

Vegetative morphology and interfire survival strategies in the Cape Fynbos grasses

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ABSTRACT

It is shown that there is a wide range of structural variation in the habit of the Arundineae and Ehrharteae of the fynbos of the Cape Floristic Region (Cape Province, South Africa). Structural differences in the bases of the fynbos grasses have been classified into four groups: swollen, knotty tillering, weak and annual. Variation in the position of the innovation buds occurs with one group having basal perennating buds, implying that all the culm material is annual, while the second group has cauline innovation buds, leading to the development of a divaricate perennial herb. The recognition of caducous, mesic (orthophyllous) and sclerophyllous leaf blades is also possible, based on leaf morphology and anatomy. These variations in growth forms allow the classification of the Cape grasses into five guilds adapted for survival in the dense fynbos vegetation that develops between the well-spaced fires in these heathlands. The following guilds have been recognized: competition avoiders that grow on rock ledges and outcrops where competition from shrubby vegetation is reduced; reseeder, that survive the protracted interfire period as seed; geophytes, that survive this period as underground organs; coppicers, that survive as small plants; and competitors, that grow tall by means of cauline innovation buds, and so are able to compete with the shrubby heath vegetation.

UITTREKSEL

Daar word aangetoon dat daar 'n wye reeks strukturele variasie in die groeiwyse van die Arundineae en Ehrharteae van die fynbos van die Kaapse Floristiese Gebied (Kaapprovinsie, Suid-Afrika) bestaan. Strukturele verskille in die basisse van die fynbosgrasse is in vier tipes ingedeel: geswolle, knoesterig stingelsuiervormend, swak en eenjarig. Daar bestaan variasie in die posisie van die verjongingsknoppe, met een groep wat basale oorwinteringsknoppe het, wat impliseer dat al die halmmateriaal eenjarig is. Daarteenoor kom die verjongingsknoppe by die tweede groep op die stingel voor, wat aanleiding gee tot die ontwikkeling van 'n uitgespreide meerjarige kruid. Die erkenning van vroegafvallende, mesiese (ortofiele) en sklerofiele blaarskywe is ook moontlik, op grond van die blaarmorfologie en -anatomie. Die Kaapse gras kan op grond van hierdie variasie in groeivorms in vyf gildes geklassifiseer word wat aangepas is om te oorleef in die digte fynbosplantegroei wat tussen die goedgespasieerde brande in hierdie heideveld ontwikkel. Die volgende gildes word erken: kompetisievermyders wat op rotslyste en klipriwwe groei waar kompetisie van struikagtige plantegroei verminder is; hersaaiers wat die langdurige periodes tussen brande as saad oorleef; geofiete wat hierdie periode in die vorm van ondergrondse organe oorleef; stomplootplante wat as klein plante oorleef; en kompeteerdere wat deur middel van verjongingslote aan die stingels, hoog uitgroei en sodoende met die struikagtige fynbosplantegroei kan kompeteer.

INTRODUCTION

The southern and south-western parts of the Cape Province of South Africa possess a distinct flora, usually called the Cape Flora (Good 1974; Taylor 1978; Goldblatt 1978; Takhtajan 1986). Goldblatt (1978) delimited the geographical area of this flora, and called it the Cape Floristic Region, with the major vegetation type being 'fynbos'. This region is virtually synonymous with the Fynbos Biome (Rutherford & Westfall 1986). This Cape Flora contrasts with the floras of adjacent biomes both in physiognomy and composition. Floristically, apart from the normally common Asteraceae and Fabaceae, it is characterized by the families Proteaceae, Ericaceae, Iridaceae and Restionaceae, with the Mesembryanthemaceae and Crassulaceae dominating in the more arid regions (Goldblatt 1978; Bond & Goldblatt 1984). The levels of endemism are remarkably high, both at species (68%) and at generic (20%) level. The Poaceae, although generally ranking highly in most floras, is only the 13th largest family in the Cape Floristic Region, even with the

inclusion of the exotic pooids introduced from Europe (Bond & Goldblatt 1984).

The Poaceae of the Cape Floristic Region are poorly understood taxonomically and ecologically. The last complete critical taxonomic revision was by Stapf (1899) for the *Flora capensis*, while Chippindall (1955) produced a guide to their identification. Conert (1970, 1971) revised the generic limits of *Danthonia*, which resulted in several new genera being recognized for the region. Recently Gibbs Russell and Ellis (Gibbs Russell 1987a, b; Ellis 1987a, b; Gibbs Russell & Ellis 1987, 1988) have started a programme on *Ehrharta*, and a co-ordinated programme on the arundinoid grasses of southern Africa is under way. Davidse and Ellis have worked on *Tribolium* and *Prionanthium* (Davidse 1988; Ellis 1989), Barker and Ellis on *Pentameris* and *Pseudopentameris* (Barker 1986; Ellis 1985a, b, c, d, 1986), while Linder & Ellis (1990) have commenced a programme on *Pentaschistis*, *Poagrostis* and allied genera. Linder (in prep.) has reviewed the phytogeographical patterns inherent in the grasses of the Cape Floristic Region, showing that several taxa may help elucidate the origins and evolution of the Cape Flora. The distribution, breeding systems and eco-physiology of the Cape grasses have not been studied, and the only ecological information appears

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to be incidental comments in descriptions of vegetation types (i.e. Taylor 1978; Kruger 1979).

