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

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

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

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

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

![Map of the study area in the Humansdorp district showing the numbered study sites in each community (see Table 1).](Image)

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

### Table 1 Vegetation and soil data for the study sites

| Site number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|-------------|---|---|---|---|---|---|---|---|
| Vegetation order | South Coast Dune Fynbos | Kaffrarian Thicket | South Coast Dune Fynbos | South Coast Dune Fynbos | Thamnochorus glaber-Nepeta diaphana | Thamnochorus fruticosus-Fractia fruticosa | Kaffrarian Thicket | South Coast Renosterveld |
| Community | Restio elenochoris-Agathosma stenopetala | Cassine aethiopica-Cassine wrightii | Restio elenochoris-Agathosma stenopetala | Cassine aethiopica-Cassine wrightii | Thamnochorus glaber-Nepeta diaphana | Thamnochorus fruticosus-Fractia fruticosa | Agathosma stenopetala | Elytropappus rhinocerotis-Metrosideros muricata |
| Dominant species | Agathosma stenopetala, A. apiculata, Restio elenochoris, R. pilippen, Passerina vulgaris | Sideroxylon inerme, Petrosedwardsia tripartita, Cassine aethiopica, Olea exasperata | Thamnochorus triandra, Stenotaphrum secundatum, Passerina vulgaris, Rhys oegon | Thamnochorus glaber, Restio trinervis | Erica diaphana, E. pecinifolia, Leucadendron salignum, Thamnochorus glaber, Restio trinervis | Themeda triandra, Triaschach leucostachys, Thamnochorus fruticosus, Elytroplax vaginulata | Themeda triandra, Elytropappus rhinoceros, Rhus carica, Potamogeton angustifolia | Themeda triandra, Sporobolus africam, Cynodon dactylon, Pemphiasis angustifolia |
| Vegetation structure | Low closed ericoid shrubland with open restioid overstorey | Mid-high closed large leaved shrubland | Closed grassland with low sparse ericoid shrub overstorey | Mid-high closed ericoid and proteoid shrubland with open restioid overstorey | Closed restioid grassland with low sparse ericoid shrub overstorey | Tall closed large leaved shrubland | Low open grassy small-leaved shrub overstorey | Closed grassland with sparse dwarf small-leaved shrub overstorey |

| Soil properties | Excessively drained, moderately fertile, fine calcareous dune sand | Excessively drained, moderately fertile, medium, calcareous dune sand | Seasonally waterlogged, moderately fertile, fine, calcareous dune sand | Excessively drained, infertile, acid, coarse sand | Seasonally waterlogged, infertile, acid, medium sand | Well drained, fertile soil | Poorly drained, (duplex) moderately fertile, loam | Seasonally waterlogged, (duplex) moderately fertile loam |
| Soil description and depth (m) | >3 | >3 | 1,5 | 1,1 | 1,5 | | | 0,5 |
| Soil form and series | Fernwood Motopio | Fernwood Motopio | Fernwood Motopio | Constantia Stenombols | Longlands Orkhoy | Clovelly | Glenrosa Willamson | Swartland Bridbach |
| Geology | Recent sand | Recent sand | Recent sand | Table Mountain Group sandstone | Table Mountain Group sandstone | Bokkeveld shale | Bokkeveld shale | Bokkeveld shale |
| H2O holding capacity (g) | 27.6 | 48.6 | 29.8 | 40.2 | 69.3 | 42.1 | 40.9 | 40.9 |
| pH | 7.7 | 7.6 | 7.6 | 4.2 | 4.3 | 5.1 | 5.3 | 5.3 |
| Na (ppm) | 44 | 193 | 130 | 34 | 119 | 196 | 182 | 379 |
| K (ppm) | 40 | 63 | 98 | 31 | 34 | 414 | 240 | 129 |
| Ca (ppm) | 1918 | 2031 | 3039 | 186 | 209 | 2168 | 756 | 712 |
| Mg (ppm) | 57 | 246 | 309 | 58 | 172 | 773 | 264 | 427 |
| S values (m-equiv.) | 10,3 | 13,3 | 18,6 | 1,65 | 3,9 | 19,16 | 7,38 | 9,10 |
| Oxidizable C (%) | 2,4 | 4,5 | 7,4 | 3,2 | 3,5 | 18,6 | 5,1 | 5,0 |
| Total N (%) | 0,075 | 0,102 | 0,305 | 0,046 | 0,089 | 0,443 | 0,124 | 0,195 |
| Available P (ppm) | 35,7 | 15,1 | 15,6 | 1,5 | 3,9 | 25,7 | 2,0 | 3,3 |

