in New South Wales (Weiss 1983). Further another species of Myrica, M. faya, native to the Azores and Madeira, has invaded more than 85 000 ha in the Hawaiian Islands (Hosaka & Thistle 1954). Therefore, any planned introduction of one of these species into areas outside their own distributions requires caution and scientific investigation if future large scale alien plant infestations are to be avoided.

Large scale infestations of alien plants with fleshy fruits may not only compete with indigenous plant species but may also alter foraging patterns and diets of avian frugivores feeding on them. Large populations of the Rameron pigeon (Columbia arquatrix) formerly existed in the indigenous forests of South Africa (Oatley 1984) and fed on the fleshy fruits of indigenous tree species (Philips 1927). The indigenous South African forests dwindled with the advent of timber exploitation late last century and by the 1950's the Rameron pigeon had become relatively uncommon in Natal forests. However, recently Rameron pigeon populations have increased, with a switch in the diet from indigenous fruits to the berries of Solanum mauritianum (Oatley 1984). The avian utilization of Solanum mauritianum berries has promoted the spread into, and the establishment of this species within timber plantations of Natal and the Transvaal. In particular light gaps created by felling operations are rapidly overgrown by the establishment of a monospecific understorey of Solanum mauritianum. Further, perturbations of the ecosystem occur by the non-removal and dispersal of indigenous fruits and a concomitant decline in the recruitment and regeneration of these species. In the southwestern Cape fruit displays of Acacia cyclops attracts large flocks of Red-winged Starling (Onychognathus morio) from November to March. After March most A. cyclops fruits have been consumed, whereas the indigenous fruits of Rhus species (R. crenata, R. glauca, R. lucida, R. lavigata, R. tomentosa) which provided a continuous supply of fruits throughout the summer (pers. obs) are consumed after March. By late March or early April Myrica cordifolia fruits are available and are consumed in preference to the Rhus fruits. During 1983-1984 the fruit crops of A. cyclops at Hermanus were poor and the avian frugivores utilized the succession of fruiting Rhus during the summer. Since a long term reliance had been placed on the fruits of Acacia cyclops, any failure on the part of this fruit crop would need to be overcome by another species. Under these circumstances the succession of fruiting Rhus species could be considered to be pivotal by default and indicates the vulnerability of ecosystems when contaminated by alien species. It is consequently felt that prior to the introduction of Acacia cyclops to the Cape last century, Rhus fruits were heavily utilized. Further, the Red-winged Starlings are usually associated with mountainous and hilly country (McLachlan & Liversidge 1971) but within the southwestern Cape are abundant in coastal A. cyclops thickets, though are rarely or never observed in coastal vegetation that is devoid of A. cyclops (pers. obs). In conclusion the fruit displays of alien plant species may not only precipitate perturbations for the plant species but also for the avian frugivore populations.

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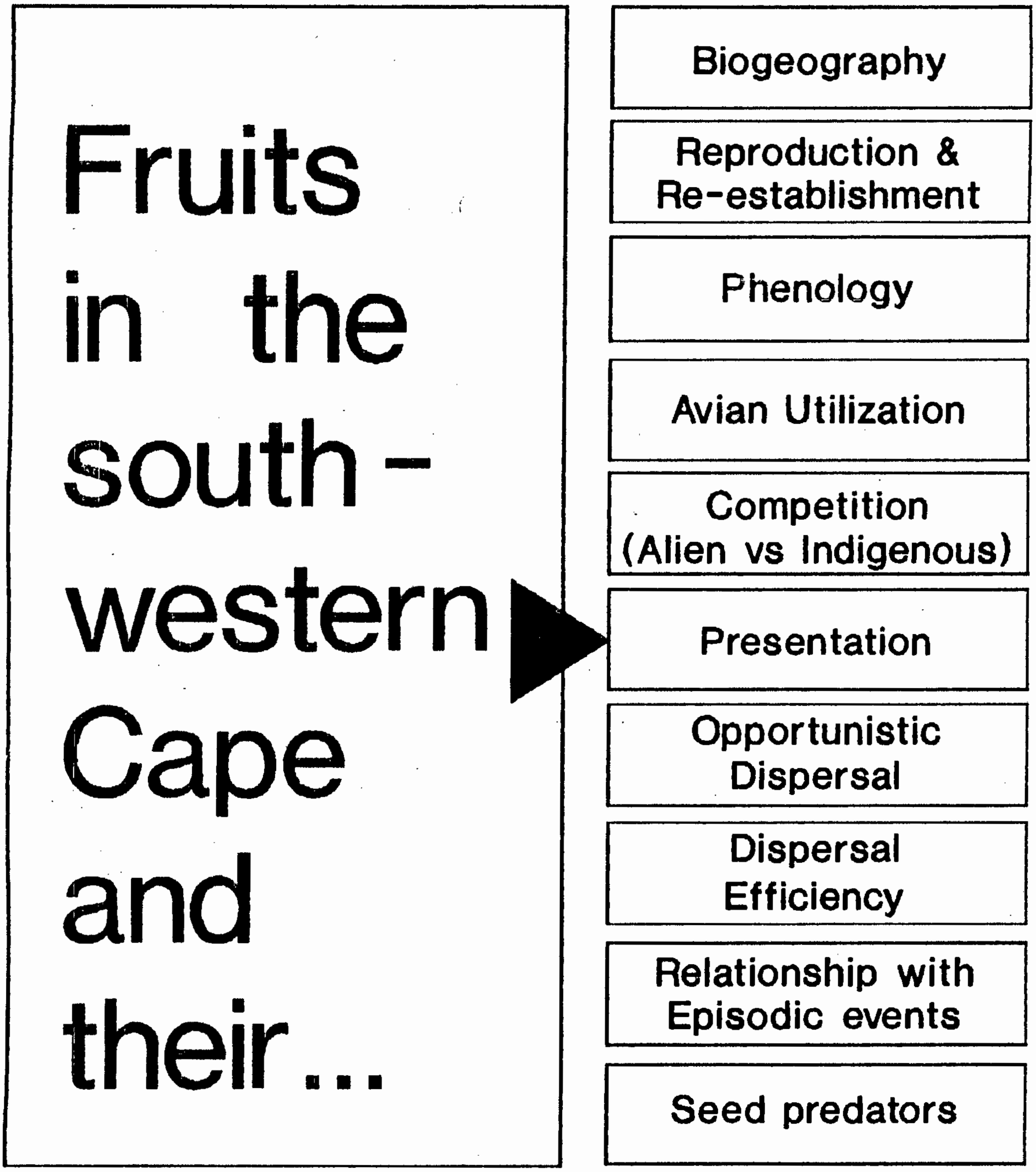
CHAPTER 6



Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Inter-relationships between leaf abundance, stem thickness and fruit presentation in some African evergreen plants

Contents

Discussion

Inter-relationships between leaf abundance, stem thickness and fruit presentation in some African evergreen plants*

Abstract

Relationships between fruit production, stem thickness and leaf and stem abundance were investigated in nine evergreen plant species in Coastal Thicket and Afromontane Forest vegetation, in South Africa. Branches bearing fleshy fruits had fewer leaves than branches without fruits; the greater the fruit production, the fewer the number of leaves. The reduction of leaves associated with fruits is considered to promote both the conspicuousness and the accessibility of fruits for dispersal by avian frugivores. This relationship was more pronounced in species which present their fruits close to their stems than in species which present their fruits in panicles. Fruiting branches had significantly thicker stems than non-fruiting branches. An increase in stem thickness may be required to support both fruits and feeding frugivores.

In press _Bot_. _J_. _Linn_. _Soc_.

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* Junior author W.R. Siegfried

Introduction

Birds are important agents for the dispersal of many plant species which usually contain their seeds in fleshy fruits (Regal 1977; Snow 1981). Such plants may increase their attractiveness for potential seed-dispersers by enhancing their displays of fruit. Thus, fruit colour (Turcek 1963; Willson & Thompson 1982), fruit type and size (McKey 1975; Stiles 1981), and suites of inter-relationships between fruit features (Knight & Siegfried 1983; Gautier-Hion *et al.* 1985) have been investigated. Apart from Denslow & Moermond (1982), Moermond & Denslow (1983), however, scant attention has been given to studying the accessibility of fruit to avian frugivores. More particularly, it appears that investigations have not been made of the plants' structures which support and enhance fruit displays. This paper reports on a study of fruit production in relation to thickness of stems and numbers of secondary stems and leaves associated with fruit displays, in nine species of evergreen plants in Coastal Thicket and Afromontane Forest vegetation in the south-western Cape region of South Africa. The report examines the following hypotheses:

(1) visual conspicuousness and accessibility of a fruit display should be enhanced by a local, limited, reduction of leaves;

(2) thicker stems should be required to support larger fruit crops and the birds exploiting the fruit crops;

(3) large fruit crops should be concentrated on branches possessing few side branches, for maximum accessibility of fruits, except for species which present their fruits terminally; and,

(4) large stem-attached fruit displays should be associated with the greatest local reduction of leaves (hypothesis 1) and the lowest number of secondary stems (hypothesis 3).

Materials and Methods

Individually-marked plants belonging to *Myrica cordifolia* (Myricaceae), *Colpoon compressum* (Santalaceae), *Rhus laevigata* (Anacardiaceae), *Pterocelastrus rostratus* and *P. tricuspidatus* (Celastraceae), *Ilex mitis* (Aquifoliaceae), *Sideroxylon inerme* (Sapotaceae), *Chironia baccifera* (Gentianaceae) and *Lycium ferocissimum* (Solanaceae) were examined during April-May 1985 at three study sites: Steenberg (34°05'S, 18°28'E), Rooi-els (34°16'S, 18°49'E) and Hermanus (34°25'S; 19°16'E). These species all have wide distributions in southern Africa, and within the south-western Cape region their fruits are consumed by local avian frugivores (pers. obs). Other aspects of the fruit displays of some of these species are described by Knight (1986)(Chapter 5).

For each species, 50 branches (30 cm in length, measured from branch apex) were collected randomly from 10 individual plants and subsequently treated as follows: length (cm) of main stem; sum of side-stem lengths (cm), henceforth termed secondary stems; total number of leaves on main stem; total number of leaves on secondary stems; total number of fruits on main stem; total number of fruits on secondary stems; diameter (mm) of main stem; diameter (mm) of secondary stems; and, total number of secondary stems for 30 cm of main stem. For purposes of this paper, a branch consists of a main stem which may or may not possess secondary stems. Occasionally tertiary stems are produced on the secondary stems and they are termed shoots.

The very small drupes of *R. laevigata* are arranged in small tight panicles, averaging 13 fruits per panicle. Hence, the number of panicles, rather than the number of fruits, was counted. For each species, fruit and leaf densities, per 10 cm of stem length (both main and secondary), were calculated for each entire branch. Samples were discarded if any fruits or leaves had fallen off a branch, prior to it being processed. Consequently, sample sizes are not the same for each species (Appendix 1).

The relationships between average fruit density, (the independent *x* variable) and the dependent *y* variables (leaf density, stem thickness and stem number) were plotted as scatter diagrams. Precise relationships between the independent and the dependent (y) variables were determined, using a suite of variable transformations which represented increasing deviations from linearity (Figure 1). Curve A (Figure 1) represents perfect linearity (x and y are untransformed), whereas in Curve B a perfect correlation will occur if the square-root of the independent variable is used. The log-log transformation (Curve H) represents the greatest deviation from linearity. An optimal correlation was determined by comparing the correlation (r) under the different variable transformations (Figure 1). Thus, the relationships between the x and the y variables were classified. Further analyses were performed to determine positions of fruit density (main or secondary stems) and differences in leaf density, stem thickness and stem numbers between fruiting and non-fruiting branches, using Mann-Whitney U tests.

Results

Amongst the nine species of plants, average fruit density ranged from 0,70 to 16,86 fruits per 10 cm in *P. rostratus* and *S. inerme*, respectively (Appendix 1). Fruit density was significantly ($P < 0,01$) greater on secondary than on main stems in seven species; there being no significant difference in *I. mitis*, and fruit density being greater ($P < 0,05$) on the main stems of *S. inerme*. Average leaf density also varied greatly between the species, from 3,85 to 42,50 leaves per 10 cm in *P. rostratus* and *L. ferocissimum*, respectively (Appendix 1). Of the nine species examined, six species had significantly inverse relationships between fruit and leaf densities (Figure 2). Further differences in leaf densities of main stems occurred between fruiting and non-fruiting branches in *M. cordifolia*, *R. laevigata*, *S. inerme*, and *C. baccifera*, with the non-fruiting branches having significantly more leaves (Table 1). In the case of secondary stems (which generally supported higher densities of fruit), leaf densities varied significantly between fruiting and non-fruiting branches in *Ch. baccifera*, *M. cordifolia* and *S. inerme* (Table 1). This supports our first hypothesis that fruit displays may be associated with a local reduction in the number of leaves.

Fruiting branches had significantly thicker secondary stems than non-fruiting branches in both *M. cordifolia* and *R. laevigata*, whereas significant differences in primary stem thickness occurred in *Ch. baccifera* and *S. inerme*

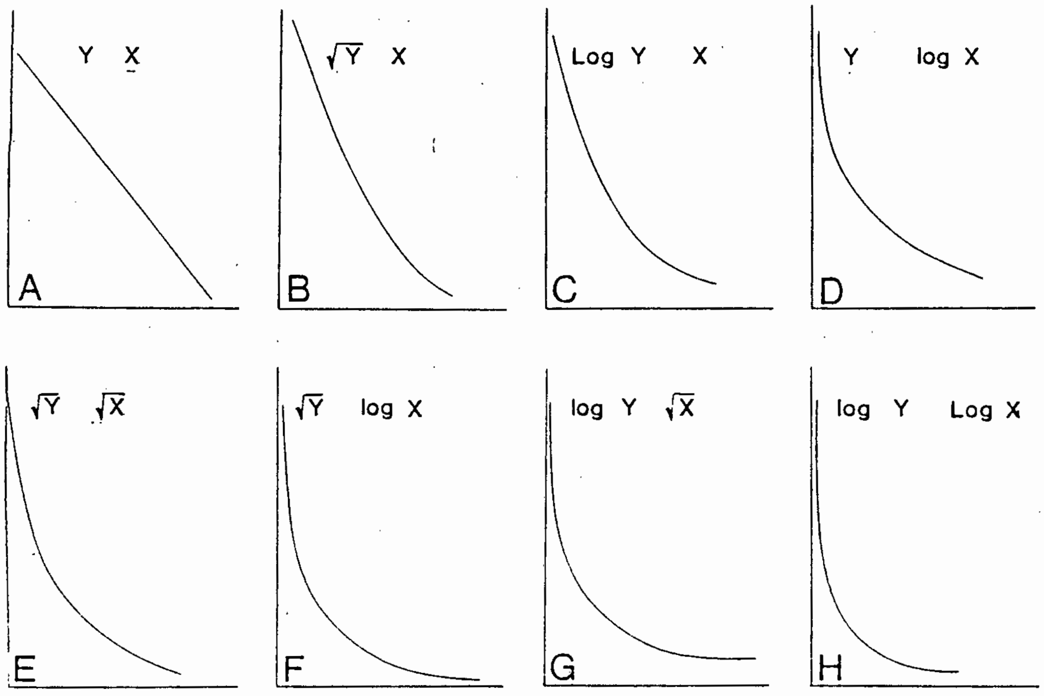

Figure 1 The suite of eight curves representing increasingly non-linear relationships, from the linear curve (A) through to the log-log curve (H), used to determine optimal correlations between fruit density and structural components of branches (see Table 2)

(Table 1). Of the seven species which display their fruits on secondary stems, fruit density increased with increasing secondary-stem thickness in *M. cordifolia*, *R. laevigata*, *P. tricuspidatus* and *Ch. baccifera* (Table 2). Hence, in this suite of seven species at least four provide support for our second hypothesis.

Sideroxylon inerme was the only species which had significantly fewer secondary stems on fruiting than on non-fruiting branches (Table 1). However, three species (*M. cordifolia*, *S. inerme* and *L. ferocissimum*) showed negative correlations between fruit density and secondary-stem numbers (Table 2). Hence, apparently, stem number is sometimes inversely related to fruit density. Although *C. compressum* showed a positive linear relationship between fruit density and an increase in secondary stem number (Table 2), this does not conflict with our third hypothesis, since its fruits are presented terminally (Appendix 1).

Only three species (*M. cordifolia*, *S. inerme* and *P. tricuspidatus*) possess stem-attached fruits. Fruit-leaf density relationships were more significant (*r* = -0,87; -0,85; and -0,77, respectively, for each of these species than for *R. laevigata* (*r* = -0,71), *L. ferocissimum* (*r* = -0,62) and *Ch. baccifera* (*r* = -0,54). Optimal fruit-leaf density relationships were found using C, E and F curves (Figure 2) for the three species having stem-attached fruits, *S. inerme*, *M. cordifolia* and *P. tricuspidatus*, respectively. In the other three species (*R. laevigata*, *Ch. baccifera* and *L. ferocissimum*), the relationships are more linear, since optimal correlations were achieved using B, B and C curves (Figure 2). The greater the degree of non-linearity, the steeper the gradient of slope between fruit and leaf density, and the greater is the proportion of leaf reduction associated with the fruits. However, since *L. ferocissimum* has a more pronounced negative relationship between fruit density and secondary stem number (*r* = -0,68) than *S. inerme* and *M. cordifolia* (*r* = -0,40 and -0,47; respectively), our fourth hypothesis, that branches with stem-borne fruits have both an emphasized fruit loss and fewer secondary stems, cannot be accepted unconditionally.

Table 1 Statistical differences (Mann-Whitney U test) between structural components of fruiting (FB) and non-fruiting (NFB) branches of five plant species, based on data in Appendix 1

	No. main-stem leaves	No. secondary stem leaves	No. main and secondary stem leaves	Main stem thickness	Secondary stem thickness	No. secondary stems
Myrica cordifolia	NFB***	NFB***	NFB***	NFB*	FB***	NS
Rhus laevigata	NFB***	NS	NFB***	NS	FB***	FB***
Pterocelastrus tricuspidatus	NS	NS	NFB*	NS	NS	NS
Sideroxylon inerme	NFB***	NFB***	NFB***	FB*	NS	NFB**
Chironia baccifera	NFB**	NFB**	NFB**	FB*	NS	NS

*** $P < 0,001$, ** $P < 0,01$, * P 0,05, NS = non-significant

Table 2 Significant correlations (P < 0,05) between fruit density and structural components of branches for nine plant species, based on curve-fits in Fig. 1

Species	Structural component of branch	Optimal curve fit (see Fig. 1)	Correlation (r)
Colpoon compressum	No. secondary stems	A	0,32*
Rhus laevigata	No. main and secondary stem leaves	B	-0,71***
Lycium ferocissimum	No. secondary stems	B	-0,68***
Chironia baccifera	No. main and secondary stem leaves	B	-0,54***
	Main stem thickness	B	0,48***
	Secondary stem thickness	B	0,45***
Myrica cordifolia	Secondary stem thickness	B	0,53***
Sideroxylon inerme	No. secondary stems	B	-0,40**
	No. main and secondary stem leaves	C	-0,85***
Lycium ferocissimum	No. main and secondary stem leaves	C	-0,62***
Myrica cordifolia	No. secondary stems	D	-0,47***
Colpoon compressum	Secondary stem thickness	D	-0,29*
Myrica cordifolia	No. main and secondary stem leaves	E	-0,87***
Rhus laevigata	Secondary stem thickness	E	-0,50***
Pterocelastrus tricuspidatus	No. main and secondary stem leaves	F	-0,77***
	Secondary stem thickness	F	0,50***
Myrica cordifolia	Main stem thickness	F	-0,31*
Rhus laevigata	No. secondary stems	F	0,61***
	Main stem thickness	G	-0,42**

*** P < 0,001, ** P < 0,01, * P < 0,05

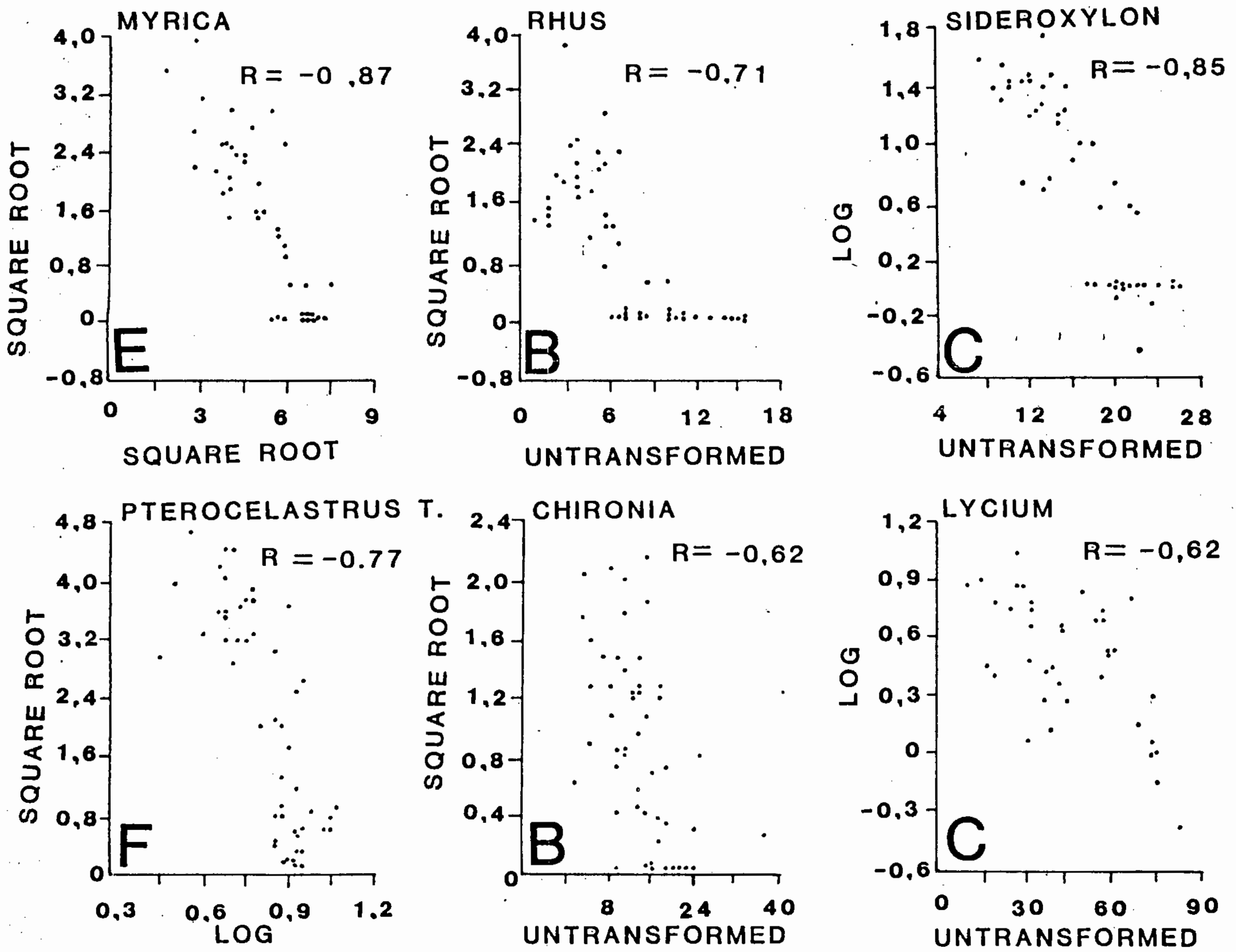

Figure 2 Significant inverse relationships between fruit density (vertical axis) and leaf density (horizontal axis) of six plant species in the south-western Cape region of South Africa

Discussion

Leaf Reduction

Since leaves may obscure fruits from avian frugivores, the fleshy fruits of many species which rely on birds for dispersal are presented as clusters (panicles) at the ends of long stalks (e.g. *I. mitis*, in this study). Alternatively, fruits may be displayed individually or in relatively small clusters, of three to four fruits, at the ends of long peduncles (e.g. *P. rostratus*) or close to the apexes of secondary stems (e.g. *Ch. baccifera*) or at their tips (e.g. *C. compressum*).