The Cape Floristic Region is ecologically very diverse. The climate is essentially Mediterranean, with most of the rain falling in winter, whereas the summers are dry. The amount and seasonal distribution of the precipitation is influenced greatly by the mountain ranges running more or less parallel to the coast. Along the coastal slopes the rainfall is about 1 000 mm p.a., with the drier summers being ameliorated by mist and regular showers. The inland leeward slopes are much drier, with rainfall often less than 250 mm p.a., and with a very hot and dry summer (Fuggle & Ashton 1979). The soils are generally deficient in nutrients, and the combination of dry summers and low soil nutrient status results in slow growth rates for the vegetation as a whole. The vegetation is a shrubland or heathland, from 0.5 to 3 m tall, with a very small herbaceous component, and virtually no annual component (Taylor 1978; Kruger 1979; Campbell 1985). Along the wet coastal ranges the vegetation is dense, with a high basal cover and no bare ground, while along the arid inland slopes the shrubs are well scattered, with ample bare ground which is colonized by annual plants after good winter rains. Although the fynbos vegetation is pyrophytic, fires are spaced well apart, with at least four years between fires, and at most about 40 years, due to the slow biomass build up. The modern average would probably be some 15 years between fires, although it appears likely that in the past the fire cycle could have been much longer (Van Wilgen 1987).

Habit and growth form in the Poaceae have received remarkably little attention in the literature, and consequently there is no generally useful terminology available to describe the vegetative structures. The terms 'tussock' and 'clump' refer to rather similar type structures, and some of the more curious, aerially branching plants have no ready terms. The Cape Poaceae show a remarkable diversity of habits, from the classical caespitose tussock grass to a complex growth form somewhat similar to a divaricate herbaceous plant. These habits appear to be adapted to a range of habitats, both spatial and temporal, in the Cape Floristic Region. They may be highly informative on the ecology and selective restraints operative in the area, and show that these grasses are closely integrated into this unique system, but they have received very little research attention.

Bond & Goldblatt (1984) list almost 200 species of Poaceae for the Cape Floristic Region. Of these, virtually all the endemic species belong to the Arundinoideae in the tribes Arundineae and Ehrharteae. The Pooideae is represented largely by exotic taxa and the Bambusoideae is absent from this biome. Panicoideae and Chloridoideae, although present in fairly large numbers of individuals, have only one endemic species between them, and are scarce in 'typical' fynbos vegetation, but they tend to dominate the grassy fynbos types of the eastern Cape (Campbell 1985; Cowling 1984). The present study is based on the Arundineae, Ehrharteae and Pooideae, indigenous and largely endemic to the Cape Floristic Region. Nomenclature follows that of Gibbs Russell *et al.* (1985), except for *Pentaschistis*, where the nomenclature of Linder & Ellis (1990) is followed.

METHODS

The distributions of the Poaceae species in the Cape Floristic Region were determined from herbarium records using the PRECIS system of the National Botanical Institute, Pretoria (Gibbs Russell 1985a), and the collections of the Bolus Herbarium, University of Cape Town. Whether these grasses were exotic or indigenous was determined following Gibbs Russell *et al.* (1985). Vegetative morphology was also examined on these herbarium specimens. The habit and growth forms of these grasses was classified by recognizing four different base types, two positions for the innovation buds and three different types of leaf morphology. This classification was tested during extensive field work in the spring and summer of 1987, and in the spring of 1988 (August–December). While engaged in these field observations it became apparent that functional correlations exist between the vegetative morphology and the response of these fynbos grasses to fire, and more particularly, to the protracted periods without fire. These long interfire periods in the pyrophytic fynbos vegetation are unusual and the vegetative morphology, together with the fire history data for specific localities led to the recognition of several interfire period survival strategies exhibited by different fynbos grass species. Five different strategies were recognized and this classification was also tested in the field during this period.

Study sites are indicated on Figure 1. The age of the vegetation since the last fire was determined from records of the Chief Directorate of Nature Conservation, from records held in the local offices of Nature Conservation officials, from observations by mountaineers and farmers, and from personal experience of the post-fire successions.

Detailed leaf, culm and base anatomical studies were made from material freshly preserved in FAA in the field, and the vouchers are housed either at PRE (for leaf anatomy) or at BOL (for base and culm anatomy). The results on the anatomy of the bases and culms will be reported separately (Linder, Thompson & Ellis in prep.). Many of the leaf anatomy results have already been published (Ellis 1980a,b, 1982a,b, 1985a–d, 1986, 1987a,b, 1988a,b), whereas studies on *Pentaschistis* leaf anatomy are in preparation (Ellis & Linder in prep.).

Data for a comparison of the Poaceae growth forms of the Cape Floristic Region with those of other biomes was based on species lists available from Gibbs Russell, developed for the analyses of southern African flora and biomes (Gibbs Russell 1985b, 1987c). Growth forms of the savanna and grassland grass species were assigned on the basis of herbarium material. These results are summarized in Figure 2 and on p. 102.

OBSERVATIONS AND DISCUSSION

Base morphology

With the exception of the bamboos, most perennial grasses have herbaceous culms that die back to the base annually and are replaced by shoots arising from axillary basal buds (Gould 1968). The perennial grass 'plant' resulting from several seasons of growth is therefore, made up of several to many lateral shoots initiated at the base.