*References to site marked on map (Figure 1)*
*Vegetation orders and communities sensu Cowling (1983a); names below binomial in column 3 are those used in the text*
*Structural characterization sensu Campbell et al. (1981)*
*Soil classification sensu MacVicar et al. (1977)*
*Weight absorbed at saturation by 100 g soil (Piper 1959)*
*Sum of exchangeable cations (1 mol dm-3 NH4 acetate leachate)*
*Walkley-Black method*
*Kjeldahl method*
*Modified Olsen (alkali extraction, pH 8) for 1–3 Bray No. 2 (acid extraction, pH 3) for 4–8*.
fourteen years respectively, according to records kept by the landowners. The thickets on shale and dune sand were probably unburnt for fifty years or longer.

Climate
The climate is warm temperate and transitional between Koppen Csa and Csb climates (Specht & Moll 1983). Most rain is cyclonic and associated with fronts from the circumpolar westerly belt. The study area is usually included in the non-seasonal rainfall region although the three summer months (December – February) are always the driest (Figure 2b). Bond (1980) has shown that semi-arid and subhumid climates in the Cape constant rainfall region have an effective moisture regime that is unequivocally mediterranean as typified by moisture surpluses in winter and deficits in summer (Figure 2b). The warmest month at Cape St. Francis is February (mean monthly temperature of 19.9 °C) and the coolest is July (14.2 °C). Highest and lowest mean temperatures are 29.7 °C (in April) and 5.0 °C (in August) respectively (Anon 1942). Frost is uncommon. The area is subject to strong winds and occasional gales at any time of the year. Evaporation and radiation are clearly highest in the summer months (Nov – Feb) (Figure 2a). As all sites are on level ground, the radiation regime was assumed to be similar for all vegetation types. During the study (1981), exceptionally heavy precipitation resulted in doubling the average annual total and rainfall was unequivocally bimodal (Figure 2c).

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

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

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

Table 2 Growth form classes

| Herbaceous growth forms | Woody growth forms |
|-------------------------|--------------------|
| Annuals | Small leaved shrubs<sup>a</sup> (Campbell et al. 1983) |
| Geophytes | Large leaved shrubs<sup>b</sup> (Campbell et al. 1983) |
| Non-geophytic forbs | Proteoids<sup>c</sup> |
| Graminoids | Thicket species<sup>d</sup> |
| Grasses (Poaceae) | |
| Cyperoids | |
| Restios (Restionaceae) | |
| Proteoids (Proteaceae) | |

<sup>a</sup>Most species have sclerophyllous leaves
<sup>b</sup>Isobilateral sclerophyll leaves (all species are Proteaceae)
<sup>c</sup>Dorsiventral sclerophyll leaves (components of Subtropical Transitional Thicket (Cowling 1983a)).

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

In this way we made qualitative observations at monthly intervals on a total of 173 species in the eight communities shown in Table 1 during the period January 1981 – April 1982. Observations were made on 3–5 individuals of each species. In addition, successive monthly measures of shoot length increments on 20 of the selected species were made to show peak growth periods. To do this we tagged two shoots and measured their lengths on each of six specimens of each shrub species. Shoot elongation on two shoots per ten tufts of each woody species was monitored. Twelve shoots of different grass tufts were tagged and the number of tillers and/or leaves per shoot were counted, depending on the species' growth habit. To measure growth of the arboreal rose succulent, <i>Aloe africana</i>, we recorded the length of the three newest leaves on six tagged specimens. Leaf fall of selected species was measured by placing traps (200 mm diameter) beneath each of two specimens. Leaves trapped during each sampling interval were air-dried to a constant mass and weighed. At each sampling we also recorded all geophytes within a set area of 95 m<sup>2</sup> in each community.

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

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

**Results and Discussion**

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

**Evaluation of methods**

In Figure 11 the two methods of determining growth are given: bar graphs denote the percentage of observed individuals growing at any one sampling time while detailed increments are expressed as five-number summaries. The bar graphs simply indicate that most of the growth of both species occurs from autumn, through winter to spring. The five-number summaries, however, reveal the bimodal nature of this cooler season growth on the loam soil. Low shoot increment in *Pterocelastrus tricuspidatus* in September (Figure 11a) and in *Sideroxylon inerme* in October (Figure 11d) coincided with a high percentage of shrubs showing growth (Figures 11b and e). This ex-
Empirifies the point raised earlier that different measures give different peaks. In this case, however, the results of the two methods are not contradictory; a high proportion of shoots could be growing but their growth, expressed as shoot increment, could be minimal.