Two main drawbacks apparently attend the presentation of fruits in panicles. First, the production of panicle stalks requires a special investment by the plant; the stalks being discarded once fruiting has been completed. Secondly, since panicles have to support not only fruits but also feeding frugivores, their fruits tend to be small and presumably attract mainly small opportunistic frugivores (Terborgh & Diamond 1970; Snow 1971, 1981; McKey 1975; Howe & Estabrook 1977). The presentation of individual fruits, as occurs in *P. rostratus* and *C. compressum*, also has a theoretical disadvantage in that it imposes a restriction on the size of fruit crops. Since large fruit crops may preferentially attract more frugivores, plants producing small crops may have fruits left undispersed at the end of a fruiting season, unless they are dispersed by specialist frugivores (McKey 1975). If fruit stalks were to be discarded, and fruits borne directly on, or close to, the stems, large crops of individually larger fruits could be presented. This, however, could be disadvantageous if the plant's leaves either obscured or reduced the accessibility of its fruits.

In deciduous plants, a change in leaf colour during the boreal autumn appears to enhance the conspicuousness of fruit displays (Stiles 1982). Since the leaves of these species are discarded in winter when the plants are dormant, their loss does not represent a disadvantage. However, in our study region true deciduousness is not normal and the leaves of broad-leafed plants live between one and six years (Kruger 1981). If maximum fruit production in these species were to coincide with senescence and maximum loss of leaves near fruiting bodies, the conspicuousness and accessibility of fruits would be promoted without sacrificing the long-term photosynthesizing potential of the plant. In this connexion, *S. inerme* staggers its fruit ripening, with full-sized unripe fruit being maintained for up to 15 months (pers. obs), and it is likely that in this species final ripening of fruit may be delayed until the associated leaves are close to the limit of their longevity and can be discarded. Scars from recent leaf incisements were visible in both *S. inerme* and *M. cordifolia* during April-May. Recent scars were also observed in the other species, but it was difficult to determine whether they were from leaf or fruit removal.

Phenological models proposed by Specht & Moll (1983) and Specht *et al.* (1983), applicable to the species we studied, predicted that broad-leafed evergreen species occurring on base-rich soils should have the greatest degree of leaf-fall immediately following autumn and spring shoot growth. If fruit ripening does precede maximum leaf-fall, the late austral autumn and early winter and late spring should be optimal periods for fruiting. In fact, in our study areas, we recorded the highest number (15-20) of species fruiting in April and May, and the sampling of our nine study species was undertaken during these months. We also noted then that new shoots were starting to grow on secondary stems of *M. cordifolia*, *C. compressum*, *P. tricuspidatus* and *S. inerme* which are most abundant in Coastal Thicket vegetation occurring on base-rich soils. This phenological pattern agrees generally with the model proposed by Specht & Moll (1983). However, our observations cannot be used to confirm their model, since shoot growth was not quantified throughout the year. Moreover, it should be borne in mind that excess or early shooting would theoretically reduce accessibility and conspicuousness of fruits to frugivores. Further, rapidly growing shoots may compete with young fruit for resources (Quinlan & Preston 1971). It appears that in apples (*Malus*), most carbon used for fruit production is fixed by leaves that are in close proximity to the fruit (Quinlan & Preston 1971). Therefore, a carbon drainage within the vicinity of fruits may occur and, at a late phase of fruit ripening, leaves may be discarded in order to concentrate resources within the fruit.

Stem Thickness

Siegfried *et al.* (1985) demonstrated that in *Erica* avian-pollinated species had significantly thicker stems than non- avian pollinated species. The increase in stem thickness of the avian-pollinated species was attributed to the increased support required by pollinators. Similar relationships should hold for fruit displays. Unlike some avian seed dispersers (Greenberg 1981) local species are not adapted for hovering (pers. obs) and, therefore, plant stems and fruit panicles must give sufficient support for perching. Consequently, fruit size and frugivore size and support all need to be related. Diamond (1973, 1975) showed that, in New Guinea, small fruits (7 mm in size) attracted the smallest fruit pigeons (47 - 163 g) and that there was a proportional increase in the size of species of fruit pigeon feeding on fruits of increasing size. Fruits of 40 mm appeared to attract pigeons of the largest size (592 - 802 g).

In our study region, avian frugivores vary in size from the Cape white-eye *Zosterops pallidus* (8 - 15 g) to the Rameron pigeon *Columba arquatrix* (324 - 500 g). White-eyes tend to forage on the smallest fruits, many of which are arranged in panicles or at the tips of branches of species such as *I. mitis* and *R. laevigata* (see Chapter 4). In contrast, the large avian frugivores are usually associated with those species which produce larger fruits on thick stems (pers. obs). Kantak (1979) postulated a similar arrangement in Mexico. The thickening of stems before fruiting in species such as *S. inerme* and *R. laevigata* may have long-term benefits in that increased support is available for future shoots which will also bear relatively large fruit crops.

Conclusion

It is likely that evergreen plants tend to present their fruits during periods when-leaf fall is greatest, so that both conspicuousness and accessibility of the fruits are enhanced for dispersal by frugivores. This process is likely to be defined best in species which produce stem-attached fruits. We predict that stem-attached fruits are more likely to occur in evergreen than in deciduous species.

Acknowledgement

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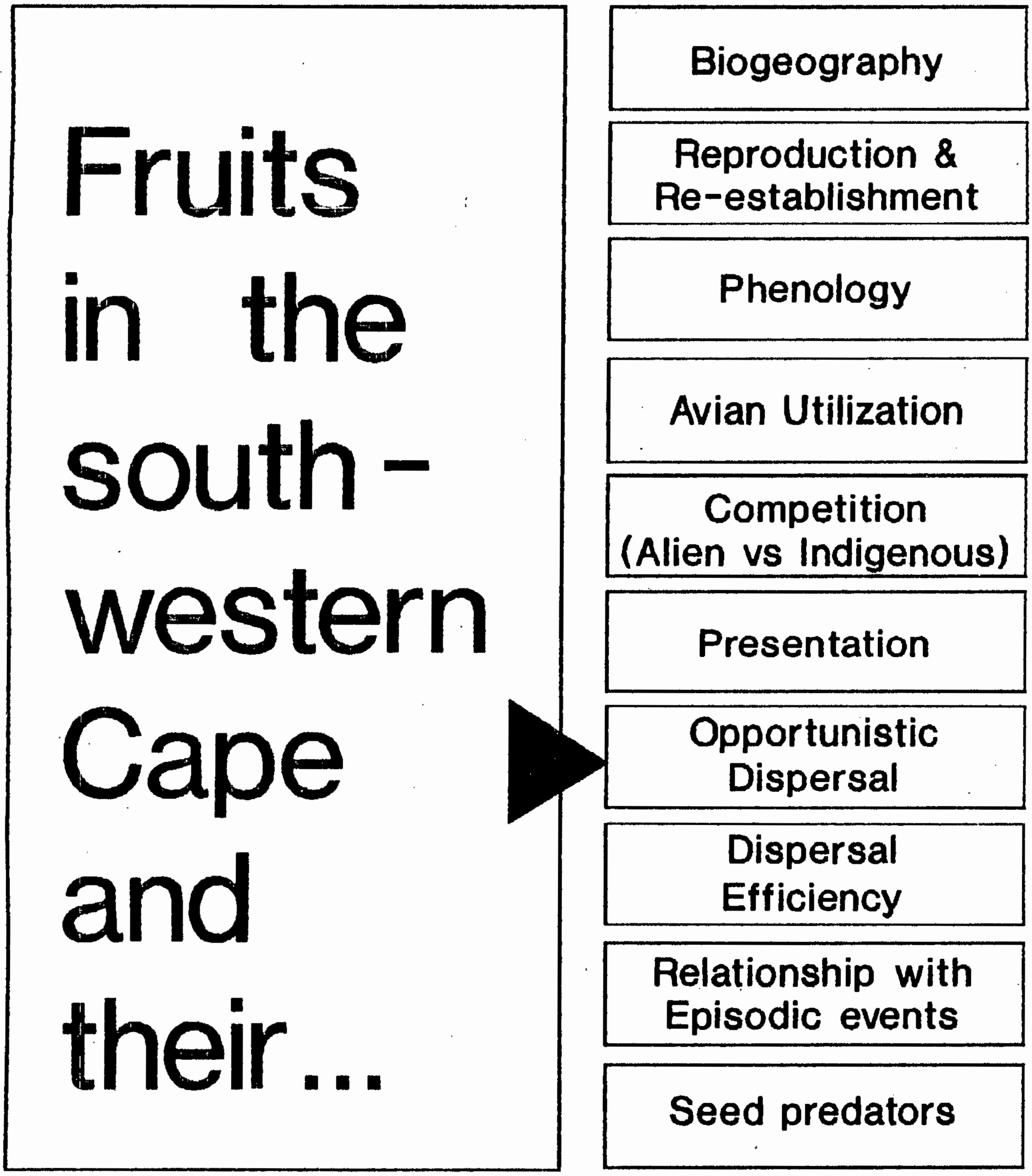
Appendix 1 Structural components of fruiting and non-fruiting branches of nine plant species in the south-western Cape, South Africa

Structural components of branches	Myrica cordifolia	Colpoon compressum	Rhus laevigata	Pterocelastrus rostratus	Pterocelastrus tricuspidatus	lex mitis	Sideroxylon inerme	Chironia baccifera	Lycium ferocissimum
Fruit characteristics									
Fruit type	Drupe	Drupe	Drupe	Capsulate aril	Capsulate aril	Drupe	Drupe	Berry	Berry
Fruit size (mm)	8	13	4	8	8	5	12	7	8
Fruit attachment	Stem	Terminal	Stalked panicle	Long peduncle	close to stem	Stalked panicle	Stem	Short peduncle	Short peduncle
Fruit colour (ripe)	Purple-black	Purple-black	Brown	Orange	Yellow	Red	Black	Orange-red	Red
Leaf characteristics									
Type	Simple	Simple	Compound	Simple	Simple	Simple	Simple	Simple	Simple
Length (mm)	5-10	30-60	34-48 (leaflet)	20-60	30-60	70-80	60-80	18-24	11-25
Width (mm)	4-8	17-27	20-26 (leaflet)	13-15	25-35	20-30	25-30	4-6	4-8
Non-fruiting branches									
No. branches examined	16	Insufficient samples	23	Insufficient samples	6	Insufficient samples	14	10	Insufficient samples
No. main stem leaves per 10 cm	16,44		9,05		3,86		21,57	10,60	
No. secondary stem leaves per 10 cm	49,44		4,26		9,69		20,57	19,60	
No. main and secondary stem leaves per 10 cm	44,55		10,13		9,18		21,41	18,33	
Main stem thickness (mm)	3,97		5,71		5,32		6,39	2,02	
Secondary stem thickness (mm)	1,24		1,57		2,73		3,68	1,16	
No. secondary stems per 30 cm of main stem	15,37		1,91		6,67		4,86	20,80	
Fruiting branches									
No. branches examined	31	48	28	49	45	47	34	41	37
No. main stem leaves per 10 cm	1,03	6,52	0,47	2,30	2,18	8,54	14,74	5,34	16,34
No. secondary stem leaves per 10 cm	23,45	15.73	5,05	4,61	7,49	11,03	10,06	13,78	48,22
No. main and secondary stem leaves per 10 cm	22,43	14,65	4,27	3,85	6,80	11,00	14,39	12,54	42,5
Main stem thickness (mm)	1.98	4,07	4,29	4,22	5,26	6,06	7.64	2.59	5.00
Secondary stem thickness (mm)	1,84	2,57	3,34	2,91	3,53	3,58	2,97	1,45	3,21
No. secondary stem per 30 cm of main stem	13,23	9.40	6,86	4,27	11,38	2,96	1,82	17,83	8,70
Fruit production									
No. main stem fruits per 10 cm	1,53	0,94	0,37	0,35	1,67	4,79	18,95	0,13	1,45
No. secondary stem fruits per 10 cm	4.76	1.83	4,50	1.08	8,53	4,91	8,22	1,72	4,64
No. main and secondary stem fruits per 10 cm	4,73	1,76	3,58	0,78	7,51	5,37	16,86	1,49	4,02

CHAPTER 7



Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Acacias and korhaans: an artificially assembled seed-dispersal system

Contents

Acacias and korhaans: an artificially assembled seed-dispersal system

Contents /continued

Acacias and korhaans: an artificially assembled seed-dispersal system*

Abstract

The seed-dispersal of two introduced acacia species by the black korhaan _Eupodotis afra_, a 700 g ground feeding otidid bird, was studied in the southwestern Cape region of South Africa. The seeds of _Acacia cyclops_ possess conspicuous pseudarils and were consumed in preference to _A. saligna_ which possess seeds lacking a functional pseudaril. Despite high levels of pre- and post-dispersal seed predation by a hemipteran and a rodent respectively, the black korhaan dispersed many _A. cyclops_ seeds to sites where they germinated and the seedlings could establish themselves. This successful seed-dispersal system has arisen without any coevolution between this plant and this bird.

Submitted _J. Funct. Ecol._

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* Junior author I.A.W. Macdonald

Introduction

The introduced Australian wattles *Acacia cyclops* and *A. saligna* (Family Fabaceae: Mimosoideae) are widespread in the southern and southwestern Cape (Stirton 1978). *Acacia cyclops* was introduced to South Africa *ca* 1857 and *A. saligna* *ca* 1848 (Shaughnessy 1986). The seeds of *A. cyclops* have a conspicuous scarlet pseudaril (derived from the funicle), whereas seeds of *A. saligna* possess a vestigial white pseudaril. Consequently *A. cyclops* has seeds that are typically bird-dispersed whereas *A. saligna* is typically ant-dispersed (van der Pijl 1972; Davidson & Morton 1982). Avian-dispersal of acacia seeds possessing colourful lipid-rich pseudarils has been investigated in Australia (Forde 1986). Seed germination and patterns of colonization by *A. cyclops* have been investigated in South Africa (Glyphis, Milton & Siegfried 1981). The occurrence of *A. cyclops* and *A. saligna* seeds in the faeces of the black korhaan *Eupodotis afra* in South Africa stimulated an investigation to test the following hypotheses:-

1) Do black korhaans selectively feed on those acacia seeds possessing colourful, lipid rich pseudarils (*A. cyclops*)?

2) Do black korhaans disperse the seeds of *A. cyclops* and *A. saligna* in a viable condition, and to sites that permit seed germination?

Materials and Methods

Field techniques

Individual faeces (recognized by their large size and general appearance) of the black korhaan were collected from two areas: Pella (33° 32′ S, 18° 30′ E) situated in Coastal Fynbos (Moll *et al*. 1984), and a site close to the Kalbaskraal Nature Reserve (33° 35′ S, 18° 36′ E) situated in Renosterveld (Moll *et al*. 1984). Sampling for korhaan faeces (N = 35) at Pella took place from February 1984 to July 1985 to assess the overall occurrence of seeds of indigenous and alien plants in the diet of the black korhaan. Twenty-seven faecal samples at the Kalbaskraal site were collected in March (1984) which is near the end of the fruiting season for both *A. cyclops* and *A. saligna*

(Milton & Moll 1982). *In situ* field experiments were undertaken at this site to test post-dispersal seed viability and germination. Ten faeces were placed in terylene bags and replaced in the precise position where the bird had deposited them. The bags were designed to prevent further seed removal and predation while still permitting uninhibited germination. The positions of a further 10 faeces were "pegged" but not "bagged", to enable the estimation of post-dispersal seed removal and presumed predation. The "bagged" faeces were recovered six months later in September 1984 after the winter rains during which maximum acacia seed germination occurs (P.M. Holmes pers. comm.). The number and condition of germinated and ungerminated acacia seeds were assessed in September for each "bagged" and "pegged" sample. Condition of seeds was given as either "alive" or "dead". Live seeds were those which were intact, while dead seeds appeared shrunken since the seed contents had rotted. Seedlings were similarly rated, dead seedlings being brown and shrivelled. For the enumeration of "pegged" samples the surface litter and top 2 cm of soil were collected from a circular area 30 cm around each peg. These samples were then sieved, with seed and seed remains being retained.

Numerical techniques

Relative proportions of *A. cyclops* and *A. saligna* seeds were tested for significant differences using the Sign test (Siegal 1956). Differences in the number of acacia propagules (seeds and seedlings) found between experiments were tested using a Mann-Whitney *U* test (Siegal 1956). Differences in propagule number, condition and state of germination for *A. cyclops* and *A. saligna* occurring in the "bagged" and "pegged" experiments were investigated using a multidimensional contingency table analysis (Knight & Siegfried 1983). The following categories were used to define each variable:-

Acacia species (*A. cyclops*, *A. saligna*)

Germination state (germinated, ungerminated)

Propagule condition (alive, dead)

Experimental condition ("bagged","pegged")

Combinations of these variables formed the models which were tested with the BMDP 4F 14-18 computer programs (Brown 1981). The most parsimonious combination of variables (= model) was selected and fitted to the data so that residual combinations of variables were non-significant (Brown 1981).

Results

Black korhaan diet

The diet of the black korhaan, as represented by the faeces collected in February, April, November, and December 1984, and June and July 1985 at Pella (Figure 1), indicates vegetable matter (excluding seeds) to be the most frequently occurring food item (Figure 1). Both seeds and invertebrates (all members of the Coleoptera) are more seasonal than vegetable matter in their occurrence in the diet of the black korhaan. Four of the 37 faeces contained a total of 112 A. cyclops seeds, whereas only 1 A. saligna seed was found. Indigenous plants bearing fleshy fruits or arillate seeds were represented by Chrysanthemoides monilifera (Asteraceae)(1 seed), Euclea racemosa (Ebenaceae)(1), Nylandtia spinosa (Polygalaceae)(46) and Pterocelastrus tricuspidatus (Celastraceae)(1). All the seeds recovered appeared to be intact and potentially viable.

Selective consumption of Acacia cyclops seeds

Seeds of A. cyclops occurred at significantly higher frequencies than did those of A. saligna in the faeces collected at both sites (Sign test; $P <$ 0,001). Acacia cyclops made up more than 99% of the acacia seeds found in faeces, despite A. saligna being both the more prolific seeder (Milton & Hall 1981) and the more numerous plant at both sites (Table 1). At Pella, A. saligna seeds were more numerous than A. saligna on and in the ground (Table 2). Therefore more A. saligna seeds would be available to the ground-feeding Black Korhaan. Since the seeds of both species have thick testa which are extremely resistant to mechanical and chemical abrasion (Milton & Hall 1981) it is not considered likely that the predominance of A. cyclops in the faeces

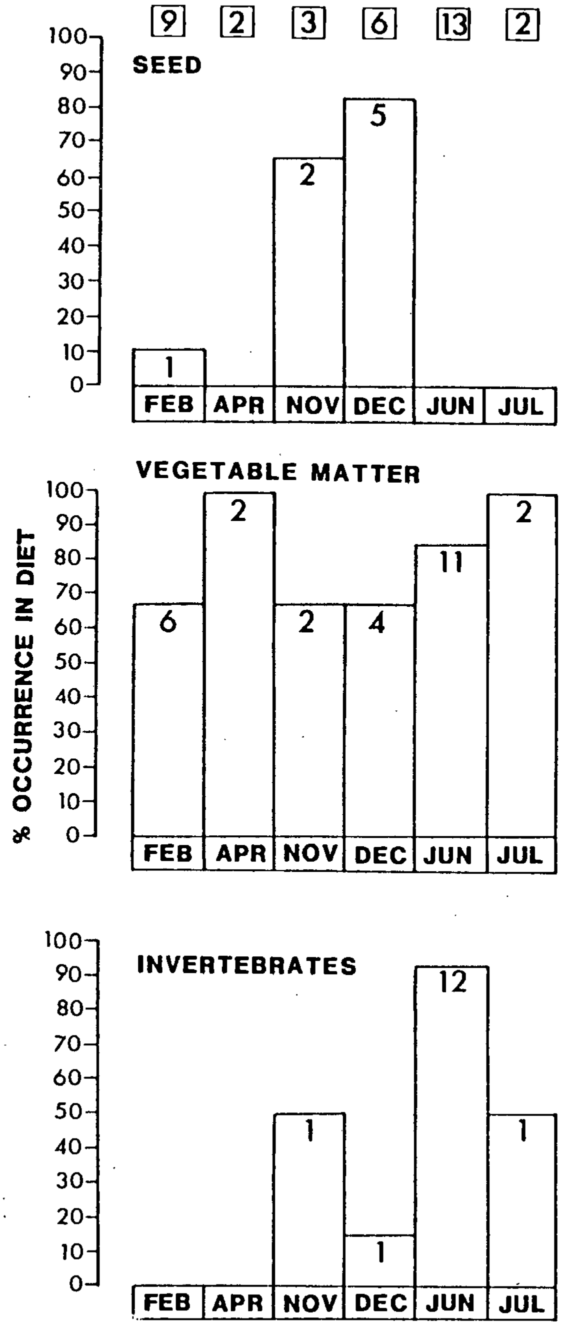

Figure 1 The percentage occurrence of seeds, other vegetable matter and invertebrates in 35 faeces obtained from black korhaans at Pella during February 1984 to July 1985. Values in squares represents the total number of samples collected for each month.