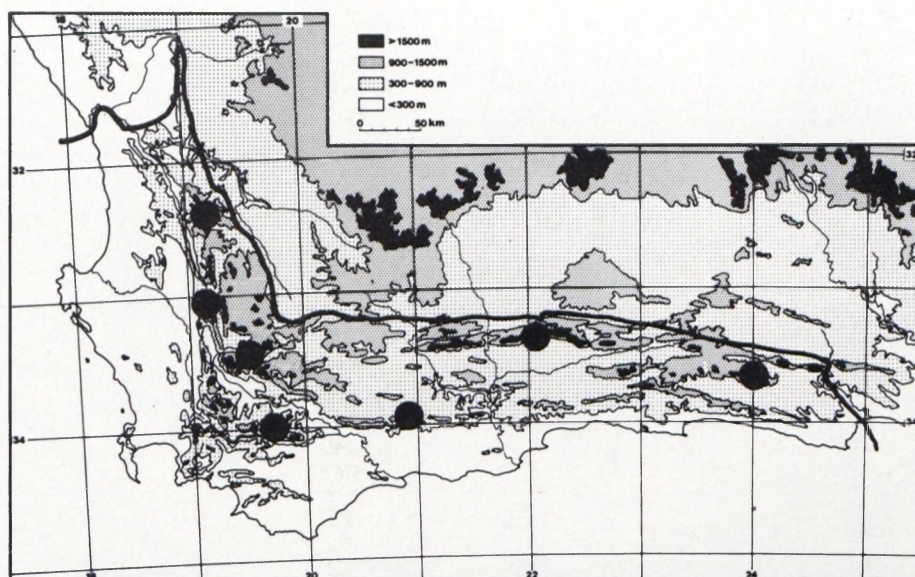


FIGURE 1.—The south-western Cape Province, South Africa. The Cape Floristic Region, as defined by Goldblatt (1978) is outlined by the line, while sample sites are indicated by the dots.

This results in the formation of clones which can reach a spread of 200 m as in *Festuca rubra* (Harberd 1961). By varying the length and thickness of the internodes of this basal portion of the culm, various structures can be developed. In the Cape grasses four different types of base can be distinguished (Figure 3).

1 Bulbous or geophytic bases

The base is modified into a distinct storage organ. This consists of the lowermost culm internode(s) which is generally swollen and tuberous, bulb- or corm-like, and which is usually covered by the fibrous bases of the old leaf sheaths (Burns 1946). The development of these bulbs and corms is rare in the Poaceae (Clayton & Renvoize 1986; Watson & Dallwitz 1988), and occurs in relatively few, unrelated species (Clark & Fisher 1987). In the Cape arundinoids several different structures are found. Bulb-like structures, formed from swollen leaf bases,

occur in *Pentstemon viscidula*, *P. argentea*, *Merxmuel-lera rufa*, and others. In *Pentstemon aristidoides* a stout horizontal rhizome is formed, while in *Ehrharta villosa* portions of the stolons become swollen to form pseudobulb-like structures. These structures are deeply sunken below the level of the soil surface, and are often woolly from the densely hairy leaf sheaths, thus protecting the shoot bases from excessive evaporation or temperature changes (Tsvelev 1976). This could also be a protection against fire damage, or a defence against predators. Plants with these bases rarely form dense tufts, usually bearing a single terminal cluster of leaves and few fertile culms. Bulbous bases are unusually common in the Cape arundinoid grasses, examples being *Merxmuel-lera rufa*, *M. decora*, *Ehrharta capensis*, *E. longifolia*, *E. dura*, *Pentstemon aristidoides*, *P. viscidula*, *P. argentea* and *P. velutina* in the Arundinoideae and *Festuca scabra* in the Pooideae.

2 Knotty tillering bases

The base consists of tightly aggregated clusters of very short internodes, positioned at or just below the soil surface. The whole structure is usually tangled with old leaf bases, which probably play a protective role for the basal buds. There is no clearly differentiated storage organ. The plants are capable of coppicing from this base after fire, and form tussocks (e.g. *Pentstemon pallidus*, *P. pyrophila* and *Merxmuel-lera arundinacea*). If the tillering base is underground, the resulting tussock is often tightly caespitose, as in *P. eriostoma*, *P. pyrophila* and *Merxmuel-lera stricta*.

3 Weak bases

In this category only a few perennial culms arise from a basal node. The basal internode(s) is not swollen into storage organs, but sometimes associated swollen rhizomes occur (e.g. *Ehrharta setacea* and *E. villosa*). The plants developed from weak bases are usually loosely tufted, short-lived perennials, with branching culms which are decumbent at the base. This stooling (Gould 1968) gives a 'cushion' type of growth. Selected examples of this type of base are *Pentstemon pallida* form B, *P. densifolia*,

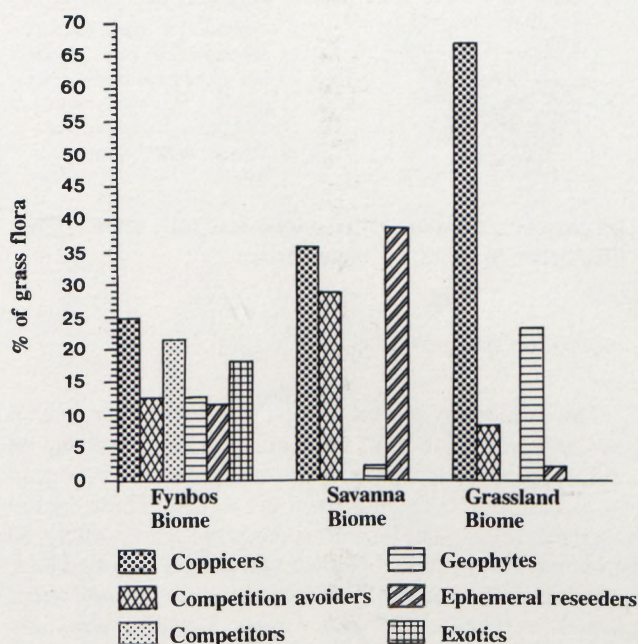


FIGURE 2.—Relative occurrence of growth forms of Poaceae in the Fynbos, Savanna and Grassland Biomes of southern Africa.



FIGURE 3.—Variation in the base structures of the fynbos arundinoid grasses. A, knotty tillering base, *Pentaschistis pyrophila*; B, geophytic base, *Merxmuellera rufa*; C, disc-like tillering base, *Pentaschistis ampla*; D, weak base, *P. densifolia*; E, annual base, *P. airoides* subsp. *airoides*. All $\times 0,4$.

P. rosea subsp. *rosea*, *P. alticola*, *P. aspera*, *P. acinosa*, *Ehrharta rupestris* and *E. setacea*. These weak bases are very similar to annual bases in that the rooting system is weak, and no thickened woody structures are found.

(*Pentaschistis rosea*, *P. pseudopallescens*), showing the link between these and weak bases.

Innovation bud position

4 Annual bases

In grasses with annual bases the primary shoot arises directly from the base, and few lateral innovation shoots develop further up the culms. The base never becomes woody. Annual grasses are rare in the mountains on the most nutrient-poor soils (Kruger 1979), but are better diversified on the arid margins of the Cape Floristic Region (*Pentaschistis airoides* subsp. *airoides*, *P. aristifolia*, *P. capillaris*, *Urochlaena pusilla*, *Ehrharta brevifolia* and *E. pusilla*). Biennials and triennials are found in the mountains. These also have the annual type of base

The culm is the axis on which the inflorescence as well as the leaves are borne. Each culm is terminated by an inflorescence, and the next season's growth is produced by lateral shoots arising from the nodes. These lateral shoots develop from innovation buds, which are enclosed and protected by the prophyll, a two-keeled modified leaf, which is located adaxially at the base of each lateral shoot (Clark & Fisher 1987). Different growth habits are determined by the position of these perennating buds and their resultant lateral shoots. Two basic variants can be recognized (Figure 4).

1 Basal innovation shoots

Basal innovation shoots develop from buds at the base of the plant. These produce culms which are annual, dying back to the upper tillering node after completion of flowering. All internodes above this node perish, and those below are persistent. This is the common situation in grasses (Gould 1968; Tsvelev 1976), and this tillering produces erect or decumbent lateral culms and the caespitose habit, usually as a result of intravaginal branching. After flowering the culms and leaves senesce, and are eventually replaced by a new basal innovation shoot. These basal innovation shoots are usually associated with knotty tillering bases. Plants with bulbous bases also innovate from the base, but these are deeply subterranean.

Grasses with this type of lateral shoot innovation essentially have an annual above-ground component.

Although generally grass leaves senesce after only a few months, many of the Cape grasses have leaves that persist for at least a year. The underground parts are strongly perennial, and may continue to grow for many years, reaching ages of up to 1000 years in *Festuca ovina* (Harberd 1962). This type of growth form is well adapted to the regular annual or biennial fires characteristic of the subtropical savannas and grasslands. In the Cape Floristic Region examples of this growth form are *Pentaschistis glandulosa*, *P. pyrophila*, *Ehrharta calycina*, and the species listed as having bulbous bases.

2 Cauline innovation shoots

Cauline innovation shoots are produced from nodes higher upon the culms. These culms are generally long-lived, and the above-ground component is perennial, resulting in an 'evergreen' plant. This is an unusual



FIGURE 4. —Variation in the position of the innovation buds in the fynbos arundinoid grasses. A, caulescent innovation buds in a 'competitor', *Pentameris squarrosa*; B, basal innovation buds along creeping rhizomes, *Pentaschistis galpinii*; C, basal innovation buds, forming a caespitose plant, *Pentaschistis curvifolia*; D, innovation buds at the ends of thin erect culms, in an old plant of *Pentaschistis colorata*, forming a cushion. All $\times 0,4$.