Table 1 The density of mature *Acacia cyclops* and *A. saligna* (plants/ha) at Pella (Beeston 1985a) and at the Kalbaskraal site (Cunliffe 1985)

Species	Pella	Kalabaskraal
A. cyclops	52	25
A. saligna	675	450

Table 2 The density of _Acacia cyclops_ and _A. saligna_ seeds on and in the soil surface layer at Pella (Beeston 1985b)

Species	No. seeds/m^2
A. cyclops @ 50% plant cover	29
A. saligna @ 20% plant cover	2913
A. saligna @ 80% plant cover	1930

results from the differential digestion of the seeds of the two species. These results support the hypothesis that the black korhaan selectively fed on seeds of *A. cyclops* which possess colourful lipid-rich pseudarils.

Seed viability and germination experiments

The mean number of propagules found in the March samples and those recovered from the "bagged" experiment were not significantly different for either *A. cyclops* or *A. saligna* (Table 3, Mann Whitney Test; $U = 118$ and $U = 156{,}5$ respectively $P > 0{,}05$). This suggests that "bagged" faeces did not experience statistically significant losses over six months. The mean number of propagules in the March samples and those recovered from the vicinity of "pegged" faeces were significantly different for *A. cyclops* (Mann Whitney Test; $U = 221$; $P < 0{,}01$), but not for *A. saligna* (Mann Whitney Test; $U = 182{,}5$; $P > 0{,}05$). The mean number of propagules in "bagged" and "pegged" faeces differed significantly for *A. cyclops* (Mann Whitney Test; $U = 100$; $P < 0{,}01$) but not for *A. saligna* (Mann Whitney Test; $U = 58$; $P > 0{,}05$).

The total number of *A. cyclops* and *A. saligna* propagules were divided into categories of propagule condition and germination state for the "bagged" and "pegged" experiments (Table 4). Based on the multidimensional contingency table analysis the following two way contingency tables were identified as possessing significant interactions:-

Germination and Propagule Condition (Alive and Dead)

Germination and Experimental Conditions (Pegged and Bagged)

Propagule and Experimental Conditions

Propagule Condition and Species (*A. cyclops* and *A. saligna*)

The integration of these five two-way associations explained 99,6% of the variation in the data defined by the multidimensional contingency table 4. The variation in the data not explained by the model is non-significant ($G^2 = 10$, $P < 0{,}05$), and therefore no other inter-relationships between variables

Table 3 Mean number of *A. cyclops* and *A. saligna* propagules found in the faeces of black korhaan under different experimental conditions.

Species	March (N = 27)	September "bagged" (N = 10)	September "pegged" (N = 10)
A. cyclops	115,6	79,1	8,7
A. saligna	4,9	3,3	0,2

Table 4 The observed frequencies for _Acacia saligna_ and _A. cyclops_ propagules divided into categories of germination state and propagule condition for each experiment. Expected frequencies are calculated from the multidimensional contingency table model and are presented in brackets.

Experimental condition	Propagule condition	Germination state	_Acacia cyclops_	_Acacia saligna_
"bagged"	live	ungerminated	324 (325,5)	32 (31,5)
		germinated	28 (26,4)	0 (2,6)
	dead	ungerminated	419 (418,5)	1 (2,5)
		germinated	20 (20,9)	0 (0,1)
"pegged"	live	ungerminated	0 (1,8)	1 (0,2)
		germinated	18 (18,2)	1 (1,8)
	dead	ungerminated	56 (56,7)	0 (0,1)
		germinated	13 (13,9)	0 (0,1)

were significant.

Given that the mean number of propagules per faeces was 106 for A. cyclops (N = 37) and 4,5 for A. saligna (N = 37) the mean percentage of A. cyclops seeds that had germinated and survived to September was 2,6% and 1,7% for "bagged" and "pegged" faeces respectively. For A. saligna the comparable statistics were 0% and 2,2% respectively. This is an under-estimate of the potential germination as, particularly for A. saligna, a large proportion of the viable seeds still remained dormant in September. These results confirm the second hypothesis that black korhaans are able to disperse acacia seeds in a viable condition to sites that permit germination.

Discussion

Black korhaans and frugivory

The diet of the black korhaan, as determined by crop analyses (Horsbrugh 1912), is known to include small grasshoppers, immature locusts, a variety of other small invertebrates, herbaceous leaves (including clover) and grasses. The black korhaan's consumption of herbaceous leaf material and fleshy fruits supplemented by invertebrates is similar to that of most other members of the Otididae (Dement'ev et al. 1951; Ali & Ripley 1969; Cramp & Simmons 1980). It should be noted that none of the above studies provides evidence of mature seeds being digested by otidids. Since this study examined faecal rather than stomach samples the results presented in Figure 1 will under-represent vegetable matter that is easily digestible. No intact or partly digested A. cyclops pseudarils were found in any faeces, thus it is probable that the black korhaan possesses an efficient digestive system for handling soft plant material and for stripping fleshy pericarp away from the seed. Horsbrugh (1912) comments on the absence of cereal grain and maize Zea mays in their diet. Wheat grain, which grew in the vicinity of both field sites, was not found in the faeces.

The consumption of A. cyclops seeds in preference to A. saligna seeds occurring on the ground suggests that these birds are foraging for the lipid-rich pseudarils (Glyphis et al. 1981). Since the acacia seeds themselves are not digested, the ingestion of A. saligna seeds may be accidental while foraging for pseudarils of A. cyclops.

Pre-dispersal seed-predation

In the "bagged" experiment ungerminated A. cyclops seeds suffered considerable mortality (56%). This loss of viability in A. cyclops seeds in South Africa is largely the result of hemipteran predation (small holes are made into the seed testa prior to seed-dispersal. This damage to the testa causes the seed to imbibe moisture and either germinate or decay (Holmes, Dennill & Moll in press). In South Africa at least one hemipteran genus appears to be involved (Zulubius, Alydidae: Alydinae) (Schaefer 1980). Limited hemipteran feeding damage has been shown to result in a 54% loss in seed viability (Holmes, Dennill & Moll in press). Such intensities of seed predation are low compared with Australia (Milton 1980) where intense hemipteran predation can occur at virtually any stage of seed production and dispersal (Gill 1985). In contrast to A. cyclops, only one A. saligna seed was found to be damaged (N = 35; Table 4). Therefore, it seems that seed damage by hemipterans is specific to A. cyclops in the Cape.

Post-dispersal seed-predation

Mean number of A. cyclops seeds per sample was nine times greater under "bagged" conditions than under "pegged" conditions, where post-dispersal seed removal/predation could occur uninhibited. A sixteen-fold increase for A. saligna seeds was found under "bagged" conditions. Seeds of both A. saligna and A. cyclops are known to comprise 50% of the diet of striped field mice Rhabdomys pumilio living in thickets of these acacias (Shelton 1975). David (1980) estimates that a single striped field mouse would require approximately 5 g of acacia seed per day to survive. Assuming 50% of the diet is acacia seeds, 2,5 g or approximately 55 acacia seeds (see Glyphis et al. 1981) could be consumed per rodent per day. At peak densities of 238 R. pumilio individuals per ha (David 1980), 13090 seeds/ha could be consumed per day.

Consequently the high level of seed removal recorded in the "pegged" experiment could be accomplished by a single species of seed-predator, namely R. pumilio. Such intensities of acacia seed removal would enhance seedling to seed ratio as was observed in the "pegged" experiment.

No live but 56 dead A. cyclops seeds were recovered from the "pegged" experiment (Table 4). In contrast 324 live and 419 dead A. cyclops seeds were recovered from the "bagged" experiment. Since dead seeds are readily distinguished from live ones by their appearance and since these seeds would provide less nutritive value, the seed predator or predators may have preferentially removed the live seeds. With an enhanced proportion of dead seeds remaining, potentially fewer seeds could germinate.

The percentages of germinated A. cyclops propagules that subsequently died were almost identical for the "bagged" and "pegged" experiments (41,7 and 41,9% respectively). This suggests that "bagging" did not affect seedling mortality rate. All dead seedlings possessed undamaged cotyledons and leaves. Consequently browsing was not thought to have been responsible for their deaths. However, all these seedlings had poorly developed rooting systems, and they may therefore have succumbed to desiccation.

Korhaan dispersal efficiency

The 20 faeces from the two experiments plus 21 of the faeces collected in March represented all the faeces present within a 0,25 ha area. Assuming an average of 106 A. cyclops seeds per faeces and 164 faeces per ha, an estimated 17384 seeds/ha were dispersed by the black korhaan. Since the black korhaan is usually a solitary bird (Kemp & Tarboton 1976) or occurs in pairs (as was observed by repeated visits to the study site), this estimated seed-dispersal would represent, at most, two birds. Based on a mass of 716 g for male korhaans and 669 g for female korhaans (Maclean 1985) the daily energy expenditures (DEE) are 655 and 627 kJ respectively as calculated from the equation given by Walsberg (1980). Such daily energy demands could be met by 1248 and 1170 A. cyclops pseudarils respectively, assuming each pseudaril has an 80% assimilation (see Willson & Harmeson 1973, Ricklefs 1974) and a 0,67 kJ energy content (P.G.H. Frost unpublished data). Therefore the two black korhaans in our study site have the potential to disperse up to 2400 A. cyclops seeds per day during the fruit season. The fruit is available for approximately three months which would give an approximate maximum number of A. cyclops seeds dispersed by the pair of some 216000. If the observed seed density at the end of the season was typical of the pair's entire territory this would indicate a territory size of approximately 12 ha.

Glyphis et al. (1981) observed that recruitment of A. cyclops occurred below bushes of indigenous plants, which they considered to represent suitable perches for frugivorous birds. However, seedlings of A. cyclops are intolerant of shade (Milton 1982), and therefore bushes of indigenous plants are unlikely to represent "high quality" sites (sensu McKey 1975) for seedling establishment. Gill (1985) observed that the distribution of A. cyclops in its native Australia is closely associated with both natural and artificial disturbances. At Pella the incidence of A. cyclops is significantly related to the frequency of occurrence of bare soil conditions (Macdonald et al. in prep.). Consequently a "high quality" dispersal site is likely to be in the open on bare soil. Male black korhaans facilitate dispersal to such sites by their habit of using termite mounds as "call-sites" (Horsbrugh 1912; Kemp & Tarboton 1976). In the absence of termite mounds or ant heaps they use any elevated, but unvegetated area as a call-site (pers. obs). Therefore male korhaans are able to disperse A. cyclops seeds to microhabitats most suitable for germination and establishment. At both study sites we observed that the majority of faeces were deposited in open areas and on bare soil. It is our observation that black korhaans avoid densely vegetated areas in the fynbos biome.

About 2,6% of dispersed A. cyclops seeds in the "pegged" experiments had germinated and was still surviving in September (Table 4). Such a dispersal efficiency is similar to that for the indigenous weedy species Chrysanthemoides monilifera (Knight in prep., Chapter 8) which has become an invasive plant in Australia (Weiss 1983). The black korhaan removes considerable quantities of A. cyclops seed from the vicinity of parent plants (where there is almost no chance for propagule establishment) to open sites suitable for germination. In addition, bird-dispersed A. cyclops seeds appear to be able to imbibe moisture and germinate within a month (Glyphis et al.

1981; Gill 1985). This would give those seeds that had been dispersed by the black korhaan a chance to germinate at the onset of the wet winter season, and thus escape protracted exposure to rodent seed-predation. A high efficiency seed-dispersal system is thus indicated.

High efficiency seed-dispersal systems for bird-dispersed plants were predicted to occur in tropical environments and in plants with fleshy fruits that are relatively large, have nutritious pericarps and which generally are single seeded. Such fruits are considered to attract only specialist frugivores and are presented in small quantities over long fruiting periods (McKey 1975, Howe & Estabrook 1977). The existence of such dispersal systems has been considered to represent some evidence for the coevolution of frugivorous birds and plants possessing fleshy fruits. However, this study indicates that such a high efficiency dispersal system may arise independently of coevolution as a consequence of fortuitous interactions initiated by man.

Conclusion

With over 2,6% success in seedling establishment of bird-dispersed seeds _A. cyclops_ demonstrates a remarkable potential to colonize new sites, even when compared with other alien acacias. This superior dispersal ability has been observed in practice (e.g. Taylor & Macdonald 1985). The relationship between the introduced _A. cyclops_ and the black korhaan represents a highly efficient seed dispersal system that has been initiated through fortuitous circumstances, and therefore is independent of any coevolutionary implications.

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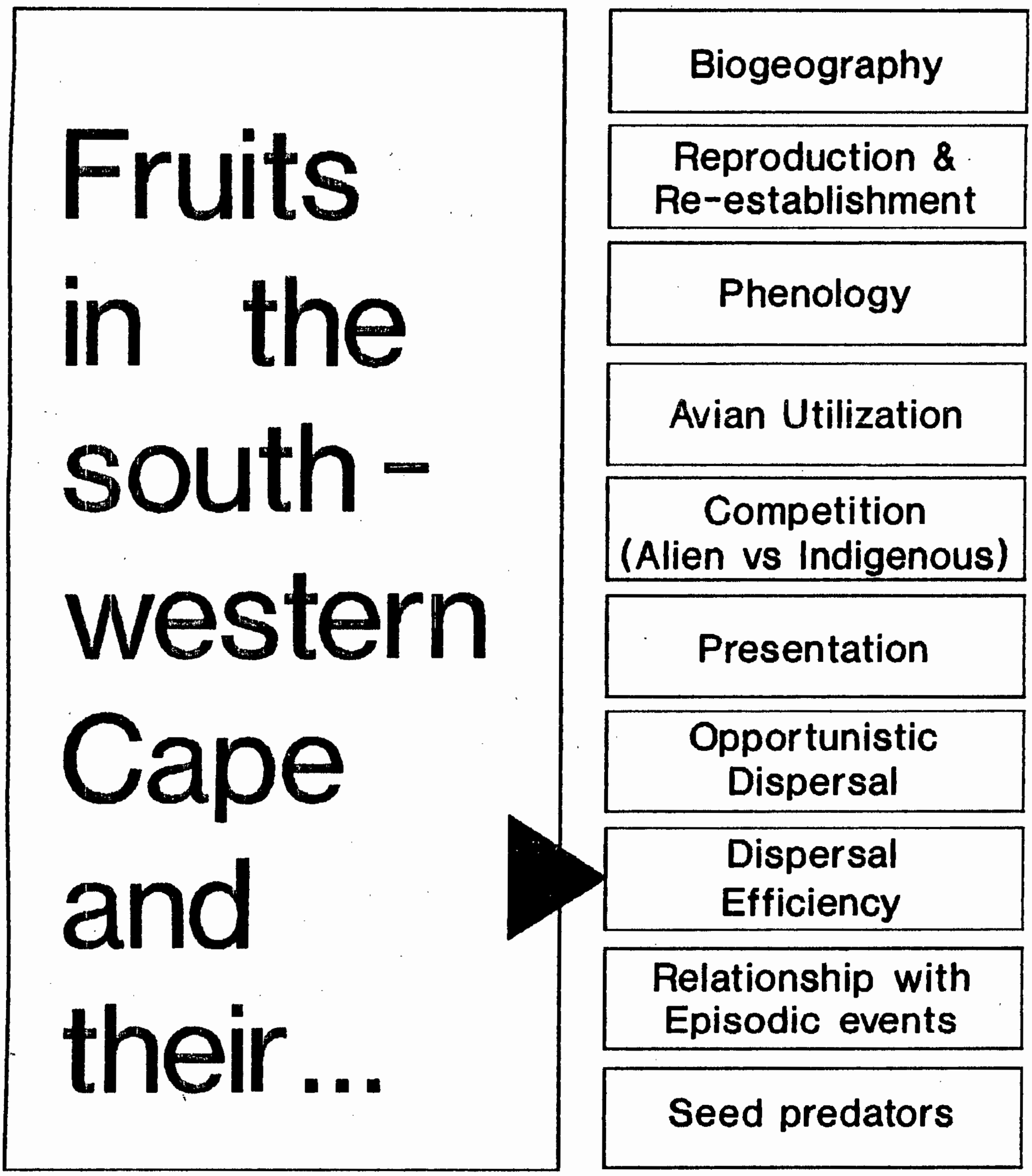
CHAPTER 8



Fruits in the south-western Cape and their...

Biogeography

Reproduction & Re-establishment

Phenology

Avian Utilization

Competition (Alien vs Indigenous)

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Seed–dispersal success of *Chrysanthemoides monilifera* in the southwestern Cape, South Africa

Contents

Seed–dispersal success of *Chrysanthemoides monilifera* in the southwestern Cape, South Africa

Contents /continued

Seed dispersal success of *Chrysanthemoides monilifera* in the southwestern Cape, South Africa

Abstract

Avian frugivory, seed dispersal and seedling establishment of *Chrysanthemoides monilifera* were studied in the southwestern Cape, South Africa. Estimated avian removal of fruit crops in six *C. monilifera* plants was compared with fruit losses due to non-dispersal, fruit abortion, and vertebrate and invertebrate seed predation. Birds removed between 14% and 27% of the total fruit crop. Bird-dispersed seeds had an experimental germination success of 10%. Hence, it was estimated that each *C. monilifera* plant produced some 287 seedlings after each fruit season. Observed recruitment in an artificially cleared area adjacent to the six *C. monilifera* plants averaged 34 seedlings per 100 m^2. This is equivalent to the estimated recruitment if all seeds were deposited in 0.5 ha. The reproductive biology of indigenous *C. monilifera* was compared with that of populations introduced into Australia.

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Introduction

Chrysanthemoides monilifera (L.) Norlindh (Asteraceae) is a widespread South African shrub producing abundant quantities of single-seeded, fleshy fruits (Coates Palgrave 1977; Knight 1986). Six subspecies of C. monilifera have been recognized (Norlindh 1943), with ssp. monilifera occurring in the southwestern Cape Province. Introduced C. monilifera plants are a major pest in Australia (Weiss 1983). If biological control of Chrysanthemoides monilifera is to be considered in Australia a full knowledge of its native reproductive biology is required. This study examines aspects of both seed dispersal and predation occurring in a native population of Chrysanthemoides monilifera.

Evaluation of dispersal success is problematic, since patterns of avian frugivory (e.g. Howe & Vande Kerckhove 1979; Howe & de Steven 1979; Kantak 1979; Wheelwright et al. 1984) have revealed little about plant establishment (Herrera 1984a). Studies on avian fruit removal in relation to seed deposition are still scarce (Howe & Primack 1975; Herrera & Jordano 1981), whereas studies on plant recruitment have omitted to record frugivory (Glyphis, Milton & Siegfried 1981; Debussche, Escarre & Lepart 1982). Herrera (1984b) and Knight & Macdonald (subm., Chapter 7), however, have examined all stages of an avian seed dispersal process.

Materials and Methods

The C. monilifera plants studied differed from ssp. monilifera in possessing translucent orange/brown, rather than purple/black, fruits. Consequently, the precise taxonomic status of the plants I studied is unknown, and they may represent either an undescribed subspecies or a subspecific hybrid. Fruit production and abortion, avian fruit consumption and seed predation were investigated in six similarly sized mature plants occurring in Mountain Fynbos vegetation (sensu Moll et al. 1984) adjacent to a remnant Afromontane Forest (sensu Moll et al. 1984) in Fernkloof Nature Reserve, Hermanus (34° 24′ S, 19 16′ E), southwestern Cape Province, South Africa. These six plants represented all the reproductively mature plants occurring locally (approximately 1 km^2). Faeces and regurgitations from baboons Papio ursinus and birds (unidentified) found (10 - 24 November 1983) in the area were collected and examined for C. monilifera seeds.

Projected canopy area (calculated in m^2 assuming each plant had a circular canopy cover) and basal stem girth (cm) was assessed for each plant. Fruit production (ripe, unripe and aborted) was sampled at the beginning of the fruit season (10 November 1983). Fruit crop size was estimated by assuming the plant to be circular and counting all fruit in a one-fiftieth arc. The accuracy of this technique was tested on two plants ca 3 km away and found to under-record by 14% and 16% respectively. Non-dispersed fruits (i.e. falling directly below canopy) were sampled using 1 m^2 seed traps made from nylon shade cloth placed under each plant (10 November - 11 December 1983) and were examined for parasitism.

A total of 14 hours (05:30 to 19:30) of avian frugivory were recorded (10 - 18 November 1983) for each C. monilifera plant. Sampling was undertaken in two-hour periods at each plant. The sequence of sampling ensured that each plant was examined over an entire day. Where possible, total number of fruits taken per avian visit was recorded.

Prior to the onset of C. monilifera germination a one-third ha area adjacent to the study plants was cleared (March 1984) of all vegetation except fully grown Virgilia divarcata Adamson (Papilionoideae) and Kiggelaria africana L. (Flacourtiaceae) trees (see Chapter 2). These trees together with telegraph poles were considered suitable perches for avian frugivores. The colonization by C. monilifera in the cleared area was monitored (March 1984 to September 1985) using 62 permanent 1m^2 quadrats, 27 of which were under perches. Since the seeds of C. monilifera are short-lived (< 6 months) due to post-dispersal seed parasitism and or/microbial damage (pers. obs), the observed seedling recruitment in 1984 was considered to be a product of the 1983 fruit set. The use of artificially cleared areas in assessing density of seedlings is justifiable since C. monilifera is a local dune pioneer (Heydorn 1975) that is used for sand stabilization purposes (e.g. Bar 1965; Begg & Henrico 1976).

Viability of seeds was tested by experimental germination. Seeds were sown in black plastic bags filled with local soil and placed on tables to prevent vertebrate predation and herbivory. Germination was monitored for seeds with and without a pericarp, seeds found under parent plants (without pericarp) and seeds recovered from bird faeces/regurgitations and baboon faeces. In an additional experiment seeds without a pericarp were stored in nylon bags at a depth of 15 cm in soil for 6 months and thereafter tested for viability.

Results

Frugivore consumption of *Chrysanthemoides*

Large quantities of *C. monilifera* seeds were found in most baboon and bird faeces/regurgitations (Table 1). Other fruits consumed include those of *Rhus* (probably *lucida*), *Halleria lucida* and *Cassytha ciliolata* (Table 1).

Chrysanthemoides fruit production

All six *C. monilifera* plants were of similar size (Table 2; Coefficient of Variation *C.V.* for each variable < 25%). Fruit mass (Table 3) varied little between plants (*C.V.*= 8,7%), but the mass of the single seed found in each fruit varied more (*C.V.*= 14,2%). Estimated fruit production between plants was similar (Table 4; *C.V.*= 14,7%), but unrelated to girth (r_{s4} = 0,09; *P* > 0,05) and canopy cover (r_{s4} = 0,01; *P* > 0,05).

Seed loss through non-dispersal

Fruit abortion varied between 10% and 36% of total fruit crop (Table 4). Of fruit recovered in seed traps 2% to 8% was found to be aborted (Table 5). This apparent discrepancy was due to aborted fruits remaining on the plant until the entire capitulum was discarded. The large quantities of fruits recovered from seed traps (Table 5), suggest that large quantities of seed were not dispersed by birds. Larger quantities of fruit would have been recovered if seed removal by baboons had been prevented. Observations on seed removal by baboons were not made, since their foraging was mostly crepuscular.

Table 1 Mean number and percentage occurrence of seeds collected from avian faeces/regugitations and baboon _Papio ursinus_ faeces in Fernkloof Nature Reserve, Hermanus.

Plant Species	Birds (N = 44)		Baboons (N = 25)	
	Mean	% Occurrence	Mean	% Occurrence
Chrysanthemoides monilifera	3,5	95,5	173,1	96,0
Rhus spp.	1,6	75,0	103,4	44,0
Halleria lucida	> 10	59,1	> 50	28,0
Cassytha ciliolata	0,4	29,5	26,0	40,0
Acacia cyclops	0,2	20,5	0,2	12,0
Olea capensis	0,2	20,5	< 0,1	4,0*
Olinia cymosa	0,1	11,4	< 0,1	4,0*
Restioid seeds	0	0	20	4,0*
Unidentified seeds	0,4	29,5	0,3	12,0

* represented in one sample

Table 2 Morphological measurements of six *Chrysanthemoides monilifera* plants at Fernkloof Nature Reserve, Hermanus.

Plant no.	Canopy cover (m^2)	Basal stem girth (cm)
1	4,01	60
2	2,27	/
3	2,06	45
4	3,40	51
5	3,20	50
6	3,02	40

Table 3 Fruit and seed mass of Chrysanthemoides monilifera fruits collected at each of six plants in Fernkloof Nature Reserve, Hermanus.

Plant no.	N (fruit)	Total mass (g) 100 fruit	100 pericarps	100 seeds
1	534	19,29	13,67	5,62
2	62	22,58	16,13	6,45
3	74	21,62	16,22	5,41
4	158	18,99	13,29	5,70
5	244	18,44	14,34	4,10
6	150	18,66	13,33	5,33

Table 4 Fruit production and seed abortion in six *Chrysanthemoides monilifera* plants occurring in Fernkloof Nature Reserve, Hermanus.

Plant no.	No. fruit sampled	Estimated total fruit production	% Aborted fruit	Estimated fruit production less fruit abortion
1	470	23500	10,21	21100
2	360	18000	26,11	13300
3	357	17850	36,41	11350
4	322	16100	13,66	13900
5	325	16250	11,69	14350
6	370	18500	15,68	15600

Table 5 Fruit losses in six *Chrysanthemoides monilifera* plants through fruit abortion and seed parasitism, as determined from trapped samples (1 m²). Values in parentheses are percentages of trapped fruit.

Plant no.	Total fruit "trapped"	No. of fruit			
		aborted	suitable for determining parasitism	with seed and fruit parasitism	with seed parasitism
1	942	19 (2,0)	534	16 (3,0)	7 (1,3)
2	392	17 (4,3)	62	3 (4,8)	2 (3,2)
3	265	6 (2,3)	74	7 (9,5)	5 (6,8)
4	391	30 (7,7)	158	11 (7,0)	2 (1,3)
5	702	49 (7,0)	244	22 (9,0)	12 (4,9)
6	900	15 (1,7)	150	11 (7,3)	1 (0,7)

Since the pericarp frequently detaches from the seed, not all fruit found in the seed traps was assessed for parasitism of the pericarp. The percentage of parasitized fruit varied considerably between plants (Table 5; *C.V.* = 36,5%) and seed parasitism even more greatly (*C.V.* = 79,9%).

Avian feeding visits to *Chrysanthemoides* fruits

Birds of 12 species were observed consuming fruit of *C. monilifera* (Table 6); sombre bulbuls *Andropadus importunus* accounting for most fruit-eating visits (1,18 hrs between individual bird visits). Based on 15 sombre bulbul visits to *C. monilifera* fruit crops, an average of 5,9 seeds was removed per visit (Table 6). Other important avian consumers of *C. monilifera* fruit included Cape bulbuls *Pycnonotus capensis* (1,92 hours between visits; 5,5 fruits removed per visit) and rameron pigeons *Columba arquatrix* (4,76 hours between visits; 16,8 fruits removed per visit). Differences in number of individual fruit visits between the 6 *C. monilifera* plants was small and ranged between 0,48 hours between visits at plant 4 and 0,42 hours between visits at plant 3 (Table 7) and were unrelated to fruit production ($r_s = 0,03$; $P > 0,05$). Visits by sombre and Cape bulbuls and Cape rock thrushes *Monticola rupestris* occurred at all plants, whereas visits of rameron pigeon were restricted to plants 1, 3 and 5 and visits of Cape robins *Cossypha caffra* to plants 3 and 6. Assemblages of avian frugivores visiting *C. monilifera* fruit crops did not vary greatly between individual plants. An overall average of 6,71 fruits was removed during each bird visit.

Germination of *Chrysanthemoides*

Bird-dispersed seeds had the highest germination success (10%) of the six treatments (Table 8). Removal of the pericarp was predicted to enhance germination, since a pericarp would promote microbial predation (Janzen 1977) which in turn may damage the seed. However, no germination was recorded for seeds without a pericarp, whereas seeds with a pericarp had 5% germination (Table 8). Seeds without a pericarp that were collected below the parent plant had, however, a 4% germination (Table 8). No germination occurred in seeds recovered from baboon faeces or in soil-stored seeds (Table 8). The

Table 6 Mean number of individual frugivorous bird visits and seeds removed per visit at six *Chrysanthemoides monilifera* plants in a Mountain Fynbos site adjacent to a remnant Afromontane Forest at Fernkloof Nature Reserve in Hermanus during 10 - 24 November 1983.

Bird species	Mean no. birds/hr	No. obs	No. fruits removed per visit	No. obs
Andropadus importunus (Vieillot)	0,85	71	5,9	15
Pycnonotus capensis (Linnaeus)	0,52	44	5,5	4
Columba arquatrix Temmink	0,21	18	16,8	4
Monticola rupestris (Vieillot)	0,15	13	3,5	2
Cossypha caffra (Linnaeus)	0,06	5	2,0	1
Sigelus silens (Shaw)	0,02	2	1,0	1
Telophorus zeylonus (Linnaeus)	0,02	2	1,0	1
Spreo bicolor (Gmelin)	0,10	8		
Turdus olivaceus Linnaeus	0,07	6		
Onychognathus morio (Linnaeus)	0,06	5		
Colius striatus Gmelin	0,06	5		

Table 6 continued

Bird species	Mean no. birds/hr	No. obs	No. fruits removed per visit	No. obs
Zosterops pallidus Swainson	0,06	5		
Streptopelia semitorquata (Ruppell)	0,04	3		
Serinus canicollis (Swainson)	0,01	1		
Serinus totta (Sparrman)	0,01	1		

Table 7 Estimated seed-dispersal and recruitment succes in six *Chrysanthemoides monilifera* plants occurring at Fernkloof Nature Reserve, Hermanus. Values in parentheses represent percentages of total fruit crop.

Plant no.	Estimated fruit production excluding abortion	Individual avian frugivore visits/hr	Estimated* total avian fruit removal	Estimated recruitments assuming 10% germination of non-parasitized fruits
1	21100	2,3	3024 (11,3)	298 (1,4)
2	13300	2,2	2893 (21,8)	280 (2,1)
3	11350	2,4	3156 (27,8)	294 (2,6)
4	13900	2,1	2762 (19,9)	272 (2,0)
5	14350	2,2	2893 (20,2)	275 (1,9)
6	15600	2,3	3024 (19,4)	304 (1,9)

*Assuming 6,71 seeds removed per individual avian visitor, and fruit would be available in sufficient quantities for 196 hrs (14 days each with 14 hrs of daylight)

Table 8 Results of germination experiments on treated *Chrysanthemoides monilifera* seeds. A sample size of 100 was used for each treatment.

Treatment	% germination
Seed with intact pericarp	5
Seed with pericarp removed	0
Baboon-dispersed seed	0
Avian-dispersed seed	10
Seed from below parent plant	4
Soil-stored seed (6 months)	0

former seeds appeared intact, whereas the latter seeds either possessed no endosperm or were fragmented. The low germination success of the short-lived seeds appears to prevent native C. monilifera plants from developing large seed banks in the soil (see Weiss & Milton 1984).

Recolonization of Chrysanthemoides

Recruitment of C. monilifera seedlings in the artificially cleared areas commenced in June 1984 in sites both under and not under perches (Figure 1). A total of 17 C. monilifera seedlings (resulting from the 1983 fruiting) was recorded in 27 1 m^2 quadrats positioned under perches. Only eight seedlings were recorded in 35 quadrats in the open. Overall seedling mortality was low (37%) and occurred soon after germination (Figure 1). No new seedlings were recorded between August 1984 and the next year's recruitment in May 1985.

Discussion

Seed dispersal by birds: theory and reality

Snow (1971) suggested that the relationships between plants possessing fleshy fruits and avian dispersal agents have evolved through counteracting selective pressures. Individual plant-bird relationships have been described as occupying positions along a gradient defined by two end-points (McKey 1975). The one end-point describes plants which produce a limited quantity of high quality (lipid-rich) fruits that are available only to specialist frugivores providing reliable dispersal to sites suitable for germination. This situation is referred to as Model 1 by Howe & Estabrook (1977). The other end-point describes plants providing large quantities of fruits that are inexpensive to produce and available to all frugivorous birds irrespective of their ability to provide reliable directional dispersal (Model 2; Howe & Estabrook 1977).

The superabundant, but low quality fruits (pericarp 90% water; pers. obs) produced by C. monilifera were mostly visited (61%) by two resident bird species which are frugivorous throughout the year (the sombre and Cape bulbul). The 20% removal of a superabundant fruit crop (Table 7) by a small suite of "reliable" frugivore species (sensu McKey 1975; Howe & Estabrook

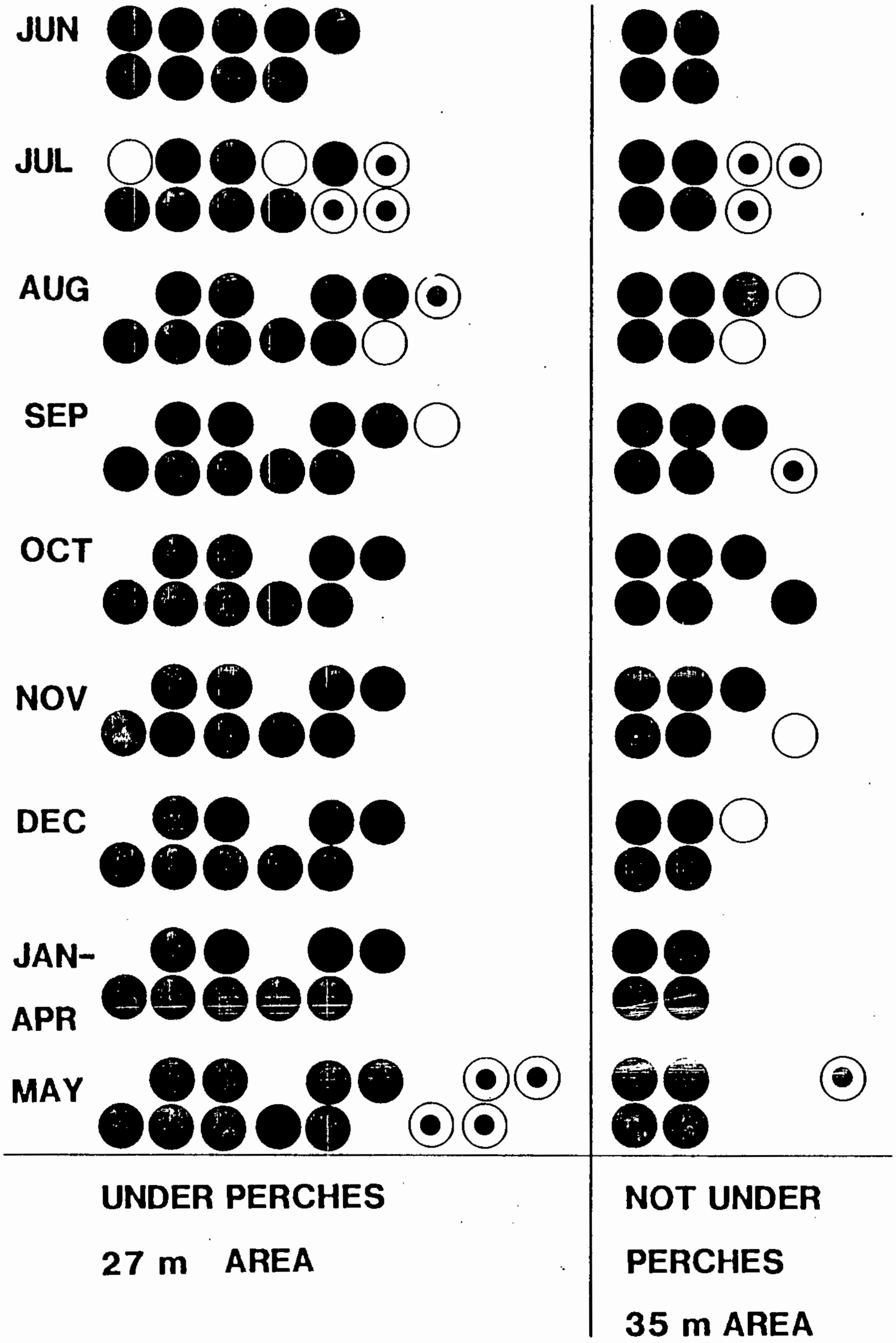

Figure 1 Observed seedling recruitment of <u>Chrysanthemoides monilifera</u> in an artificially cleared area, both under and not under perches. Each solid dot represents one plant, a circle represents a mortality not previously recorded, whereas a dot in a circle represents a new recruit not previously recorded.

1977) suggests that a high quality dispersal system occurs despite a low quality (Model 2) fruit crop. An analogous dispersal system has been described for Prunus mahaleb in Spain (Herrera & Jordano 1981). Most other field studies (Howe 1980, 1981, 1983; Frost 1980; Herrera 1982, 1984c; Howe & Smallwood 1982; Jordano 1982, 1983; Moore & Willson 1982) have found little evidence supporting these coevolutionary models. Consequently coevolution between a plant and its vertebrate dispersal agent is unlikely to occur (Herrera 1984a) unless restricted to the convergence of vertebrate-dispersed plants into generalized dispersal syndromes based on fruit characters such as size and colour (Van der Pijl 1972; Janson 1983; Knight & Siegfried 1983; Wheelwright & Janson 1985; Knight 1986).

Seed dispersal success

Assuming that 10% of bird-dispersed C. monilifera seeds germinate (Table 8), ca 287 seedlings (or 1,9% of total fruit crop) are produced by each plant after a single fruiting season (Table 7). The observed seedling recruitment by six C. monilifera plants (0,34 seedlings per m^2; Figure 1) could be explained if the dispersal of all seeds were limited to a 0,5 ha area or a dispersal distance of 40 m. Small dispersal distances are consistent with the majority of observations of frugivores. Fruit-eating visits by the rameron pigeon were a notable exception. Typically a bird foraged for ca three to eight mins then flew to a nearby perch. Regurgitation followed in ca 15 mins. This behavioural pattern was occasionally disrupted by visiting more than one fruit crop before returning to a perch. Flight direction was usually northerly, and to where the majority of perches occurred (viz. the artificially cleared colonization site). Regular avian use of perches would explain the 2,5 fold increase in seedling densities recorded at these sites (Figure 1). Since most (i.e. 60%) of seeds that germinated survived the first year, the initial establishment of C. monilifera is not habitat specific within the cleared area. Low seedling mortality is not usual in a pioneer species (Harper 1965) but contributes to the observed colonization by native C. monilifera of ecotonal and disturbed vegetation.

Suppression of seed dispersal success

Vertebrate predation

A major loss (63,5 - 71,8 %) of *C. monilifera* seeds occurred between fruit production minus avian fruit removal and that recovered from the traps (*cf.* Tables 5 and 7). This seed loss is probably attributable to baboons. Foraging by baboons typically resulted in broken branches which reduced the *C. monilifera* plants to half of their pre-fruiting size. Baboons are assumed to be seed predators since no seeds found in their faeces germinated in either the experimental sowing (Table 8) or in the field (pers. obs). Local *C. monilifera* seeds were permeable and dehydrated under open, sunny conditions. Consequently acids occurring in the baboon guts may also permeate into *C. monilifera* seeds. Weiss (1983) demonstrated rodents to be important seed predators in Australia. Local rodent seed predation was thought to be minimal since few freshly fragmented seeds were found below parent plants. Repeated rodent seed removal experiments were thwarted by baboon disturbance.

Invertebrate predation

Invertebrate parasitism reported here (Table 5) was low compared with local seed damage (S.J. Milton, pers. comm.) and parasitism reported by Neser and Morris (1985). It is possible that when fruits were inspected, parasitism had not developed beyond the egg stage. Seed parasitism of this nature would explain the damage found to soil-stored seed (Table 8). The parasitism reported by Weiss & Milton (1984) occurred in soil-stored seed. Munro (1950) reported *Chrysanthemoides*-specific tephritid fly (*Mesoclanis*) parasitism. Either *Mesoclanis dubia* or *M. magnipalpis* are thought to be responsible for the seed parasitism reported here.

Invertebrate herbivory will reduce both the overall fitness of the plant and reduce its reproductive potential. *Mesoclanis ovalis* and *M. polana* are flower predators of *C. monilifera*, whereas basal damage to local plants was consistent with *M. bruneata* predation. Other invertebrate predators include flower-attacking blister beetles (Meloidae), stem-boring longhorn beetles (Cerambycidae), and new shoot damage by argiopid spiders constructing nests.

Chrysanthemoides in South Africa and Australia

Life tables for *C. monilifera* occurring in South Africa and Australia are summarized in Figure 2. Densities of mature plants found in Australia exceed those studied locally. Fruit crop sizes of the local plants were smaller than those reported in Australia, but larger than those reported elsewhere in South Africa (Weiss & Milton 1984, Forde 1986). The proportion of seed falling to the ground and therefore available to a transient seedbank is locally smaller due to seed predation by baboons (Table 1). Seed predation in Australia is restricted to crimson rosella *Platycercus elegans*, ants and rabbits (Weiss 1983). Although Weiss (1983) gives no exact figures on bird-dispersal of fruit, it approximates that occurring locally (*ca* 20% of total fruit crop). The major difference in the life table is the nature of seed banks. Unlike in Australia, persistent local seed banks are either small (45 seed/m^2; Weiss & Milton 1984) or non-existent. Germination of seed is greater locally (8% of seed falling to ground) than in Australia (2%), and development to juvenile stage was 10 times more successful. In Australia density-dependent seedling competition may occur. Despite the difference in the reproductive biology (Figure 2), *C. monilifera* is potentially invasive in both its native and introduced environment.

Implications for management

Chrysanthemoides monilifera has the potential to become invasive, even in its native habitat due to prolific seed production and effective avian seed dispersal (Tables 4 & 7). Since *C. monilifera* is also naturalized in Sicily and California (Bond & Goldblatt 1984) further global introductions should be avoided. Invasiveness of *C. monilifera* may be a result of escaping predators rather than being ideally suited to its new environment (Weiss 1983). Consequently there is hope for biological control for Australian populations, although genetic variability may pose problems in identifying control agents (Kluge *et al*. 1986). *Mesoclanis* is a possibility since it is restricted to one asteraceous genus (Munro 1950) in a flora noted for its wealth of asteraceous genera (107; Bond & Goldblatt 1984).