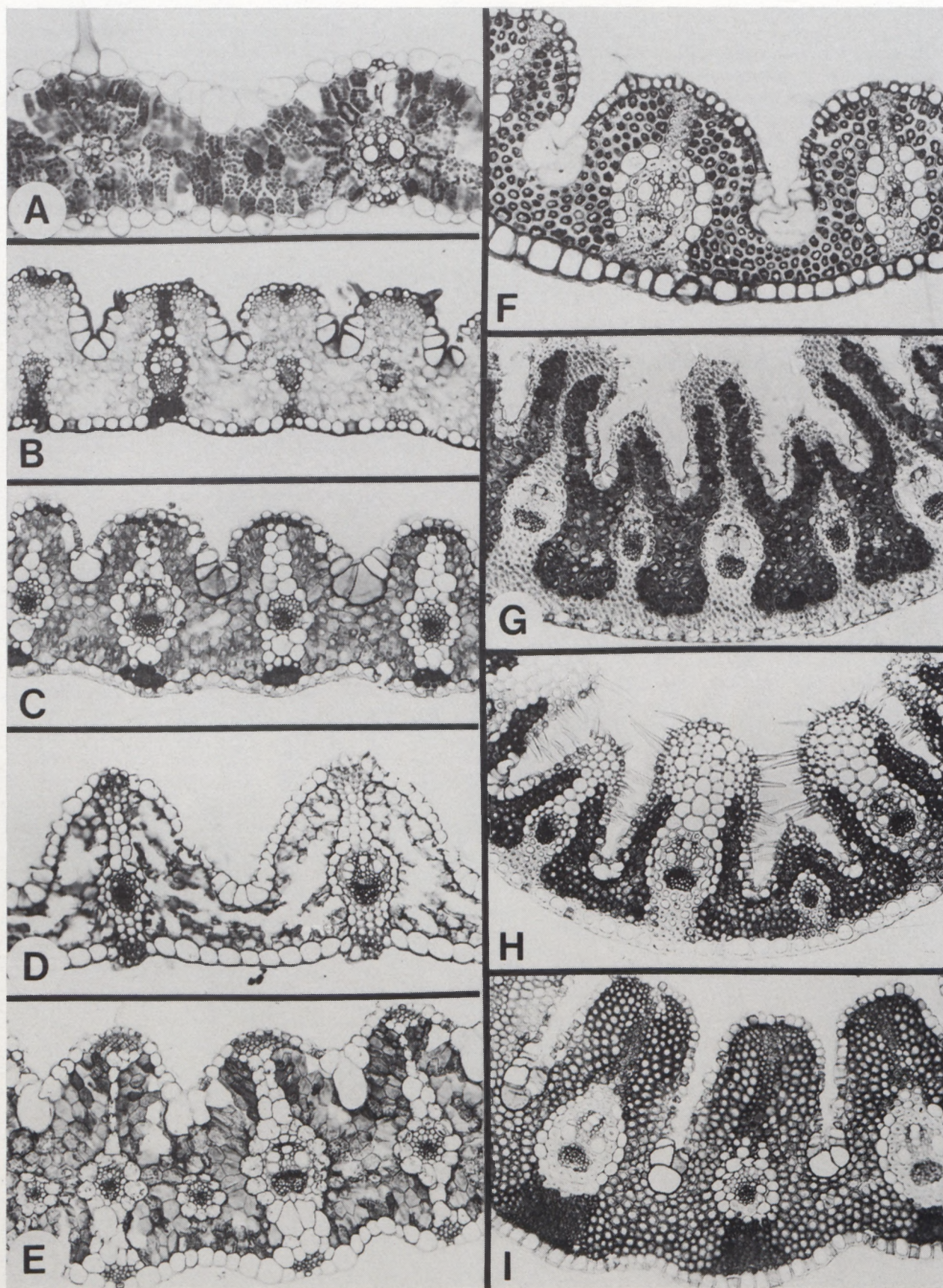


FIGURE 5.—Transverse sections of the leaves of the fynbos arundinoid grasses, illustrating variation in leaf type. A–E, mesic or orthophyllous leaf type; F–I, sclerophyllous leaf type. A, *Ehrharta brevifolia*, with large chlorenchyma cells and intercellular air spaces; B, *Pentaschistis papillosa*, with discrete sclerenchyma girders and strands; C, *Tribolium uniolae*, chlorenchyma cells relatively large and angular but air spaces reduced, intermediate type; D, *Festuca scabra*, typical pooid mesic anatomy with very diffuse mesophyll and widely spaced vascular bundles; E, *Chaetobromus involucreatus*, mesic leaf anatomy; F, *Ehrharta setacea*, compact mesophyll of isodiametric cells; G, *Pentaschistis eriostoma*, compact mesophyll, bundles close together and continuous hypodermal sclerenchyma; H, *Pentameris macrocalycina*, compact mesophyll of small cells and few intercellular air spaces, sclerenchyma girders well developed; I, *Merxmüllera rufa*, compact sclerenchyma typical of sclerophyllous leaf type. All $\times 250$.

situation in herbaceous grasses (Gould 1968). Branching culms are very rare in the Pooideae, but there are exceptions in the Andropogoneae (Clayton & Renvoize 1986), Paniceae and particularly the woody Bambuseae (Roshevits 1937). The branching may be profuse with secondary and even tertiary branches. The bases of the species with cauline innovation shoots are either of the weak or of the knotty tillering type. These species also appear to be able to innovate from the base, and so survive fires by coppicing.

Three different patterns appear to occur in the cauline innovating species. In one group, the culms are more or less erect, and the branches well spaced. This results in a 'divaricate herb', which might function in allowing the plant to grow taller than species with only basal innovation shoots (i.e. *Pentaschistis aspera*, *P. acinosa*, *P. scandens*, *Pseudopentameris macrantha*, *P. brachyphylla*, *Pentameris thuarii* and *P. squarrosa*). In the second group the culms are more or less decumbent (at least at the base), and the branches mostly occur near the base of the culms. These plants develop into cushions, often low on the ground. Good Cape examples of this are *Pentaschistis densifolia*, *P. rosea* subsp. *purpurascens* and *P. alticola*. In the third group the plant is initially caespitose, with basal innovation shoots. As the plant becomes older, the innovation shoots are found further from the base of the plant, and a distinct, and sometimes quite long, stem section is found between the woody rootstock and the branching system. This transforms the plant from caespitose to tangled. This pattern is shown most clearly by *P. colorata*, but is also seen in Cape plants of the widespread *Themeda triandra*.

Leaf morphology

The leaf anatomy and morphology of grasses is very important taxonomically, but ecologically three leaf forms may be distinguished in the Cape Floristic Region (Figure 5).

1 Caducous leaf blades

In some species of *Ehrharta* the leaf blade is either early deciduous, or is represented by a small mucro at the apex of the sheath. The leaf sheaths are generally well developed, and together with the culms constitute the photosynthetic organs of the plants. These suffrutescent species are remarkable structural mimics of the Restionaceae.

2 Sclerophyllous leaves

Sclerophyllous leaves (Ellis 1988a) persist for more than one growing season, and possibly even for several years. These are tough, leathery leaves, typically permanently inrolled and filiform or acicular with no abaxial stomata and very compact mesophyll of small isodiametric chlorenchyma cells with minute intercellular air spaces. Sclerenchyma tissue is abundant and may be either lignified or with cellulose walls (Figure 5F–I). This type of leaf appears to be analogous to the sclerophyllous leaves which are characteristic of the vegetation of the Cape Floristic Region, particularly with vegetation growing on the nutrient-deficient sands of the mountains. This type

of blade structure probably helps to 'safeguard' the scarce nutrient resources. All species of *Merxmüllera* and *Pentameris*, as well as many species of *Pentaschistis* have this type of blade.

3 Mesic leaves

Mesic leaves do not persist for more than one growing season. They are typically soft and expanded with abaxial stomata and diffuse mesophyll, and with an extensive air space system. Sclerenchyma tissue is only associated with the vascular bundles as strands or girders (Figure 5A–E). This leaf type is common on soils with better nutrient status. The pooid exotics all have mesic type leaves, and indigenous taxa with mesic leaves (e.g. *Chaetobromus* and *Tribolium*) are lowland taxa associated with intermediate nutrient status soils. However, many species of *Pentaschistis* with mesic leaves are widespread in the Cape mountains. These mesic leaves of the Cape fynbos grasses appear to be analogous to the 'orthophyllous leaves' of Campbell (1985) although the first term refers to habitat and the second to the texture of the leaves.