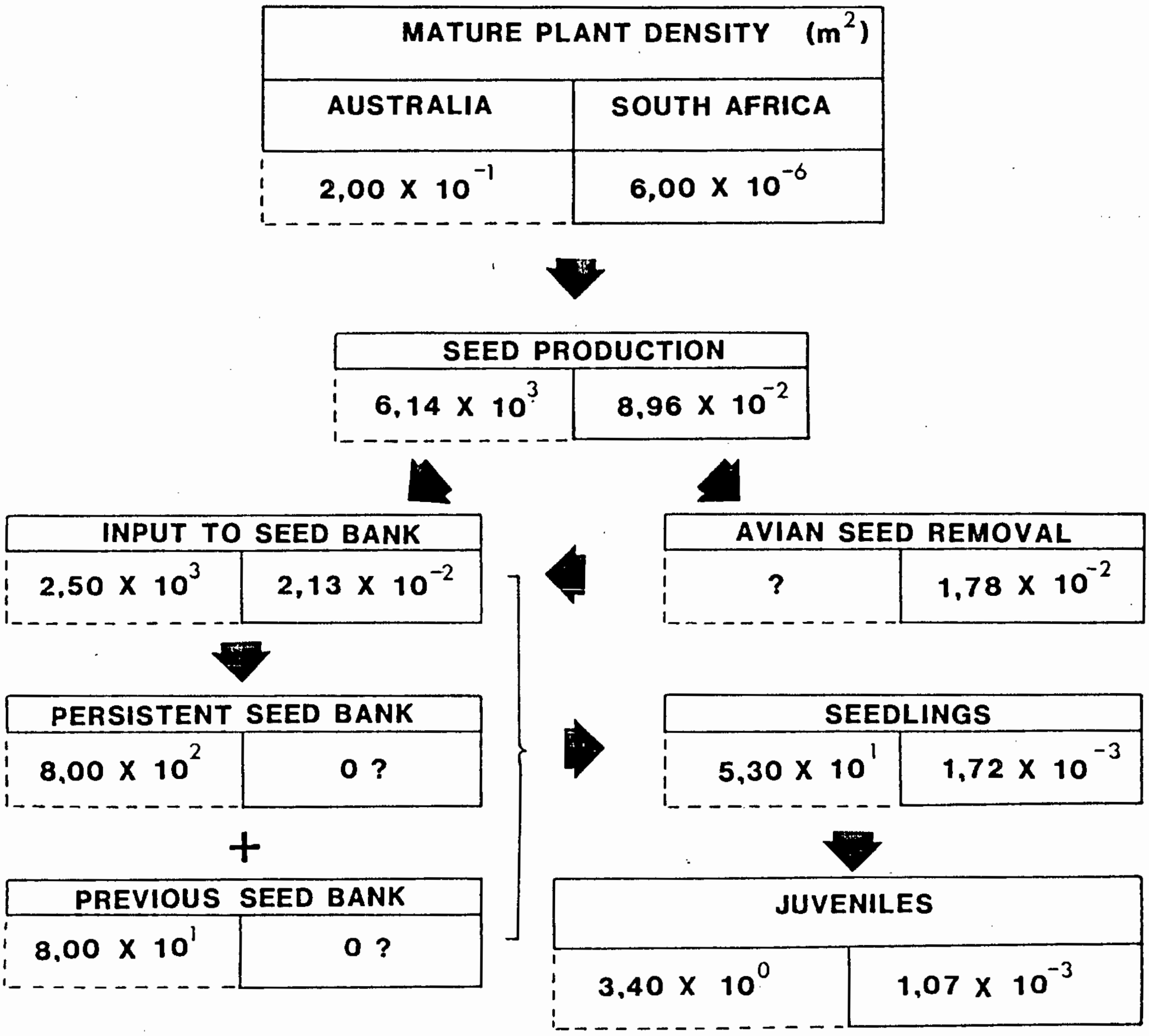

Figure 2 Diagrammatic life tables for *Chrysanthemoides monilifera* occurring in South Africa and Australia. Values at each reproductive phase are given on a m^2 yr^{-1} basis. Diagram based on Weiss 1983.

Conclusion

In its native habitat *Chrysanthemoides monilifera* can be effectively dispersed by local resident frugivores despite relatively low-quality fruit crops. These results conflict with theoretical predictions formulated by McKey (1975) and Howe & Estabrook (1977), but are similar to results reported by Herrera and Jordano (1981). Seed loss in *C. monilifera* is locally high and largely the result of baboon and invertebrate predation. The invasiveness of *C. monilifera* in other parts of the world is likely to be due to its escape from predators rather than possessing characters ideally suited to the physical conditions of the new environment.

Acknowledgements

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CHAPTER 9

Fruits in the south-western Cape and their...

Biogeography

Reproduction & Re-establishment

Phenology

Avian Utilization

Competition (Alien vs Indigenous)

Presentation

Opportunistic Dispersal

Dispersal Efficiency

Relationship with Episodic events

Seed predators

A model of episodic, abiotic dispersal for oaks (*Quercus robur* L.)

Contents

A model of episodic, abiotic dispersal for oaks (*Quercus robur* L.)

Contents /continued

A model of episodic, abiotic dispersal for oaks (Quercus robur L.)

Abstract

The role of flooded rivers as dispersal agents for Quercus robur L. was investigated adjacent to the Disa River in the Orange Kloof forestry station, Cape Peninsula, South Africa. Three months after the floods, a systematic sampling of acorns was undertaken using 100, 4m x 4m quadrats. It was found that those quadrats in areas that had been flooded contained more than four times the number of acorns found in the quadrats of the unflooded areas. Further, flooded areas had a greater percentage of intact acorns and seedlings. It was also found that acorns beneath an oak canopy germinated poorly and that ungerminated acorns had a higher mortality. Since the flooding of this river must be considered a rare event, the efficiency of large scale, episodic dispersal was compared to the continuous low density dispersal carried out by the alien squirrel Sciurus carolinensis Gmelin.

S. Afr. J. Bot. 1985, 51: 265-269.

Introduction

The Disa River between Orange Kloof forestry station and Houtbaai, on the Cape Peninsula, South Africa, burst its banks on three separate occasions during the heavy winter rains of 1983. At Newlands, close to the main catchment of the Disa River, 200 and 100 mm of rainfall was recorded on 26 and 27 June, respectively (Figure 1). Although such events are infrequent they may represent a considerable potential for the downstream dispersal of large buoyant fruits or seeds such as the acorns of the alien oak (Quercus robur L.). Dispersal of this oak within its natural, northern temperate range is associated with birds (particularly members of the Corvidae), rodents (particularly squirrels, Sciuridae), pigs (Suidae) and deer (Cervidae), whereas the importance of water-dispersal is considered to be minimal (Ridley 1930). The number and condition of oak propagules (acorns and seedlings) were sampled to determine the importance of these events for oak dispersal and seed germination in South Africa. The contribution of water-dispersal was compared to possible dispersal by the introduced squirrel (Sciurus carolinensis Gmelin). Both of these processes were related to maintaining the presence of oaks at Orange Kloof.

Materials and Methods

Field techniques

Physical and botanical descriptions of Orange Kloof forestry station are given in McKenzie et al. (1978). On 26 and 27 September a single systematic procedure was employed using 100 quadrats each 4m x 4m and set at 4m intervals in a 10 x 10 matrix (Figure 2). Two hypotheses were advanced:- (a) that the frequency of propagules occurring in each quadrat are uniformly distributed, (b) safe storage and germination are independent of post-dispersal site conditions. For each quadrat two site conditions were recorded:- (a) the presence or absence of the flood indicated by stream debris and erosion, (b) the presence or absence of an acorn-bearing oak canopy. Frequencies of oak propagules were categorized into (a) intact acorns which were potentially viable, (b) damaged acorns which were unlikely to be viable, (c) acorns that had germinated and the seedlings appeared intact, (d) acorns that had

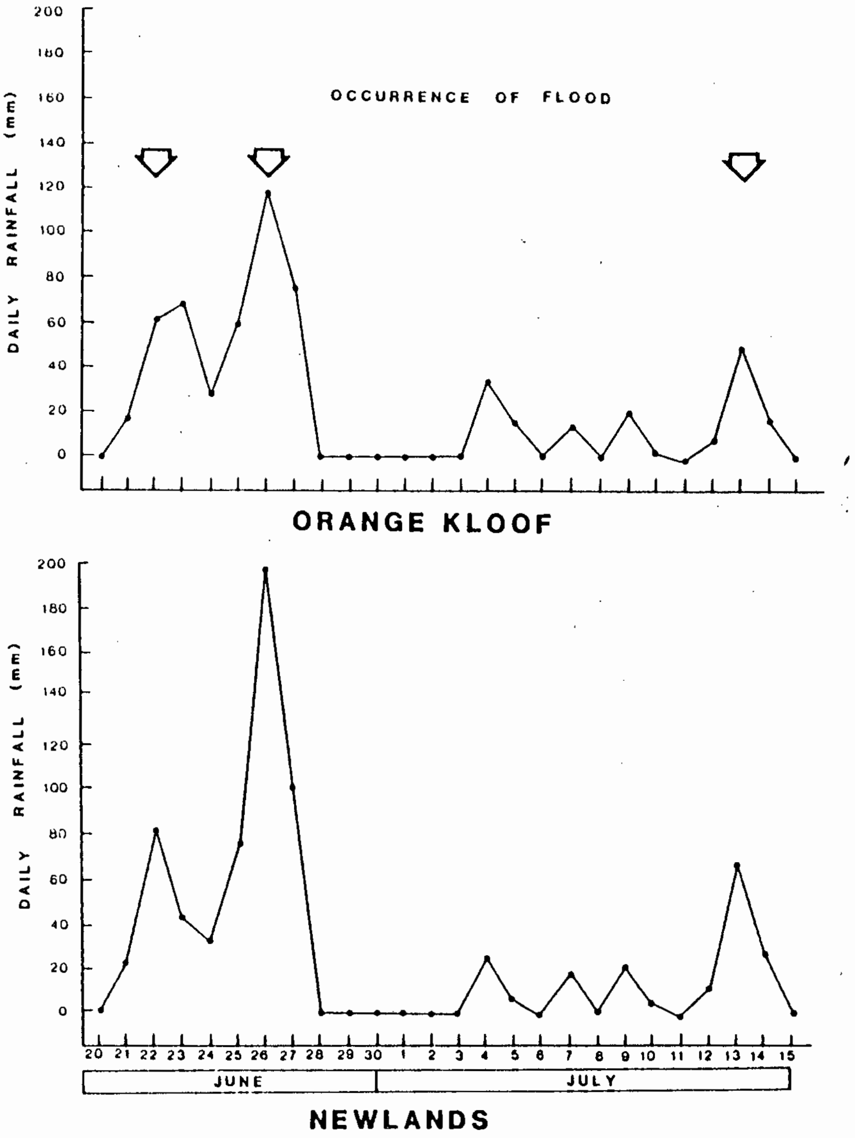

Figure 1 Daily rainfall recorded during June and July 1983 at Orange Kloof and at Newlands, an area adjacent to the catchment areas of the Disa River.

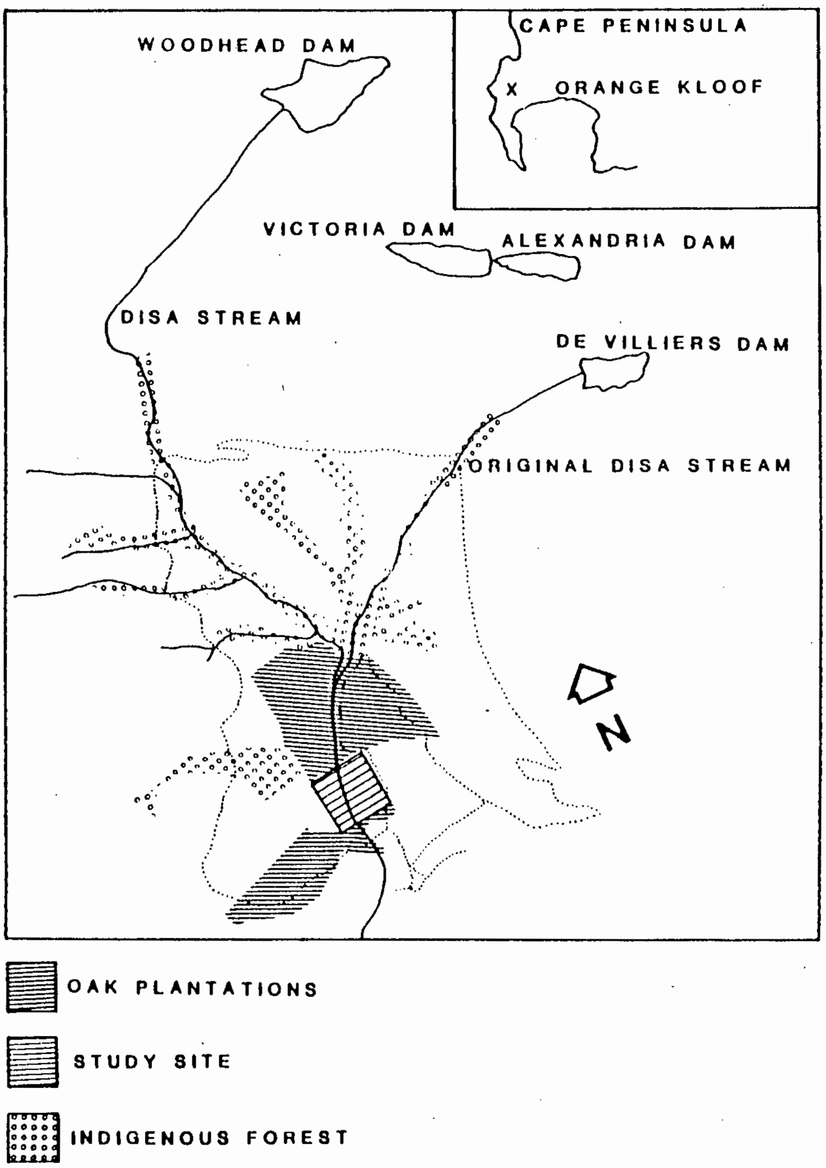

Figure 2 The position and alignment of sampling quadrats with regard to the boundaries of the Orange Kloof Forestry Station and its vegetation patterns.

germinated, but the seedlings were either damaged or had died. Acorns and seedlings that were categorized as damaged were considered to be potentially inviable. Germination experiments to test the viability of acorns were not undertaken, nor an assessment of pre-dispersal damage to acorns. A total of 6019 oak propagules were examined from 100 quadrats. All damaged acorns were examined for likely causes of mortality (microbial, invertebrate and mammal). Since the agent of mortality was sometimes difficult to determine (actions of one agent precipitated final destruction by another agent) no statistical analyses were undertaken on these data.

Numerical techniques

A simulated model was generated so that each quadrat had an equal opportunity for receiving propagules and so that the sampling frequencies had a Poisson distribution. The generated acorn frequencies are henceforth referred to as the expected frequencies. Expected and observed acorn frequencies were tested for spatial associations with a chi-square goodness-of-fit (Placket 1974), and directional spatial autocorrelations (Cliff & Ord 1969, 1973: Ward 1978). Spatial autocorrelations in north - south, east - west, north-west - south-east and north-east - south-west directions. The relationships between site conditions were investigated with multidimensional contingency table models (Knight & Siegfried 1983). Each variable was identified by one of the following symbols, with corresponding categories in brackets.

W = Potential for water dispersal (present, absent)
O = Beneath an oak canopy (present, absent)
S = Germination states (seed, seedling)
C = Propagule condition (intact, damaged)

Combinations of these variables (W, O, S and C) formed the models which were tested with the BMDP 4F 14-17 computer programs (Brown 1981). Tests of partial and marginal association identified potentially important associations (Knight & Siegfried 1983). The most parsimonious combination of variables (= model) was selected and fitted the data so that the residual combinations of variables were non-significant.

Results

The observed acorn frequencies possess spatial association ($X^2 = 6459,01$; $P < 0,001$), while no associations occur in expected frequencies ($X^2 = 85,49$; n.s.; Table 1). Therefore, each quadrat does not have an equal opportunity for receiving propagules. Spatial autocorrelation (Table 2) confirms overall spatial association within observed frequencies ($z = 3,79$; $P < 0,01$) but not in expected frequencies ($z = 1,23$; n.s.). Most spatial association within observed frequencies occurs in a north - south direction ($z = 3,40$; $P < 0,01$) and a north-east - south-west direction ($z = 3,01$; $P < 0,01$). The 58 unflooded quadrats had 1 437 propagules ($X^2 = 24,77$; $SD = 33,49$), while the 42 flooded quadrats had 4 582 propagules ($X^2 = 109,10$; $SD = 60,82$). Since Orange Kloof slopes downwards in a south - south-west direction the alignment of the 42 flooded quadrats occurred in directions possessing significant spatial associations.

Site conditions for each quadrat (presence of floods or oak canopies) together with frequencies for the four oak propagule categories and expected frequencies are presented in Appendix 1. The accumulated observed frequencies for intact and damaged seeds and seedlings under the four site conditions are presented in Table 3 and analysed as a multidimensional contingency table. The following combination of variables (= model):

CSW + CO + SO + WO

fits the data so that the residual is non-significant ($X^2 = 9,31$; $P > 0,05$) and accounts for 99,67% of the data. The expected frequencies derived from this model are also presented in Table 3 and are similar to observed frequencies. The CSW variable combination explains 87,77% of the data (residual remaining significant: $X^2 = 308,37$; $P < 0,05$) and indicates flooded quadrats to (W) to be associated with intact propagules (C) and germination state (S). Since W, S and C are inter-related with each other (e.g. the association of C with S is strengthened by the CW and the WS associations and *vice versa*) I can reject the hypothesis that the safe storage and germination of acorns are independent of site conditions. This model also indicates that the presence of an acorn-bearing oak canopy (O) is independently related to

Table 1 Test for overall spatial association of 6019 oak propagules within 100 quadrats for observed and expected frequencies

Statistic	Observed	Expected
N	100	100
$\bar{X}$	6019	6019
$\underline{s}$	62,7	7,2
χ^2	6459,0	85,5
$\underline{df}$	99	99
$\underline{P}$	$< 0,001$	n.s.

Table 2 Results of spatial autocorrelation (*r*) for 6019 oak propagules within 100 quadrats for observed and expected frequencies

Direction	Statistic	Observed frequency	Expected frequency
N-S	*W*	176	180
	r	0,35	0,18
	z	3,40	1,78
E-W	*W*	178	180
	r	0,17	0,04
	z	1,70	0,45
NW-SE	*W*	160	162
	r	-0,11	-0,14
	z	0,89	1,16
NE-SW	*W*	160	162
	r	0,33	0,13
	z	3,01	1,26
Overall	*W*	674	684
	r	0,19	0,05
	z	3,79	1,23

Where *W* is number of quadrat interactions, and critical values of *z* for significance levels are:- *z* = 2,00 *P* = 0,05; *z* = 3,00 *P* = 0,01 (Ward 1978)

Table 3 The observed frequencies for site and propagule conditions. Expected frequencies are calculated from the multidimensional contingency table model and are presented in brackets

Flood	Under oak	State	Condition		
W	O	S	C		
			Damaged		Total
absent	absent	acorn	338	63	401
			(333,3)	(60,8)	(394,1)
		seedling	49	52	101
			(43,0)	(64,8)	(107,8)
	present	acorn	683	52	735
			(687,7)	(54,2)	(741,9)
		seedling	111	89	200
			(117,0)	(76,1)	(193,1)
present	absent	acorn	1145	383	1528
			(1164,7)	(370,2)	(1534,9)
		seedling	117	713	830
			(108,1)	(715,0)	(823,1)
	present	acorn	1402	177	1579
			(1382,3)	(189,9)	(1572,2)
		seedling	160	485	645
			(168,9)	(482,9)	(651,8)

the propagule condition (C), germination state (S) and areas of flood (W).

The most conspicuous agents responsible for acorn mortality within areas of flood and oak canopy are presented in Table 4. Microbial decay was the single most common cause of acorn mortality. Acorns within areas of flood appear most prone to microbial damage. Invertebrate damage was most common in unflooded areas beneath an oak canopy. Consequently microbial damage within flooded areas may have pre-empted invertebrate predation. Acorn predation by mammals, exclusively squirrels, is generally minimal, but may be locally important within unflooded areas that are beneath an oak canopy.

Discussion

Since the dispersal of acorns to suitable germination sites is not uniform and seed storage and germination are enhanced within areas of flood, the discussion will focus on marginal totals for each significant pairwise combination of variables included in the multidimensional contingency table model.

CS: Propagule condition/germination state

The majority of acorns were damaged (84,1%), whereas most seedlings were intact (75,4%). Therefore it appears that either acorns that are potentially viable have already germinated, or a rapid germination pre-empts a high acorn mortality. Germination may be an escape from predation. Since only a single sample of oak propagules was undertaken, temporal rates of acorn predation could not be determined.

CW: Propagule condition/water dispersal potential

Flooded areas had more intact acorns (38,0%) than unflooded areas (18,0%). Although invertebrate predation is greater within unflooded areas (unflooded = 42,7%; flooded = 33,1%), microbial damage is elevated in flooded areas (unflooded = 46,1%; flooded = 62,6%). Therefore rapid germination is still required at a post-dispersal stage.

Table 4 The importance of three agents in the mortality of acorns, expressed as percentages

Flood	Under oak	Microbe damage	Invertebrate damage	Mammal damage	Propagule total	Number of quadrats
absent		46,1%	42,7%	11,2%	1021	58
present		62,6%	33,1%	4,3%	2547	42
	absent	61,8%	31,8%	6,5%	1483	68
	present	55,1%	38,7%	6,1%	2085	32
absent	absent	46,6%	34,0%	19,2%	338	41
absent	present	45,8%	47,0%	7,2%	683	17
present	absent	66,2%	31,9%	2,7%	1145	27
present	present	59,7%	34,7%	5,6%	1402	15
average		57,9%	35,8%	6,3%	3568	100

SW: Germination state/water dispersal potential

The percentage of propagules that germinated in flooded areas (32,0%) is greater than that in unflooded areas (21,0%). This may either reflect lower acorn predation or quicker germination within areas of flood. Since rapid water dispersal would remove acorns from areas of high invertebrate predation, mortality rates will be reduced and germination success is enhanced. A rapid dispersal to areas of abundant moisture created by the floods may further enhance germination success.

CO: Propagule condition/presence of an oak canopy

Fewer intact acorns were recorded in areas below an oak canopy (25,4%) than in areas not under an oak canopy (42,4%). Janzen (1971,1972) demonstrated high invertebrate predation below the canopy of a parent plant, and the need for dispersal away from these areas. Relative invertebrate damage below oak canopies is greater (38,7%) than in other areas (31,8%). Consequently the relative damage by microbial agents is lower below oaks and invertebrate predation may pre-empt microbial damage. On the other hand signs of damage by mammals below and not below oaks scarcely varies (6,1 and 6,5%, respectively).

SO: Germination state/oak canopy

A higher percentage of acorns germinated in areas away from oak canopies (33,0%) than did acorns beneath canopies (27,0%). Since variables **S**, **C** and **W** are all independently related to **O**, this relationship is not a reflection of greater acorn predation below oaks (CO association). It is possible that areas below oaks may have reduced soil moisture (especially if compared to flooded areas) and consequently a slower germination.

WO: Potential for water dispersal/oak canopy

The majority of propagules found away from oak canopies occurred in flooded areas (82,4%). Within flooded areas slightly more propagules were found away from oak canopies (51,5%) than below them (48,5%). If only intact propagules are considered, areas away from oaks have an even greater proportion of propagules (62,3%). In unflooded areas 65,1% of the propagules occur below oaks. The remaining 34,9% must presumably be "dispersed" by either squirrels or gravity (rolling down slope). Nineteen percent of these propagules appeared to have mammal inflicted damage; it is therefore plausible that this 34,9% is largely the contribution of squirrels to the dispersal of oak. Of this 34,9%, only 23,0%, of the propagules were intact, whereas 46,8% viability was recorded for corresponding areas that were flooded. It may therefore be presumed that water is the 'efficient' dispersal mechanism; in terms of escaping from areas of potentially high acorn mortality and promoting quicker germination of acorns.

Synthesis

Figure 3 summarizes the results in diagrams representing the need for dispersal and the advantages offered by a water facilitated dispersal. It is likely that without the removal of acorns (by both squirrels and water) from below an oak canopy, the high mortality of acorns would prevent the continued presence of the oak population. Water dispersal of acorns is a large scale but infrequent process, analogous to a catastrophe. This process represents a relatively low mortality of acorns (53,5%) while dispersing them to areas of elevated soil moisture and rapid germination. However, since this process is restricted to a downstream direction (approximately north - south at Orange Kloof), population replacements can only occur downstream (south) and the oak population cannot become permanently established. The continuous but low intensity dispersal by squirrels is likely to incur a considerably greater mortality, and therefore may not maintain a sufficiently large population of oak. Since this process is not limited to downstream directions it overcomes the directional limits of episodic water dispersal. The episodic dispersal may overcome deficiencies of high mortality incurred by squirrel dispersal. Thus abiotic water dispersal and biotic squirrel dispersal may be seen as complementary for maintaining the presence of oaks at Orange Kloof.

In consequence it may take only a few upstream acorn dispersals by squirrels and subsequent germination of seeds and establishment of oak plants for a large scale downstream dispersal of acorns to occur during episodic flooding. Since the oak has been considered an 'aggressive, invasive species

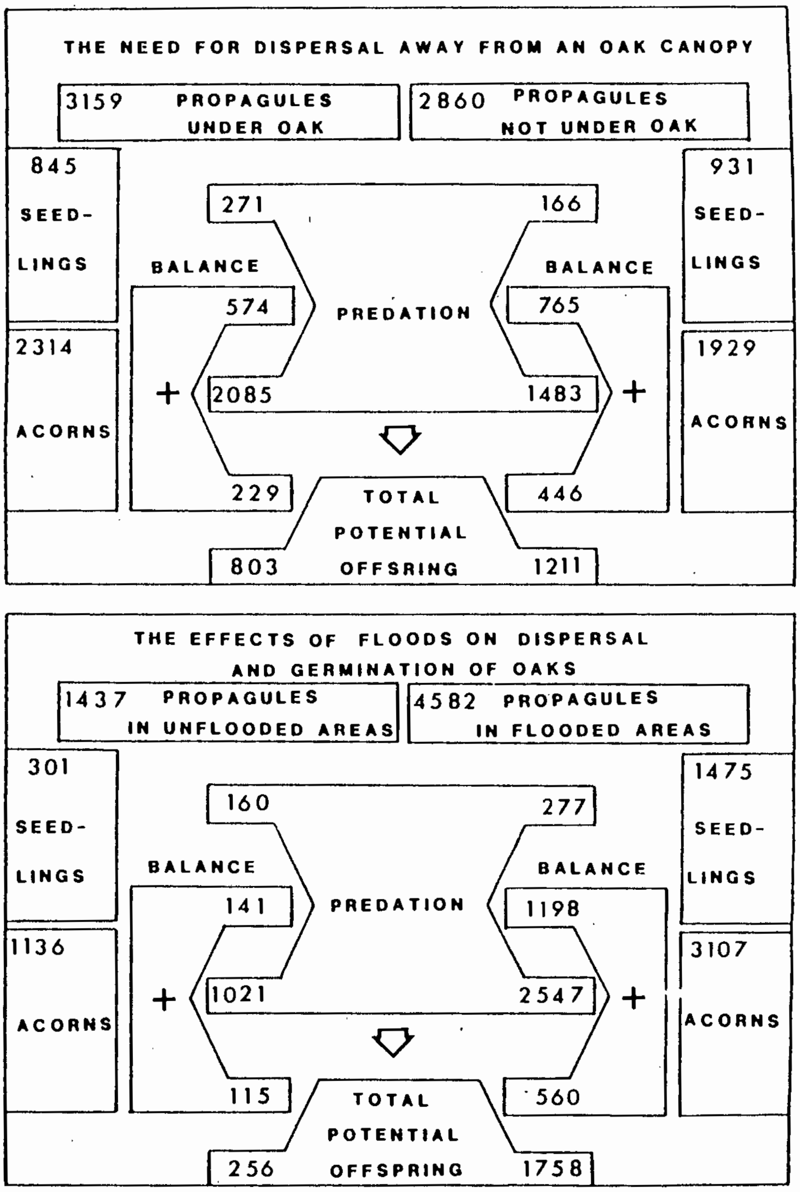

Figure 3 Diagrams representing the need for dispersal away from an oak canopy and the advantages of water dispersal.

in at least some parts of southern Africa' (Macdonald 1983), it could be important to have some knowledge of its population dynamics and dispersal. Assuming oaks were to expand their numbers during periods of excessively wet winters and cooler summers, control of oak may become more efficient if upstream areas are given priority for clearing. Since the oak was introduced by Jan van Riebeeck in 1656 (Donald 1978), it has been considered an integral part of the 'Cape Culture' and therefore human sentiment would have to be considered by those planning and instituting control measures.

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Appendix 1 Frequencies of viable and non-viable acorns and seedlings for each quadrat. Total observed and expected frequencies, together with site conditions are presented

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn		Seedling		Observed total	Expected total
			Inviable	Viable	Inviable	Viable		
1	1	2	46	3	0	3	52	48
2	1	2	44	2	2	1	49	60
3	1	2	49	6	8	8	71	57
4	1	2	47	13	11	5	76	58
5	2	1	110	18	0	25	153	62
6	2	1	41	14	5	22	82	49
7	2	1	32	30	11	31	104	56
8	1	1	10	0	0	0	10	59
9	1	1	3	0	0	0	3	49
10	2	2	65	40	37	38	180	69
11	1	2	30	1	8	0	39	61
12	1	2	24	0	0	1	25	59
13	1	2	8	4	0	2	14	59
14	2	2	32	8	5	14	59	59

Appendix 1 (continued)

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn Inviable	Acorn Viable	Seedling Inviable	Seedling Viable	Observed total	Expected total
15	2	2	104	8	8	28	148	61
16	2	2	220	8	0	46	274	51
17	2	1	36	21	4	38	99	61
18	1	1	2	0	0	1	3	49
19	1	1	10	1	7	0	18	73
20	2	2	51	31	31	52	165	64
21	2	2	237	2	5	38	282	69
22	1	2	23	5	3	0	31	63
23	2	2	21	3	5	29	58	53
24	2	1	24	18	1	21	64	57
25	2	1	105	2	8	17	132	61
26	2	1	88	10	5	40	143	58
27	1	1	5	0	0	1	6	70
28	1	1	2	0	0	3	5	51

Appendix 1 (continued)

			Acorn		Seedling			
Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Inviable	Viable	Inviable	Viable	Observed total	Expected total
29	2	1	28	90	17	86	221	68
30	2	2	97	38	32	35	202	65
31	2	1	10	38	2	35	85	62
32	1	2	6	0	3	1	10	54
33	2	1	19	18	12	17	66	61
34	2	1	19	19	4	29	71	60
35	1	1	10	1	3	0	14	83
36	1	1	0	0	1	1	2	63
37	1	1	5	0	0	0	5	59
38	1	1	0	0	0	1	1	62
39	2	2	111	8	5	80	204	66
40	2	2	11	0	0	2	13	56
41	1	2	93	5	34	5	137	57
42	1	2	36	3	6	17	62	53

Appendix 1 (continued)

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn		Seedling		Observed total	Expected total
			Inviable	Viable	Inviable	Viable		
43	2	2	101	8	0	31	140	53
44	2	1	24	17	1	28	70	66
45	1	1	7	0	0	0	7	69
46	1	1	0	0	1	0	1	53
47	1	1	22	1	0	0	23	63
48	1	1	28	38	19	19	104	61
49	2	1	37	2	0	29	68	67
50	1	1	0	2	0	0	2	46
51	1	2	0	0	0	0	0	61
52	2	2	101	12	12	24	149	54
53	2	2	57	2	15	38	112	67
54	1	1	0	0	0	3	3	71
55	1	1	5	2	0	5	12	55
56	1	1	0	1	0	0	1	46

Appendix 1 (continued)

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn		Seedling		Observed total	Expected total
			Inviable	Viable	Inviable	Viable		
57	1	1	11	5	0	0	16	61
58	2	1	27	11	9	13	60	53
59	2	1	18	7	5	26	56	68
60	1	1	3	0	9	0	12	55
61	1	2	19	0	12	7	38	65
62	1	2	18	2	10	9	39	76
63	2	2	79	2	5	12	98	60
64	1	1	0	1	0	2	3	65
65	1	1	49	2	0	0	51	68
66	1	2	64	5	0	8	77	54
67	1	1	9	0	0	0	9	60
68	2	1	34	5	7	22	68	60
69	1	2	68	0	0	5	73	72
70	1	1	63	5	0	7	75	76

Appendix 1 (continued)

			Acorn		Seedling			
Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Inviable	Viable	Inviable	Viable	Observed total	Expected total
71	2	2	115	7	0	18	140	64
72	2	1	45	27	3	33	108	61
73	1	1	1	0	0	0	1	61
74	1	2	108	3	14	17	142	74
75	1	1	0	2	0	1	3	68
76	1	1	7	0	2	0	9	66
77	2	1	26	5	2	28	61	54
78	2	1	29	8	0	18	55	64
79	1	1	8	0	1	1	10	65
80	1	1	9	0	0	1	10	59
81	2	1	38	5	2	41	86	63
82	2	1	36	8	2	26	72	56
83	1	1	5	0	0	1	6	55
84	1	1	0	0	1	0	1	56

Appendix 1 (continued)

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn		Seedling		Observed total	Expected total
			Inviable	Viable	Inviable	Viable		
85	1	1	0	1	0	0	1	51
86	2	1	68	5	0	18	91	60
87	2	1	44	2	2	11	59	65
88	1	1	16	0	0	0	16	56
89	1	1	4	0	0	0	4	60
90	1	1	3	0	1	0	4	68
91	2	1	32	0	3	23	58	55
92	1	1	6	0	0	1	7	55
93	1	1	35	0	2	2	39	52
94	2	1	46	3	8	15	72	55
95	2	1	74	0	1	12	87	59
96	2	1	55	0	3	9	67	57
97	1	1	0	0	0	2	2	44
98	1	1	0	0	1	0	1	50

Appendix 1 (continued)

Quadrat number	Flooding 1= absent 2= present	Under Oak 1=no 2=yes	Acorn Inviable	 Viable	Seedling Inviable	 Viable	Observed total	Expected total
99	1	1	0	1	0	0	1	71
100	1	1	0	0	1	0	1	55

CHAPTER 10

Fruits in the south-western Cape and their...

- Biogeography
- Reproduction & Re-establishment
- Phenology
- Avian Utilization
- Competition (Alien vs Indigenous)
- Presentation
- Opportunistic Dispersal
- Dispersal Efficiency
- Relationship with Episodic events
- Seed predators

Coping with seed parasitism; A possible response by *Protasparagus aethiopicus*

Contents

Results

Coping with seed parasitism; a possible response by *Protasparagus aethiopicus*

Abstract

Seeds of *Protasparagus aethiopicus* berries are subject to heavy parasitism by a lepidopteran larva. The level of parasitism increases with an increase in seed number per fruit. One-seeded berries have the highest probability of escaping parasitism (0,97), whereas two- and multi-seeded (three seeds or more) berries have lower probabilities for escaping (0,42 and 0,25; respectively). Since the seeds are in all cases similar in size, one-, two- and multi-seeded berries possess different seed-to-pulp ratios, with multi-seeded berries having the highest seed-to-pulp ratio. Successful larval development is inversely related to seed number, with a 97% larval mortality in one-seeded berries, 86% in two-seeded and 17% in multi-seeded berries. A mechanism for limiting successful parasitism in *Protasparagus aethiopicus* berries was examined at four study sites and at three stages of fruiting. The ratios of one-, two- and multi-seeded berries were found to vary both seasonally and at different sites, whereas parasitism of multi-seeded berries remained consistently high.

Oikos 1987, 48: 15-22.

Introduction

Based on theoretical considerations, models describing reciprocal evolution between plants with fleshy fruits and frugivorous birds have been proposed (Snow 1971; McKey 1975; Howe & Estabrook 1977; Howe & Smallwood 1982). However, field research has rarely supported these models (Frost 1980; Herrera 1981a; Herrera & Jordano 1981; Jordano 1982). Fruiting seasons, seed size, seed number and nutritional quality of pulp are all considered to be adaptations on the part of the plant to increase the success of vertebrate mediated seed dispersal (McKey 1975; Howe & Estabrook 1977). Herrera (1981b) demonstrated that intraspecific variations in seed numbers of Smilax asper berries are the product of plant competition for avian dispersers. Jordano (1984) indicated that intraspecific variation in seed size and seed number of Rubus ulmifolius resulted in a differential quality of dispersal carried out by different avian species. Although results of both Herrera (1981b) and Jordano (1984) are consistent with McKey (1975) and Howe & Estabrook (1977), Herrera (1984a) demonstrated that the seed number of Berberis hispanica berries are not necessarily an adaptation to increasing the number of seeds dispersed by birds, but may be associated with seed-parasitism by a tephritid fruit fly larva.

Preliminary observations in 1980 on Protasparagus aethiopicus (Wag-'n-bietjie) indicated that a large number of apparently intact berries possessed no intact seeds. This study also revealed that one-, two-, and multi-seeded (three seeds or more) berries existed on the same plant, but that the proportions of seed numbers varied both seasonally and spatially. Multi-seeded berries are considered to have three or more seeds, three seeds is the usual maximum, however, on rare occasions a single ovule has divided into two, with the result that four seeds are distributed within three locules. The percentage pericarp investments based on dry weight decreased with an increase in seed number. One-seeded berries had 70% pericarp, two-seeded had 50% and multi- seeded had 36% pericarp investments (pers. obs). The parasitism of these berries was likely to represent a single species, since the larva itself, the oviposition marks and the exit holes appear to be identical in all cases. The anatomy of the larva was consistent with that of a lepidopteran (Pinhey 1975), but repeated attempts to rear the moths were unsuccessful. The species richness of insects within the Cape Floral Kingdom is vast and parallels that of its floristic richness (8504 plant spp.; Bond & Goldblatt 1984). Of the total insect fauna, only a small population has been described for both larval and adult phases (e.g. Skaife 1979) and consequently a definitive identification of the micro-lepidopteran larvae involved was impossible. The present study was undertaken to quantify the parasitic damage to *P. aethiopicus* seeds at different sites and fruiting seasons, and to determine if these plants possessed any mechanisms whereby parasitism was reduced.

Materials and Methods

Natural history of *Protasparagus aethiopicus*

Protasparagus aethiopicus is a thorny vine occurring in coastal thicket vegetation (Jessop 1966), and is particularly common in the southwestern Cape region of South Africa. Flowering of *P. aethiopicus* in my study area at Hermanus was almost continuous between November and June. Development from flowering to fruit was variable, but was usually completed between twelve and twenty weeks. Within specific habitats both flowers and ripe fruits are produced at the same time, but considerable phenological differences occur between different habitats. Based on 36 hours of observations, the ripe berries of *P. aethiopicus* are consumed only by the Sombre Bulbul *Andropadus importunus* and the Cape Bulbul *Pycnonotus capensis* (pers. obs). Both birds appear to be resident throughout the year and are also territorial for much of the year. The foraging behaviour of both bulbul species drew attention to the possibility that not all *P. aethiopicus* berries are suitable for consumption. During foraging, both bulbul species gently rotate the berries in their beaks and thereafter the berries are frequently discarded. Approximately one out three berries are consumed, and discarded berries accumulated beneath the fruiting plant. These accumulated berries are a product of frugivore foraging, since unremoved berries wither *in situ* and remain on the branches for many months, even when the branch itself dies. A preliminary study indicated that most of the discarded berries examined appeared to be parasitized and multi-seeded.

Sampling

Sampling of P. aethiopicus berries for lepidopteran parasitism was undertaken at four sites and repeated three times during the fruiting season. Three of the sites were in dune scrub-thicket situated at Westcliff (34° 36′ 00" S, 19° 13′ 30" E); Mosselrivier (34° 24′ 30" S, 19° 16′ 30" E) and Die Mond (34° 25′ 00" S, 19° 18′ 20" E). Westcliff is a rocky exposed west facing cliff site characterized by open low scrub. Flowering and fruiting of P. aethiopicus was earlier than at other sites and samples of fruit were obtained on 3/3/84, 30/3/84 and 20/4/84. Mosselrivier is situated in a wind protected riverine thicket, with vegetation between two and three meter high. Fruiting of Mosselrivier was almost three weeks later and samples were obtained on 31/3/84, 10-21/4/84 and 2/5/84. The third dune site was situated in dense three-meter Sideroxylon inerme thicket-dune forest, and P. aethiopicus fruiting was one to two months later than at Mosselrivier. Samples were obtained on 2/5/84, 5/6/84 and 25/7/84.

The fourth site, Grootbos, is a remnant coastal forest (Taylor 1961) close to Stanford (34° 33′ 40" S, 19° 23′ 30" E) where P. aethiopicus occurs as an entirely subcanopy vine. This site was first inspected and sampled on 2/8/84 and, although ripe fruit may have been presented earlier, most fruit was still unripe and subsequent sampling was undertaken on 3/9/84 and 1/10/84. In all cases sampling of fruit was undertaken such that early, middle and late phases of fruiting were included. At each site a single 10 cm fruiting panicle was collected from each of five tagged branches. An entire fruit panicle was removed at each sampling to avoid replicate sampling of the same fruit at a later date. The nature of the P. aethiopicus vines make it impossible to determine if all five sampled branches represented separate genotypes. During sampling, panicles with approximately 80% ripe berries was selected so that berries of an equal ripeness were compared. A total of 1795 ripe berries was collected and individually examined for larval exit holes, and dissected, annotating the number of full sized seeds. In the parasitized berries, damaged seeds, exit holes and state of larvae (dead or alive) were recorded.

Analysis

Maximum likelihood statistics were used to identify relationships between the nature of parasitism (not parasitized, parasitized but larva had left berry, parasite present but dead, present and alive) and seed number (one-, two- and multi-seeded berries). The null hypothesis was that seed number and parasitism were independent of each other. A sequential cell removal of this two-way contingency table was used to identify the sources of significance (Knight & Siegfried 1983). A four-way contingency table analysis integrated the occurrence of parasitism (presence or absence), number of seeds, phase of season (early, middle or late) for each site (Westcliff, Mosselrivier, Die Mond and Grootbos). Each of these four variables was given an identifying initial:- parasitism was P, seed number was N, phase of season was S, and site location was L. Two-way relationships, e.g. seed number N with parasitism P, could in this way be summed with other two- and even three-way relationships to create models that described the data. The proportions of one-, two-, and multi-seeded berries were also plotted together with seasonal parasitism for each site.

Results

Parasitism and seed number

One-seeded berries accounted for 66,0% of all fruit dissected, whereas two- and multi-seeded berries accounted for 20,9% and 13,1%, respectively (Table 1). Out of 1184 single-seeded berries only 31 or 2,6% were found to be parasitized (Table 1), whereas two- and multi-seeded berries had 57,6% and 75,0% parasitism, respectively. The frequencies of unparasitized berries and parasitized berries possessing larvae that were either dead, alive or have already left through an 'exit hole' are summarized in Table 1 and were also found to be related to seed number ($\underline{G}^2 = 1170,65$; $\underline{P} < 0,001$). The expected frequencies of this contingency table are also presented in Table 1. Use of the sequential cell removal technique indicated that parasitized multi-seeded berries possessed far more exit holes (140) than expected (20,4), and the removal of this cell reduced the maximum likelihood statistic ($\underline{G}^2 = 603,23$; $\underline{P} < 0,01$). Removal of cells representing dead larvae in two- and multi-seeded

Table 1 Frequencies and nature of parasitism in one- two- and multi-seeded *Protasparagus aethiopicus* berries. Values in parentheses are expected frequencies.