Interfire survival strategies

The vegetation of the Cape is a shrubby heathland, dominated by Restionaceae, Ericaceae and Proteaceae (Taylor 1978). These fynbos plants are evergreen, generally highly divaricated, and they form a relatively dense shrubbery of 1–3 m tall. The vegetation burns on a variable cycle of between four and 40 years, as vegetation less than four years old rarely has adequate fuel to burn (Van Wilgen 1987). Grasses in general are well adapted to withstand fire, and tropical grasses in particular, become moribund if not burnt regularly. These tropical grasses generally are subject to annual, biennial or triennial fires and their growth forms and habits undoubtedly are determined largely by this regular incidence of fire.

Ecological studies on the vegetation of the Cape Floristic Region have generally emphasized the various methods by which the flora survives the sporadic fynbos fires (e.g. Manders & Cunliffe 1987). However, in the case of the grasses, in addition to surviving the fires themselves, survival in the dense, shrubby fynbos vegetation that develops during the long interfire periods appears to be a major constraint. Immediately after fire, perennial grasses generally are an important component of the regenerating fynbos vegetation, even though this family is virtually absent in mature fynbos prior to burning. After a burn the vegetation gradually becomes denser, generally passing through dominance by the Restionaceae, then the Ericaceae, and finally the Proteaceae (Kruger 1977). This mature, dense vegetation excludes herbaceous species, and so also the grasses. There appear to be five ways in which the grass species of the Cape have responded to this situation.

1 Competition avoiders (Table 1)

These species exploit habitats where taller woody plants cannot grow. Such habitats are either in streams, or in rock crevices and ledges. In these harsh conditions the grasses compete with mosses, a few herbaceous evergreen species and geophytic orchids. The protection from fire offered by these habitats appears to be incidental. Some species are totally restricted to these habitats (e.g. *Pentaschistis*

TABLE 1. — Distribution of growth form and survival strategy in the competition avoider Cape grasses. The vegetation types are approximate and follow Moll *et al.* (1984)

Species	Base type	Innovation buds/shoots	Leaf type	Habitat
<i>Pentaschistis rigidissima acinosa</i>	weak; forming low cushions	cauline	sclerophyllous	Mesic Mountain Fynbos, cliffs and ledges
<i>Pentaschistis capensis</i>				Lower altitudes in streams and waterfalls
<i>Pentaschistis malouinensis</i>		basal		Mesic Mountain Fynbos
<i>Pentaschistis aspera papillosa</i>	weak	cauline only	mesic	Mesic Mountain Fynbos, low altitude
<i>Pentaschistis densifolia pusilla</i> <i>Anthoxanthum dregeanum tongo</i> <i>Brachypodium distachyon</i>	weak; often with rhizomes	basal and cauline		Mesic Mountain Fynbos
<i>Pentaschistis eriostoma</i>	tillering	cauline	sclerophyllous	variable

rigidissima, *P. acinosa*). Other species colonize soil exposed after fire, but soon succumb to the rapidly growing shrubby vegetation. *Pentaschistis densifolia*, *P. malouinensis*, and often *P. eriostoma* fall into the latter category.

Typically, the avoiders are short, cushion forming plants with weak bases, cauline innovation shoots, and sclerophyllous leaves. They are generally restricted to higher altitudes in the mountains (possibly because of the availability of crevices). *Pentaschistis eriostoma* and *P. malouinensis* are both rather widespread, and ecologically flexible. *P. eriostoma*, in particular, can vary from a typical vegetation avoider at higher altitudes, to a classical tussock grass on the arid fringes of the Cape Flora. Some vegetation avoiders deviate from the above description by the possession of mesic leaves, and often also basal innovation shoots. *Pentaschistis densifolia* and *P. pusilla* are arundinoid examples, while most of the 'avoider' pooids also fall into this category (*Anthoxanthum dregeanum*, *A. tongo* and *Brachypodium distachyon*).

The only true graminoid hydrophyte in the Cape is *Pentaschistis capensis* which is found over a wide altitude range, but always growing on rocks and stones in perennial streams, often draped over waterfalls. For this species it is then not clear whether it is avoiding drought or competition from woody vegetation.

2 Reseeders (Table 2)

This group can be defined as those taxa that survive the interfire period as seed. The seed germinates after fire and

grows into annual or short-lived perennial plants that survive for 1–3 years before being forced out by the recovering fynbos vegetation. The grass plants die, leaving their seed till the next fire, which may not be for 25 years, and possibly longer. Whether the species survive as seed banks, or whether they depend on regular dispersal is not clear. If they survive as seed banks, the mechanisms by which the seed is protected for such an extensive period requires attention.

Within the Cape Floristic Region several different reseed strategies exist. True annuals (ephemerals) are found only on the arid fringes of the Region. This includes the West Coast Strandveld (Moll *et al.* 1984) and the Succulent Karoo (Acocks 1988). In these vegetation types soil nutrient levels are higher, but low rainfall prevents the development of a dense basal cover, so that there is ample open ground between the scattered bushes, where annual grasses can grow following adequate rainfall. *Pentaschistis airoides* subsp. *airoides*, *P. aristifolia*, *P. capillaris*, *Urochlaena pusilla*, *Stipa capensis*, *Ehrharta brevifolia*, *E. longiflora*, *E. pusilla*, *Tribolium utriculosa* and *T. echinata* are annual arundinoid species of these arid regions. This is possibly the closest analogue to the true Mediterranean conditions of southern Europe and northern Africa to be found in the winter rainfall region of the Cape. These are not strictly postfire annuals and usually function as interfire annuals as well.