Seed	No Larvae	Larvae left	Larvae alive	Larvae dead	Total
One	1153	0	1	30	1184
	(904,3)	(102,2)	(15,8)	(161,6)	
Two	159	15	16	185	375
	(286,4)	(32,4)	(5,0)	(51,2)	
Multi	59	140	7	30	236
	(180,3)	(20,4)	(3,2)	(32,2)	
Total	1371	155	24	245	1795

berries further reduced the overall $\underline{G}^2$ to 219,33 and 134,55, respectively. In the case of two-seeded berries there were more dead larvae than expected, whereas in multi-seeded berries there were fewer dead larvae than expected (Table 1). A further two cells contributed to the overall significance of the Table 1 and represented live larvae found in two- and multi-seeded berries. The removal of each cell reduced the $\underline{G}^2$ to 74,81 and 35,64, respectively. In both cases observed frequencies exceeded expected frequencies (Table 1).

Parasitism at different sites and seasons

The frequencies of parasitized and unparasitized berries for the different seed number, season and sites are presented in Table 2, and were analysed as a multi-dimensional contingency table. The following combination of variables was found to be the most suitable multi-dimensional contingency table model explaining the data:-

LSN + NP + SP

and fitted the data such that the residuals were non-significant ($\underline{G}^2 = 94,69$; $\underline{P} > 0,05$) and accounted for 95% of the data. The expected frequencies derived from this model are also presented in Table 2 and were overall fairly similar to the observed frequencies. The LSN combination of variables indicated that location (L), season (S) and seed number (N) were associated with each other and inter-related. Consequently, seed number varies with both season and location, and such associations were strengthened by mutual interdependence. The NP part of the model indicated that associations exist between seed number (N) and parasitism (P), whereas SP indicated associations between season (S) and parasitism (P). The associations of seed number (N) and season (S) with parasitism (P) were, however, independent of each other.

Early fruiting at Westcliff (3/3/84) was characterized by a large number of multi-seeded berries. However, the levels of parasitism were high in multi-seeded berries, but relatively low for two-seeded berries (Figure 1a.). By the middle of the season (30/3/84) levels of parasitism had increased in spite of the few multi-seeded berries being produced. At the end of the fruiting season almost 95% of the berries were one-seeded and parasitism was minimal

TABLE 2 Four-dimensional contingency table relating occurrence of lepidopteran parasitism, with seed number, fruit season and site location Values in parentheses are expected frequencies derived from the multi-dimensional contingency table model.

Parasite	Seed No.	Season	Site			
			Westcliff	Mossel Rivier	Die Mond	Grootbos
Para-sitized	One Seed	Early	0 (3,1)	0 (3,1)	13 (4,7)	2 (14,4)
		Middle	1 (1,1)	2 (2,2)	4 (1,7)	4 (5,1)
		Late	0 (0,3)	0 (0,2)	0 (0,2)	5 (0,8)
	Two Seed	Early	22 (29,0)	67 (60,3)	25 (22,3)	8 (9,7)
		Middle	35 (29,6)	21 (27,4)	21 (20,8)	6 (7,1)
		Late	2 (2,1)	0 (1,6)	6 (10,5)	3 (1,6)
	Multi Seed	Early	38 (38,5)	48 (44,6)	9 (8,7)	10 (9,6)
		Middle	27 (23,8)	13 (20,8)	8 (9,7)	8 (6,7)
		Late	1 (0,8)	1 (1,2)	14 (18,2)	0 (0,4)
Non-para-sitized	One Seed	Early	58 (55,9)	57 (54,9)	76 (85,2)	270 (258,6)
		Middle	46 (46,9)	94 (94,8)	72 (75,3)	220 (219,9)
		Late	56 (56,7)	26 (26,8)	38 (38,8)	140 (145,2)
	Two Seed	Early	16 (10,0)	13 (20,7)	4 (7,7)	4 (3,3)
		Middle	18 (24,4)	28 (22,6)	16 (17,2)	6 (5,9)
		Late	6 (6,9)	6 (5,4)	39 (35,5)	3 (5,4)
	Multi Seed	Early	5 (5,5)	2 (6,4)	0 (1,3)	0 (1,4)
		Middle	4 (8,2)	14 (7,2)	4 (3,3)	0 (2,3)
		Late	0 (1,2)	1 (1,8)	29 (25,8)	0 (0,6)

(Figure 1a.). The reduction in investment in two- and multi-seeded berries may be the principal factor contributing to the reduction of parasitism between early season (43% fruit parasitism) and late season (5% fruit parasitism). Overall parasitism of fruit averaged 38%.

Early fruiting at Mosselrivier (31/3/84) was characterized by a dominance of two- and multi-seeded berries. However, parasitic pressure was heavy with 62% of berries being parasitized (Figures 1a and b). Frequencies of parasitism during early fruiting at Mosselrivier and middle fruiting at Westcliff closely approximated each other (sampling occurred on successive days) (Figures 1a and b). During the fruiting season at Mosselrivier there was a steady increase in the frequency of one-seeded berries, whereas the overall parasitism declined. At the end of the fruit season few berries were parasitized (3%). An overall of 39% of P. aethiopicus berries were found to be parasitized and were therefore similar to that recorded at Westcliff. The decline in parasitism from early to late season was more pronounced at Mosselrivier than at Westcliff.

At Die Mond, one-seeded berries (70%) characterized early fruiting (2/8/84) and therefore differed from the two previous sites (Figure 1c). In spite of the occurrence of two- and multi-seeded berries the one-seeded berries were subject to a high level of parasitism which was significantly greater than expected based on the multi-dimensional contingency table model (standardized deviation = 4,5). It was likely that a large number of lepidoptera was still requiring berries in which to oviposit and it seems that even one-seeded berries were employed in the presence of a general scarcity of P. aethiopicus berries. The overall level of parasitism for early fruiting at Die Mond was far lower than at other sites (37%) and may be a consequence of a large investment in one-seeded berries. During mid-season fruiting the proportion of one-seeded berries dropped by 9% and also the overall level of parasitism (11%). At the end of the fruit season single-seeded berries accounted for only about 30% of total berries and parasitism was only 16%. During the entire season an average of 27% of berries was found to be parasitized.

At Grootbos, most berries were one-seeded (93 %) and almost all two- and multi-seeded berries were parasitized (Figure 1d). The overall level of

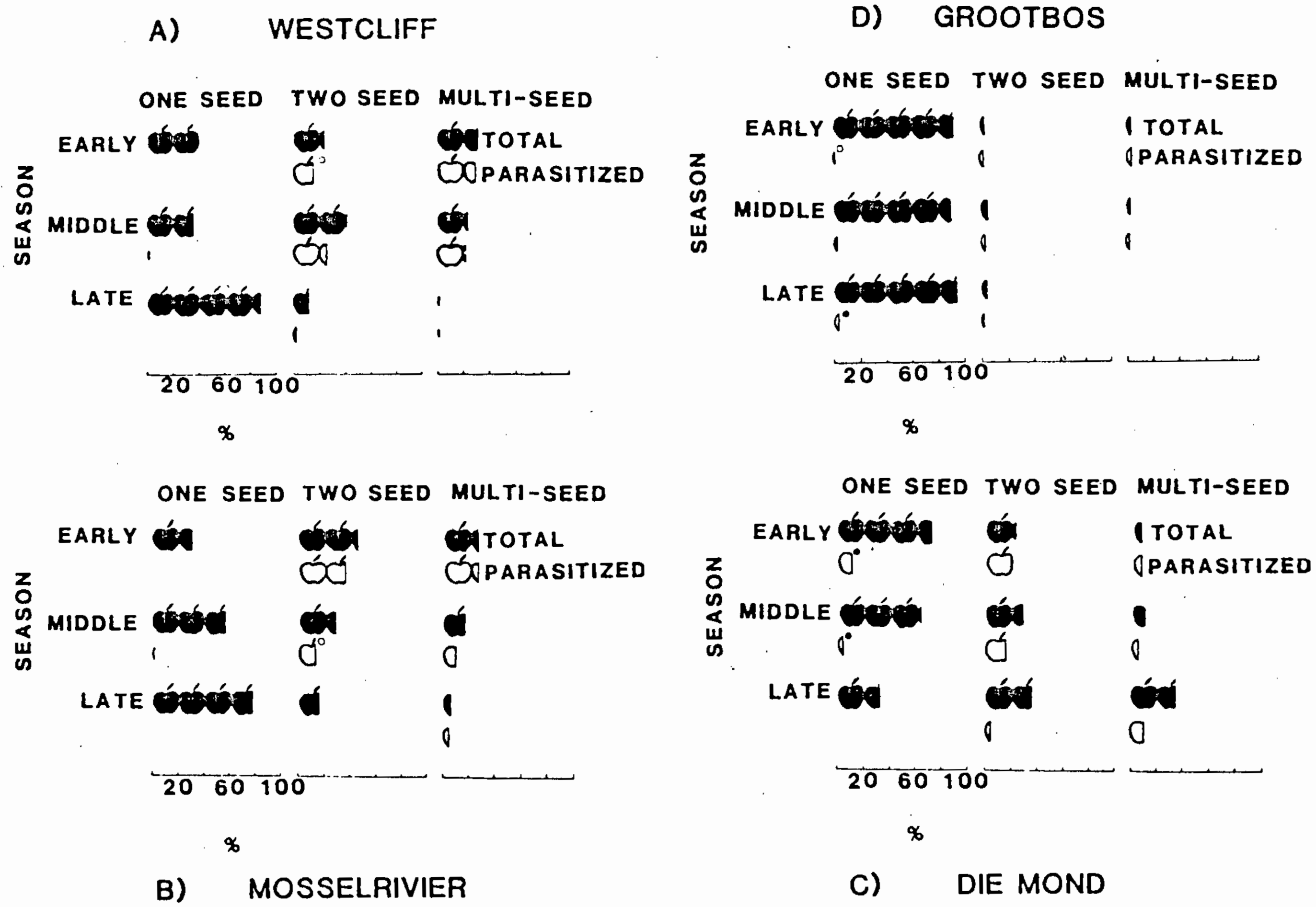

Fig. 1. Percentage of total *Protasparagus aethiopicus* berries that possessed one-, two- or multi-seeded berries at each study site (A-D) and season (early, middle and late). Each whole berry represents 20%. The open berries represent the percentage of total berries that were found to be parasitized. A dot next to the parasitized fruits indicates that there were more parasitized fruits than expected ($P < 0.05$), whereas the circle indicates that there were fewer parasitized fruits than expected.

parasitism in one-seeded berries was also greater than expected and therefore parasitic pressure by the lepidoptera was probably greater than at the three coastal sites. Further, the incidence of one-seeded parasitism increased during the fruit season and was considerably greater than expected at late season (standardized deviation between observed and expected was 5,1). The strategy of fruiting in spring and investing in mostly one-seeded berries appeared to have incurred the lowest levels of average parasitism (7%).

Discussion

The pericarp investment of fleshy fruits is a necessary incentive to attract potential avian dispersal agents. Based on theoretical predictions derived from fruit-frugivore models (Snow 1971, McKey 1975, Howe & Estabrook 1977) plants should favour an increase in number of seeds per fruit, whereas dispersers which ingest the fruit and disperse the seeds should favour a decrease in seed number. Herrera (1981b) has demonstrated that Smilax aspera berries had on average fewer seeds in plant communities rich in fruit-bearing species than in species-poor communities. With regard to Protasparagus aethiopicus, those plants possessing the lowest seed proportions (average of 1.01 seeds per berry) occurred at Grootbos, yet there were no other fleshy fruits available to "compete" with during the fruiting (2/8/84 to 1/10/84). In contrast plants at Mosselrivier possessed the greatest seed proportion (average of 1,75 seeds per berry) in spite of having to "compete" with twelve species which presented fruit simultaneously and equally or more abundantly than P. aethiopicus. Therefore, contrary to Herrera (1981b), interspecific competition is unlikely to be influencing seed proportions in P. aethiopicus.

Since the results obtained in this study indicate that multi-seeded berries are preferentially selected for lepidopteran parasitism (Table 1, and the significant NP association in the multi-dimensional contingency table model) and, further, that successful larval development, as indicated by the presence of exit holes, is almost exclusive to multi-seeded packages. It is therefore, unlikely that multi-seeded berries would be selected for during periods of high parasitic pressure, confirming Herrera's (1984a) proposition. Since in all berries with exit holes all the seed matter in the fruit is utilized, it appears that seed supply to the lepidopteran larvae is likely to be limited.

The lack of exit holes in one- and two- seeded berries is further evidence that multi-seeded berries are required for successful development of lepidopteran larvae. It must also be noted that the pericarp itself is never used as a food source by the larvae.

These results duplicate those obtained by Herrera (1984a), except that the parasite involved is a lepidopteran rather than tephritid fly. Although parasitized P. aethiopicus berries appear to be identical in colour and size to unparasitized fruit, the pericarp is distinctly bitter compared to unparasitized berries, suggesting that microbes may be associated with the parasite, rendering the berries less attractive to frugivorous vertebrates (Janzen 1977). Norris (1936) indicated that fruit-piercing moths may introduce microbes into fruit. A complex system of frugivore, fruit parasitism, and microbial damage has also been described for the Hawthorn Crataegus monogyna (Manzur and Courtney 1984).

A certain problem exists with regard to differential parasitism, not dealt with by Herrera (1984a), This is the mechanism whereby an invertebrate recognizes multi-seeded berries from two- and one-seeded berries. From Figure 2 it can be seen that the shape and size of one-, two- and multi-seeded berries differ. Size differences occur, since seed size varies little and, therefore, multi-seeded berries need to be bigger than one-seeded berries. It is conceivable that a lepidopteran could discriminate between the different sizes or shapes of berries, or possibly by the presence of grooves (Figure 2). One-seeded berries are spherical, with no grooves, two-seeded berries are kidney shaped with a single groove, and multi-seeded berries are triangularly shaped with three grooves. It could be speculated that oviposition is less likely to be successful where the pericarp is thick, as in one-seeded berries and more successful where the pericarp is thin as in multi-seeded berries. The abortion of one or two ovules to produce two- and one-seeded berries could represent a simple mechanism for limiting parasitism (Herrera 1984a). Differential pollination treatments have been shown to produce different ovule numbers through ovule abortion mechanisms (Banyard & James 1979; James 1979). Similar mechanisms through the operation of recessive lethal genes could occur in Protasparagus aethiopicus. However, the cues for executing such mechanisms remain unresolved, since fruiting of P. aethiopicus is seasonally un-

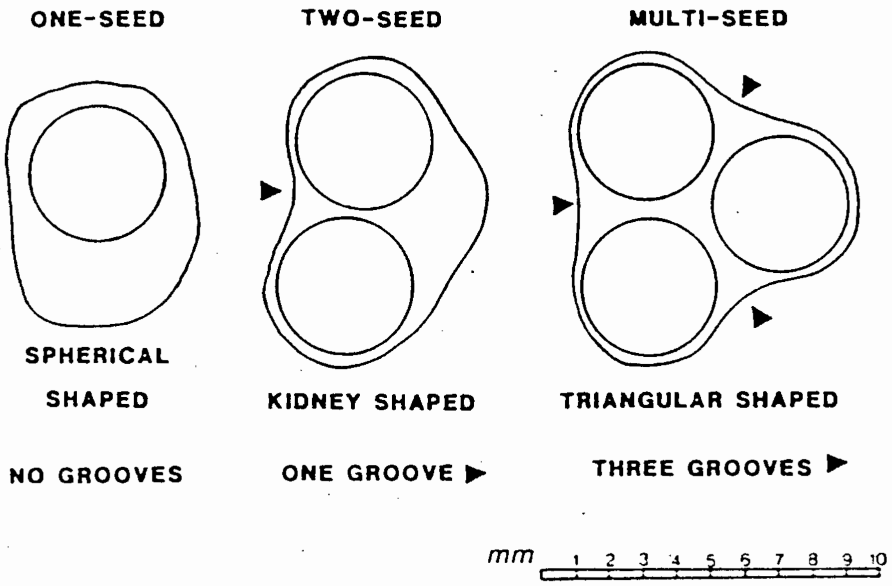

Fig. 2. Size and shape of one-, two- and multi-seeded *Protasparagus aethiopicus* berries.

predictable (Knight, in prep; Chapter 3) and duplicate work could not be undertaken in 1985. It is possible that a high degree of fruit parasitism initiates ovule abortion, or that differential abortion through a fruit season is fixed and a product of past selective pressure (Levin & Turner 1977). The product of either mechanism is the same, and at all four study sites, the levels of parasitism within two- and multi-seeded berries are reduced through the season (Figure 3).

It is considered that under seasonal environments ripe berries are most likely to be attacked by invertebrates during spring (Thompson & Willson 1978, 1979; Herrera 1982), whereas winter is likely to possess the fewest invertebrate pests (Stiles 1980; Herrera 1982). Codling moths (which are important fruit pests) appear to pass winter in a pupa stage and the first young moths emerge in September (Skaife 1979). A second generation of moths emerge in December to January, and possibly a third in March (Skaife 1979). Spring fruiting at Grootbos may therefore be subject to the highest level of parasitism. Indeed, virtually all multi-seeded berries at this site were parasitized, and even one-seeded berries were parasitized at a greater than expected frequency (Table 2, Figure 1c). It is likely that the relatively more expensive option of investing in one-seeded berries prevented a higher degree of parasitism.

Herrera (1982) suggested several options in defending ripe fruit. At Grootbos it appeared that the option of "reducing nutritive profitability of fruit" has been selected rather than the option of "ripening berries when pest pressure is lowest". This latter option appears to have been selected, judging by winter fruiting, at Mosselrivier and Die Mond sites. It is possible that water availability was limited in the deep sands occurring at Grootbos, whereby ripe berries could not have been produced at the end of summer. Further evidence for limited water availability was that plants at Grootbos showed leaf loss during the summer months which may represent drought related deciduousness. In contrast, the Mosselrivier and Die Mond sites are situated adjacent to permanent rivers and therefore water was available throughout the summer. The parasitic pressure during middle and late fruiting at Die Mond was so low that the plants were able to increase their investments in two- and multi-seeded berries and even so the observed parasitism still

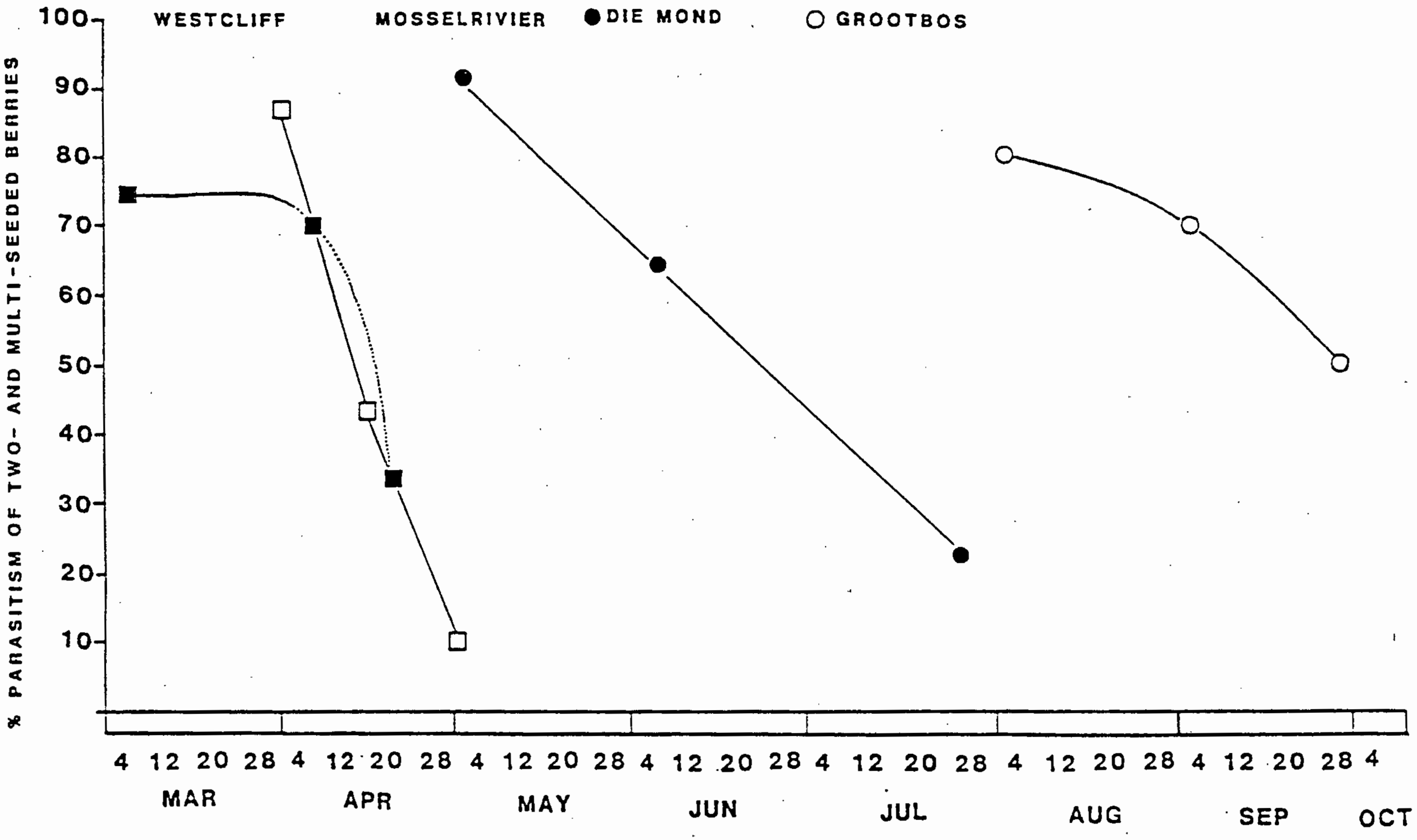

Figure 3 Percentage of two- and multi-seeded <u>Protasparagus aethiopicus</u> berries that are parasitized at different seasons and sites.

declined (Figure 1c). Early fruiting at Westcliff and Mosselrivier was characterized by relatively high investments in multi-seeded berries which were parasitized to a large extent. Thereafter the plants appeared to reduce the nutritive profitability for lepidopteran parasitism by increasing their investments in one-seeded berries. However, at Grootbos the increased incidence of one-seeded fruit parasitism during the fruit season may indicate that the lepidopterans may become less selective in their choice of fruits for parasitism. This pattern is similar to the frugivore utilization of Crataegus monogyna fruits reported by Courtney and Manzur (1985). The different strategies of seed investment at different sites are significant, since the associations SN and LN were both included in the multi-dimensional contingency table model. However, the observed decrease in parasitism during the fruit season (SP association, Figure 3) was not simply a reflection in seasonal changes in seed number investments (SN), since the associations SP and SN were independent of each other in the multi-dimensional contingency table model.

Conclusion

This study has demonstrated that the pressures on Protasparagus aethiopicus to maximize seed output whilst limiting pre-dispersal parasitism are not constant throughout a fruiting season, nor are they equal at different sites. The observed changes in seed number per berry at different seasons and sites may well be the product of past selective pressures in producing the "optimal" number of seeds per fruit (see Levin & Turner 1977) or a direct response to early parasitism of berries, through the operation of recessive lethal genes at an early stage of fruit production. This study indicates that the major consumers and dispersers of fruit (usually birds) under certain circumstances have a reduced influence in the morphology and phenology of fleshy fruit, if compared to environmental and parasitic or predation constraints (Herrera 1984a, b, c).

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Summary and Synthesis

Summary and Synthesis

The research undertaken found little evidence for the support of the co-evolutionary models proposed by McKey (1975) and Howe & Estabrook (1977), either at the community or the individual species level (Objective 1). Avian-dispersed plants were found to be particularly common in Afromontane Forest and Coastal Thicket (Objective 2). Even in Mountain Fynbos, resprouting plants that are adapted for vertebrate-dispersal may be abundant immediately post-fire. A classification of plant species was developed which attempted to integrate plant-dispersal with the establishment of new generations of plants (Objective 3). In addition a manipulative experiment was designed to estimate the overall success of the avian seed-dispersal of a common, indigenous plant species. In the four autecological studies avian seed-dispersal processes were compared to the effects seed predators have in the pre- and post-dispersal predation of seed (Objective 4). Finally the presentation of fleshy fruit occurring in indigenous plants was compared to those occurring in alien plants (Objective 5). Based on these results certain predictions regarding the potential for successful avian-dispersal of alien plants were presented. The most important results arising from each chapter are summarized below:-

Chapter 1: Vertebrate-dispersed plants were found to be common in Afromontane Forest and Coastal Thicket. In Karoo vegetation a high incidence of non-wind, but mechanically dispersed plants was found. Coastal and Mountain Fynbos vegetation types had the lowest occurrence of vertebrate-dispersed plants of all vegetation types studied in the southwestern Cape.

Chapter 2: Vertebrate-dispersed reseeding plants were found to represent 2,8% of the total number of recolonizing species found in an artifically cleared area of Mountain Fynbos vegetation adjacent to Afromontane Forest. The proportional representation of reseeding vertebrate-dispersed species was, however, greater (4,1%) in areas where suitable avian perches had been provided. The representation of resprouting vertebrate-dispersed plants as well as most other non-vertebrate-dispersed species did not vary greatly between sites with and without perches.

Chapter 3: The seasonal availability of fruit suitable for consumption by birds was found to be most predictable in Coastal Thicket vegetation. In contrast the availability of such fruits was relatively scarce and restricted to autumn and spring in Afromontane Forest. Availability of fruits of alien plant species was also highly seasonal. In general the fruit seasons of co-occurring plants were shorter in the southwestern Cape that those reported for the eastern Cape.

Chapter 4: The avian use of different plant species bearing fleshy fruits was found to largely reflect their overall fruit availability in the environment. Those plant species found to be prefered by avian frugivores possessed fruits that were either continuously available or seasonally predictable. For the majority of plant species, frugivory was restricted to or dominated by a single avian species. Further, during periods when fleshy fruits were in apparent scarcity a predicted increase in aggressive interactions between avian frugivores was not found. Instead such interactions were most frequent during periods of fruit abundance, due to increased use of fruits by predominantly insectivorous birds.

Chapter 5: Two gradient models are presented which describe the nature of presentation of vertebrate-dispersed fleshy fruits with respect to both alien and indigenous species. In a suite of 14 species it was found that alien species have fruit presentations that are short, but intense, whereas many indigenous species have less intensive, but prolonged fruit presentations. The indigenous species appeared to have a greater variety of fruit displays than alien species.

Chapter 6: Fruit production on individual branches in a suite of evergreen plant species was found to be negatively related to the abundance of leaves. Reduction of leaves in the vicinity of fruiting is thought to promote the conspicousness of fruit for dispersal by birds. Such relationships between fruit production and leaf abundance were most pronounced in species that have fruits closely attached to their stems. Branches with abundant fruit were also usually characterized by thicker stems.

Chapter 7: The seeds of the introduced *Acacia cyclops* possess conspicuous pseudarils and were consumed by the Black Korhaan *Eupodotis afra* in preference to those of *A. saligna* which lack a functional pseudaril. Despite high levels of pre- and post-dispersal seed predation by a hemipteran and a rodent respectively, the black korhaan dispersed many *A. cyclops* seeds to sites where they germinated and the seedlings could establish themselves. The successful dispersal of *A. cyclops* by the Black Korhaan has been initiated through fortuitous circumstances, and therefore is independent of any coevolutionary implications.

Chapter 8: Birds were found to remove *ca* 14% to 27% of total fruit production of *Chrysanthemoides monilifera* a common coastal shrub of South Africa. Seeds recovered from avian faeces had an experimental germination success of 10%. Hence, it was estimated that each *C. monilifera* plant had the potential to produce some 287 seedlings after each fruit season. Observed recruitment in an artificially cleared area adjacent to the six *C. monilifera* plants averaged 34 seedlings per 100 m^2. This is equivalent to the estimated recruitment if all seeds were deposited in 0,5 ha.

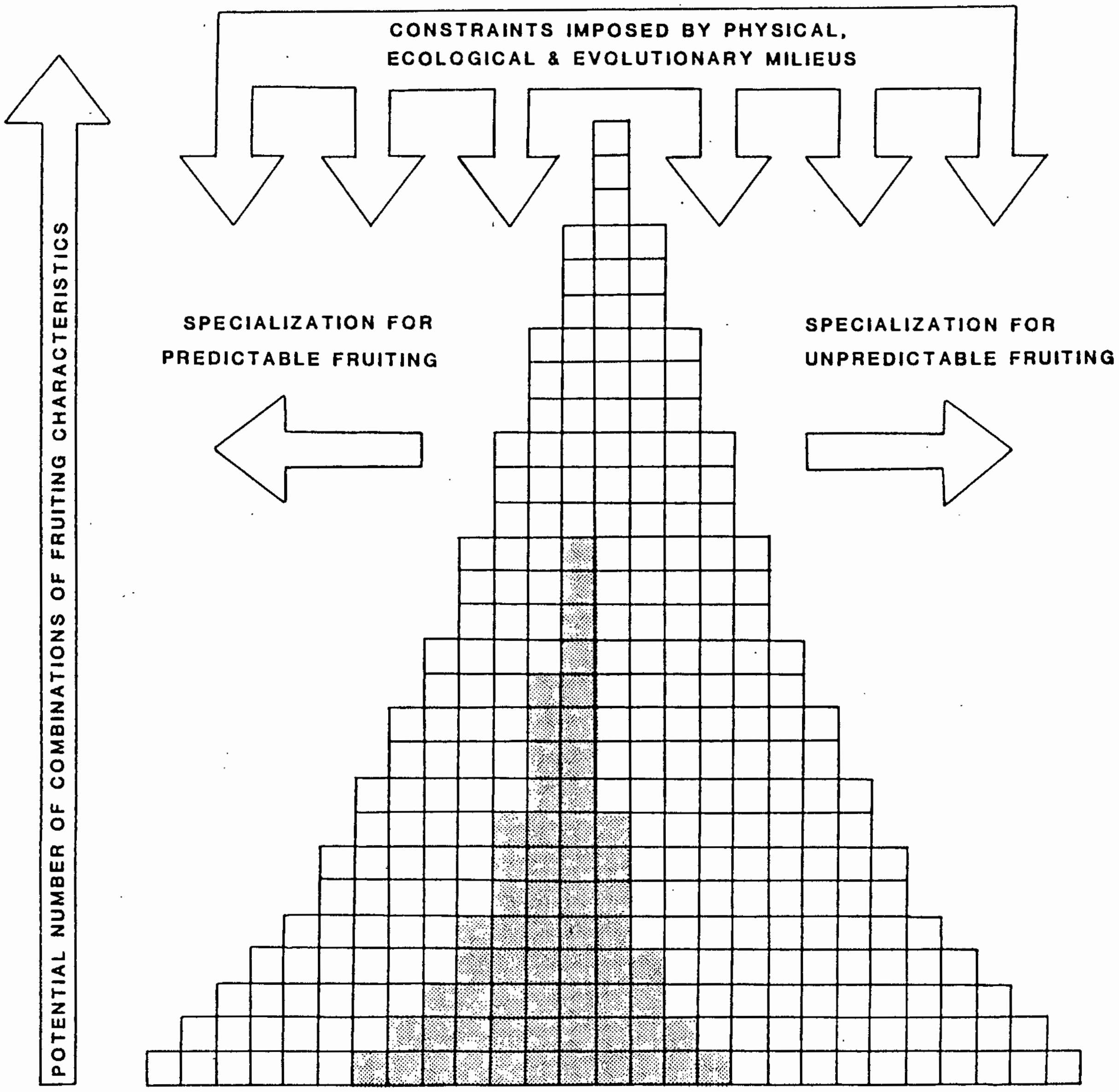
Chapter 9: In a study on the dispersal of the introduced oak *Quercus robur* it was found that areas exposed to flooding by the nearby river had four times the number of propagules found in unflooded areas. Flooded areas had a greater percentage of intact acorns and seedlings. It was also found that acorns found below an oak canopy had the highest mortality. The efficiency of dispersal through episodic flooding was compared to the continuous and low intensity dispersal carried out by the alien squirrel *Sciurus carolinensis*.

Chapter 10: One-seeded berries of *Protasparagus aethiopicus* were found to have the highest probability of escaping parasitism by a lepidopteran larva. An increase in seed investment per fruit appeared to be accompanied by an increase in a probability of parasitism. Further, successful larval development appeared to be inversely related to seed investment. By reducing seed investment in its berries *P. aethiopicus* is thought to suppress the successful development of the parasite. Consequently, seed investment in *P. aethiopicus* berries are more likely to reflect selective pressure from a seed predator rather than for attracting a seed-dispersal agent.

Based on the above studies little evidence for the coevolutionary models proposed by McKey (1975) and Howe & Estabrook (1977) was found either within a Coastal Thicket community (Chapter 4) or for individual species (Chapters 7, 9 & 10) occurring in the southwestern Cape. To date no alternative framework for proposing hypotheses on the evolution of fruit/frugivore interactions has been presented. Chapter 5 proposed a dichotomous model for the presentation of fleshy fruits with plant species occupying positions along a gradient of fruit availability (predictable to unpredictable). Plant species with extremely prolonged fruiting will provide the most predictable fruiting, whereas species that fruit yearly and in the same season have conditionally predictable fruiting, and species with "mast" seasons represent the most unpredictable fruiting. Such categories of species were identified (Chapter 3) and are likely to be dispersed by different frugivore species (Chapter 4). This scheme is useful for delineating a proposed framework for addressing future research in fruit-frugivore interactions (Figure 1). With increasing specialization in either direction (predictable or unpredictable presentation of fruits) fewer plant species are able to occur, assuming that each species possesses its own fruiting identity and competitively segregates itself from other species (this is analogous to niche theory). In essence, each species possesses a unique combination of fruit characteristics, and the number of potential combinations (represented by cells in Figure 1) will be reduced with specialization. For example, evolving very long fruiting periods (and thereby supplying a predictable fruit resource) will reduce the potential for phenological displacement of fruiting among different species. In contrast, unpredictable fruiting species are likely to be restricted to large and/or conspicuous displays if they are to secure the services of avian dispersal agents.

Using the above framework the 22 plant species observed to be eaten by birds (Chapter 4) were classified with respect to fruit colour, fruit crop size, fruit quality and phenology (active ripening). From this simple analysis (Figure 2) only two plant species were observed to share the same combination of fruit characteristics, namely Rhus lucida and R. glauca, which are known to hybridize with each other (Adamson & Salter 1950).

Figure 1 A proposed framework for addressing future research into fruit-frugivore interactions. The figure should be read as a series of histogram bars representing the potential number of fruit combinations that can exist (and therefore the number of species or species forms) that exist along a gradient of fruit predictability. Each cell represents the availability of a single combination of fruit characteristics. The shape of the matrix of cells will vary depending on the nature of the plant's physical, ecological and evolutionary milieus (represented by the downward pointing arrows). The shaded areas of the matrix represent the likely areas where introduced plant species will occupy.


CONSTRAINTS IMPOSED BY PHYSICAL, ECOLOGICAL & EVOLUTIONARY MILIEUS
SPECIALIZATION FOR PREDICTABLE FRUITING
SPECIALIZATION FOR UNPREDICTABLE FRUITING
POTENTIAL NUMBER OF COMBINATIONS OF FRUITING CHARACTERISTICS

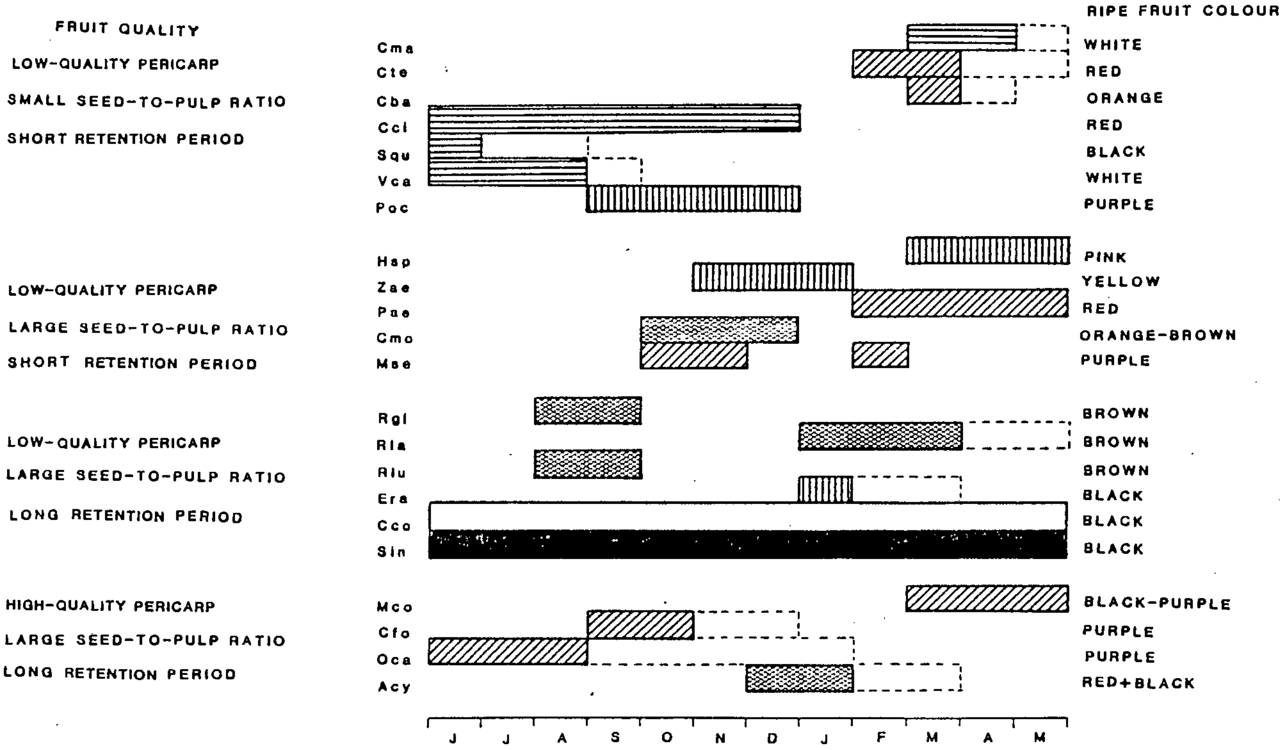


Figure 2 The relationship between fruit quality, crop size (indicated by shading; solid > 100 000 fruits per plant, cross hatch 10 000 - 100 000 fruits, diagonal 1 000 - 10 000 fruits, horizontal 100 - 1 000 fruits, vertical 10 - 100 fruits, speckled < 10 fruits per plant), fruit colour and phenology (active ripening). Plant species are: Hsp = *Haemanthus* species, Zae = *Zantedeschia aethiopica*, Pae = *Protasparagus aethiopicus*, Rgl = *Rhus glauca*, Rla = *R. laevigata*, Rlu = *R. lucida*, Cmo = *Chrysanthemoides monilifera*, Cma = *Cassine maritima*, Cte = *Cassine tetragona*, Era = *Euclea racemosa*, Cba = *Chironia baccifera*, Cci = *Cassytha ciliolata*, Mco = *Myrica cordifolia*, Cfo = *Chionanthus foveolata*, Oca = *Olea capensis*, Cco = *Colpoon compressum*, Sin = *Sideroxylon inerme*, Squ = *Solanum quadrangulare*, Vca = *Viscum capense*, Acy = *Acacia cyclops*, Mse = *Myoporum serratum*, Poc = *Phytolacca octandra*.

Vacancies within the framework are fewer than the number of permutations that are mathematically possible or than suggested in Figure 1. This is due to constraints imposed by each species' evolutionary background and its physical and evolutionary milieu. Evolutionary constraints include the convergence of fruit colour and size for bird dispersal (Chapter 1) and inter-relationship between fruit production and morphology of plants (Chapter 6). The nutrient deficiency of soils in Mountain Fynbos vegetation may impose environmental constraints by preventing more than one season of fruiting between fires for resprouting species possessing fleshy fruits (Chapter 2) with the result that only unpredictable fruiting can be selected. Lack of available moisture during the summer months may impose other environmental stresses on both fruit development and seedling establishment and therefore restrict the potential for phenological displacement of fruiting (Chapter 3). Ecological constraints include defence of fruit against seed predators such as invertebrates (Chapter 10), vertebrates (Chapter 8) and combinations of these two agents with microbes (Chapters 7 and 9).

Such constraints severely reduce the number of combinations of fruit characteristics available but, even so, vacancies may still exist (analogous to vacant niche theory). Vacancies are therefore available for exploitation by alien plant species, or in the long-term by the evolution of new species. Success in occupying these vacancies depends on overcoming the combination of constraints imposed by the physical, ecological and evolutionary milieus. Generally speaking, introduced plants will have more problems in overcoming environmental constraints and less problems with ecological constraints than indigenous plants. One of the most pressing ecological constraints facing an introduced plant species bearing fleshy fruits is securing the services of avian dispersal agents. This may manifest itself in apparently bizarre plant-bird relationships such as the dispersal of Acacia cyclops by korhaans (Chapter 7) and swallows (Broekhuysen 1960); birds not usually considered to be frugivorous. Evolutionary constraints will be the most difficult to identify due to different generation turnovers occurring between frugivore and plant species (Herrera 1984).

A major difference between this segregation hypothesis and niche theory is that the proposed framework can be used independently of the species concept and that the occupation of vacancies is similar to the process of colonization. In the proposed framework one species is not necessarily constrained to a single 'vacancy': hence the phenological variation that occurs in populations of *Protasparagus aethiopicus* reported in Chapter 10 and the genetic lability reported for the morphology of fleshy fruits (Chapter 5) can be accommodated. Species possessing numerous subspecies or hybrids such as *Chrysanthemoides monilifera* (Chapter 8) are likely to spread across several vacancies if the framework defined is geographically large. The character of the framework is, therefore, totally determined by the geographical extent of the study, its physical environment and species composition.

Potential for mobility within the framework is also considerable for plants that are taxonomically recognized as single species. For example, *Colpoon compressum* occupying Coastal Thicket and the Mountain Fynbos form which at present are taxonomically considered as a single species occupy diametrically opposite positions in the framework: Coastal Thicket *C. compressum* is rarely encountered without any ripe fruit, whereas the Mountain Fynbos form has a single post-burn fruiting season and therefore fruit is generally available only every 12 to 15 years. Occupation of these vacancies by populations of plants may also depend on the presence of other species. For example *Ficus* spp. usually have asynchronous fruiting which often maintains fruit availability during periods when other fleshy fruits are not available (Prys-Jones 1984). Where *Ficus* spp. coexist with *Sideroxylon inerme* the fruit availability of *S. inerme* is seasonally restricted (P.G.H. Frost & R.P. Prys-Jones pers. comm.). The mediterranean type regions of southern Africa are without any *Ficus* spp. (Coates Palgrave 1978), and as a possible consequence *S. inerme* plants appear to have a fruiting phenology not dissimilar to that of *Ficus*. In the absence of *Ficus* spp. *S. inerme* appears to have colonized vacancies occupied by *Ficus* spp. elsewhere.

Compared to the dichotomous models of McKey (1975) and Howe & Estabrook (1977) this approach of identifying unique combinations of fruit characteristics, occurring in plants through a process of segregation, is thought to offer a more realistic insight into effects natural selection may have on the presentation of fleshy fruits for bird dispersal. More particularly it may be useful for identifying alien species that have a potential for effective dispersal by local avian frugivores, and for explaining the considerable variations that exist in the presentation of fleshy fruits, even in plants that are considered to be taxonomically the same species. Further advantages of this approach is that it integrates more closely the plant's reproductive and dispersal biology with its physical, ecological and evolutionary milieus.

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