Fynbos postfire reseeders are not true annuals, in that they do not germinate annually, although the plants themselves only grow for a single growing season. *Pentaschistis pseudopallescens*, *P. rosea* and possibly

P. alticola are biennial or triennial, which flower in the second year after fire. They occur above 1 000 m on nutrient-poor and leached soils in the western Cape mountains, and it is possible that these slow development times may be due to the poor soil nutrient status, and the harsh growing conditions. *P. pallida* form B and *P. trisetata* are reseeders which flower in the first year and are found at lower altitudes, in warmer conditions, and on less leached soils. Both groups appear to be facultative perennials, depending on the severity of the summer droughts. If the plant survives the summer, and is not shaded out by the growing vegetation, it may flower for a second year. These species may totally dominate the vegetation after the fires. They all have weak or annual bases, basal innovation shoots and mesic leaves.

3 Geophytes (Table 3)

This group of species behaves like typical geophytes, appearing early in the first winter or spring after fire and flowering profusely soon after commencing growth. By the second post-fire season they are not as prominent and flower less profusely. When they become overshadowed by the regenerating woody vegetation, they appear to survive the protracted interfire period by means of their swollen, subterranean storage organs. It appears as if flowering depletes the base, but that subsequent photosynthesis may replenish the storage products (Hodgkinson & Williams 1983). However, research is still required to follow the cycle of flowering and photosynthate accumulation and translocation, both in these grasses and in analogous groups, such as *Watsonia* in the Iridaceae. The factors controlling flowering and dormancy are not understood. The stored products allow the plants to flower almost

immediately after fire, while the reseeders apparently have to spend the first year accumulating sufficient reserves to support a flowering episode.

The Cape flora is remarkably rich in geophytic grasses. These species tend to dominate areas that are frequently burnt or bush-cut, like fire-breaks. This survival strategy is undoubtedly effective and the methods of overcoming damage by herbivores are poorly understood. These geophytic grasses are probably an important food source for mole-rats, a possibility which needs to be investigated (Lovegrove & Jarvis 1986). Examples are *Pentaschistis viscidula*, *P. argentea*, *P. velutina*, *Merxmüllera rufa*, *M. decora* and *Ehrharta longifolia*. Morphologically, they all have bulbous, subterranean bases, basal innovation shoots and sclerophyllous leaf blades, although these leaves are unusual in having abaxial stomata. *Pentaschistis aristoides* probably also belongs to this group, but is unusual in that the base is developed as a rhizome. *Ehrharta dura*, *E. microlaena*, *E. capensis* and *Festuca scabra* differ from the typical type described above by their mesic leaf anatomy.

4 Coppicers (Table 4)

These species survive the interfire period as persistent, almost dormant, moribund plants. After a fire, they coppice from the base and then flower late in the first spring or summer. The plants then persist above ground without, or with very little, subsequent flowering. They are often evident in the mature vegetation, persisting in the vegetative state as weak moribund tussocks. Presumably, if the interfire period is too long, the plants will eventually die. This form is then usually found at higher

TABLE 2. — Distribution of growth form and survival strategy in the ephemeral reseed Cape grasses. The vegetation types are approximate and follow Moll *et al.* (1984)

Species	Base type	Innovation buds/shoots	Leaf type	Habitat
<i>Pentaschistis trisetata</i>	annual; true annual	basal	mesic	Lowland Fynbos
<i>Pentaschistis pallida</i> form B <i>barbata</i>	weak; short-lived perennials	basal and cauline		
<i>Pentaschistis rosea</i> <i>pseudopallescens</i> <i>pungens</i>	weak; biennials and short-lived perennials		mesic to intermediate	Mesic Mountain Fynbos
<i>Pentaschistis airoides</i> subsp. <i>airoides</i> <i>aristifolia</i> <i>capillaris</i> <i>Ehrharta brevifolia</i> <i>delicatula</i> <i>longiflora</i> <i>pusilla</i> <i>triandra</i> <i>Tribolium echinata</i> <i>utriculosa</i> <i>Urochlaena pusilla</i>	annual; true ephemerals		mesic	Succulent Karoo and Strandveld

TABLE 3.—Distribution of growth form and survival strategy in the geophytic Cape grasses. The vegetation types are approximate and follow Moll *et al.* (1984)

Species	Base type	Innovation buds/shoots	Leaf type	Habitat
<i>Pentaschistis</i> <i>aristoides</i> <i>argentea</i> <i>velutina</i> <i>viscidula</i> <i>Merxmuellera</i> <i>decora</i> <i>lupulina</i> <i>rufa</i> <i>Ehrharta</i> <i>longifolia</i>	bulbous; corms	basal	sclerophyllous; with abaxial stomata	Mesic Mountain Fynbos
<i>Ehrharta</i> <i>dura</i> <i>microlaena</i>			mesic	Mountain Fynbos, lower altitudes
<i>Ehrharta</i> <i>capensis</i> <i>melicoides</i> <i>Festuca</i> <i>scabra</i>				

TABLE 4.—Distribution of growth form and survival strategy in the coppicing Cape grasses. The vegetation types are approximate and follow Moll *et al.* (1984)

Species	Base type	Innovation buds/shoots	Leaf type	Habitat
Pentaschistis colorata tortuosa eriosoma ampla Pentameris macrocalycina dregeana obtusifolia	tillering	cauline	sclerophyllous	Mesic Mountain Fynbos
Pentaschistis pyrophila				
Pentaschistis curvifolia malouinensis	basal			
Ehrharta calycina Pentaschistis rupestris glandulosa			mesic	
Pentaschistis pallida form F tomentella				Dry Mountain Fynbos
Pentaschistis cirrhulosa calcicola				
Merxmuellera arundinacea dura cincta stricta	tillering		sclerophyllous	Renosterveld

altitudes where the mature vegetation is not very dense, and where recovery rates are slower.

Pentaschistis pyrophila and *Pentameris obtusifolia* are typical examples utilizing this survival strategy. They have knotty tillering bases, basal innovation shoots and sclerophyllous leaf anatomy. Other species which utilize this strategy, but not exclusively so, are *Pentaschistis colorata*, *P. tortuosa*, *P. eriostoma* and *P. ampla*. *Pentaschistis curvifolia*, *P. malouinensis* and *Ehrharta calycina* may also best be placed into this group, despite their weak bases.

This group overlaps to some extent with other strategies, and is often difficult to define. Many species that form large, persistent tussocks in the more open vegetation at lower altitudes are probably best placed into this group, despite the absence of direct evidence of coppicing after fire. This would include *Pentaschistis rupestris*, *P. pallida* form F, *P. glandulosa*, *P. tomentella*, *P. cirrhulosa*, *P. calcicola*, *Merxmuellera arundinacea* and *M. cincta*. These lower altitude species are generally not shaded out during the interfire period, but this is because of the sparse vegetation in which they grow, rather than any special morphological adaptations that they may have.

5 Competitors (Table 5)

This small, specialized group of grasses appears to be able to compete with low mature fynbos. The plants have

branching culms capable of almost indefinite growth. After flowering has terminated the growth of a culm, a lateral branch continues growth from an upper leaf innovation bud. New leaves are continually formed near the top of the culms with the basal portions being covered by senesced leaf sheaths. These plants may either be tall (up to 2 m) and erect, as in *Pseudopentameris macrantha*, *Pentameris macrocalycina* and *P. thuarii*, or trailing through the vegetation as in *Pentameris squarrosa*, *Pentaschistis scandens* or some of the *Ehrharta* species. These species do not appear to gain in biomass with successive seasons (probably due to limiting nutrients) but gain in height with a reduction in culm diameter and leaf size. In old plants the leaves may be less than 1/4 the length of those produced in the first post-fire season, but the plant may have doubled in height. Flowering is most frequent in the first year after fire and gradually diminishes in later years.

The group of suffrutescent species belonging to the Villosa and Ramosa groups of *Ehrharta* are also competitors, mostly at higher altitudes. These are remarkably similar to the Restionaceae, with reduced, caducous leaves and photosynthetic culms.

Members of this specialized group all have the weak type of base and cauline innovation shoots. The leaves vary from sclerophyllous for most of the higher altitude taxa, or caducous (associated with suffrutescent culms) in some species of *Ehrharta*, to almost mesic in some

TABLE 5. — Distribution of growth form and survival strategy in the competitor Cape grasses. The vegetation types are approximate and follow Moll *et al.* (1984)

Species	Base type	Innovation buds/shoots	Leaf type	Habitat
Ehrharta ramosa rehmannii gigantea	weak	cauline, tall, erect plants	caducous blades	Mountain Fynbos
Ehrharta villosa				Lowland Fynbos
Pentameris dregeana macrocalycina longiglumis obtusifolia Pentaschistis colorata tortuosa			sclerophyllous	Mesic Mountain Fynbos
Pentameris squarrosa thuarii Pseudopentameris macrantha brachyphylla			intermediate	Mesic to wet Mountain Fynbos, lower altitudes
Ehrharta setacea rupestris		cauline, short plants	sclerophyllous	Mountain Fynbos, high altitudes
Ehrharta barbinodis		cauline	intermediate	Succulent Karoo

low-altitude competitors. It is not clear how long these species are capable of persisting in unburnt vegetation, as some show signs of senescence. However, this may depend on the density of the local variant of fynbos. It is this group which shows the greatest deal of convergence with the Restionaceae.

Comparison with other biomes

The spectra of interfire survival strategies found in the Cape are compared in Figure 2 with those of the Grassland and the Savanna Biomes as defined by Gibbs Russell (1985b, 1987c). Direct comparison is difficult, as the enormously different physiography of the different biomes may bias for different growth forms. In addition, the relative frequency of fires in the other biomes suggests that tall and dense interfire vegetation is not a factor, as fire intervals are never as long as 10 years. However, a comparison is still illustrative of how diverse the Cape grasses are in vegetative morphology and ecology in comparison with tropical grasses. From Figure 2 it is abundantly clear that correlated with the extended fire intervals in the fynbos is the occurrence of the 'competitor strategy', which is totally absent from the other biomes. Competition avoiders in the other biomes are all hydrophytes, but in the Cape Floristic Region only one species is a hydrophyte, the rest being lithophytes restricted to ledges and crevices. These are, therefore, true vegetation avoiders, compared with the tropical hydrophytes. Geophytes are remarkably common in the Grassland Biomes as well as the fynbos, and the underground storage of photosynthate in grasses may be worthwhile investigating in more detail. Reseeders are understandably more significant in the Savanna Biome than in both fynbos and grassland where rainfall is usually not limiting. However, the relatively large number of exotic pooids in the fynbos tends to obscure this fact.

CONCLUSIONS

The Poaceae endemic to the fynbos show a range of structural and morphological adaptations which allow them to survive in a variety of niches in the Cape vegetation. Some growth forms allow direct competition with the shrubby Cape Fynbos, while others allow plants to survive the dense interfire vegetation either as seed, as geophytes or as small dormant plants. The models postulated here should contribute to the development of a better understanding of the unique selective forces operative in the fynbos.

The Poaceae in the Cape show a vegetative plasticity not expected from grasses. Unusual growth forms have previously been documented in some arundinoid grasses such as *Steyermarkochloa* (Davidse & Ellis 1985) and *Arundoclaytonia* (Davidse & Ellis 1987) but, apart from the woody bamboos, extensive cauline branching is basically unknown in the family. The arundinoids do have a wide range in habit, from annuals to reed-grasses like *Phragmites* (Renvoize 1981). It is therefore not unexpected that the arundinoids have developed the specialized habits to cope with the Cape Fynbos, whereas the indigenous pooids and other subfamilies have been relatively unsuccessful in the Cape. Exotic pooids, on the other hand, are particularly successful in the Cape but, noticeably, not in the natural flora but in areas of physical disturbance.

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