**Effects of substrate on phenophase**

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

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

The tendency for earlier initiation of phenophases in the loam soils might be explained by the higher water-holding capacity of the loam (42.1 g per 100 g H₂O) relative to the dune sand and acid sand (27.6 and 29.8 g per 100 g H₂O respectively) (Table 1). After a light rainfall, more moisture would be held in the loam than in the excessively drained sand.

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

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

Geophytes

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

Annuals

Almost all annuals observed grew and flowered in early autumn, later winter and spring (Appendices 2, 4, 6 and 7). Thus growth of annuals in the study area coincided with an essentially winter growing season for agricultural crops.
Phenophases and growth (five-number summaries and bar graphs — see text) of large-leaved sclerophyll shrubs in Kromme River thicket (a), (b), (d) and (e); and dune thicket (c) and (f). Leaf fall is expressed as the mean of two values (bars). Key: see Figure 3.

**Table 3** List of species occurring on more than one substrate type. Their phenodiagrams are shown in corresponding figures (Fig.) and appendices (App.)

| Species occurring on more than one substrate type | Site numbers* |
|--------------------------------------------------|---------------|
|                                                   | 1 Dune sand   | 2 Dune sand | 3 Dune sand | 4 Acid sand | 5 Acid sand | 6 Loam | 7 Loam | 8 Loam |
| Pterocelastrus tricuspidatus                      | (Fig. 11)     | (Fig. 11)   | (Fig. 11)   | (Fig. 11)   | (Fig. 11)   | (Fig. 11) | (Fig. 11) | (Fig. 11) |
| Sideroxylon inerme                                 | (Fig. 11)     | (Fig. 11)   | (Fig. 11)   | (Fig. 11)   | (Fig. 11)   | (Fig. 11) | (Fig. 11) | (Fig. 11) |
| Themeda triandra                                  | (Fig. 4)      | (Fig. 4)    | (Fig. 4)    | (Fig. 4)    | (Fig. 4)    | (Fig. 4) | (Fig. 4) | (Fig. 4) |
| Metrosia muricata                                 | (Fig. 8)      | (Fig. 8)    | (Fig. 8)    | (Fig. 8)    | (Fig. 8)    | (Fig. 8) | (Fig. 8) | (Fig. 8) |
| Helichrysum tereifolium                           | (App. 2)      | (App. 2)    | (App. 2)    | (App. 2)    | (App. 2)    | (App. 2) | (App. 2) | (App. 2) |
| Lysa orientalis                                   | (App. 4)      | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4) | (App. 4) | (App. 4) |
| Briza maxima                                      | (App. 6)      | (App. 6)    | (App. 6)    | (App. 6)    | (App. 6)    | (App. 6) | (App. 6) | (App. 6) |
| Babiana patersoniae                               | (App. 7)      | (App. 7)    | (App. 7)    | (App. 7)    | (App. 7)    | (App. 7) | (App. 7) | (App. 7) |
| Sporobolus africanus                              | (App. 4)      | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4) | (App. 4) | (App. 4) |
| Tephrosia capensis                                | (App. 2)      | (App. 2)    | (App. 2)    | (App. 2)    | (App. 2)    | (App. 2) | (App. 2) | (App. 2) |
| Oxalis polyphylla                                 | (App. 4)      | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4)    | (App. 4) | (App. 4) | (App. 4) |

*See Table 1 for detailed soil descriptions

**Restioids**

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

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

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

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

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

Grasses

Counts of tillers and/or leaves per shoot of the C4 grasses Themeda triandra (Figure 4), Tristachya leucothrix, Stenotaphrum secundatum and Sporobolus africans (Figure 5) showed more than one peak of maximum growth. Other C4 grasses which showed growth interrupted by a period of inactivity were Cynodon dactylon and Eragrostis capensiss (Appendix 4). In contrast, Elionurus muticus (Appendix 4) and Diheteropogon filifolius (Appendix 3) had only one growth season, occurring in summer.

Growth measures of the C3 grass species, Pentastichis angustifolia and Lasiochloa longifolia indicated mostly autumn/early winter growth (Figure 6) while Helictochiton hirtulum grew in autumn and spring (Appendix 7). These findings support the generalized notion of cool season growth of C3 species and warm season growth of C4 species (e.g. Teeri & Stowe 1976; Ehleringer 1978; Boutton et al. 1980).

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

The ability of both growth pattern types of C4 grasses to grow during the summer enables them to dominate in the eastern, summer rainfall area of southern Africa (cf. Vogel et al. 1978). However, the capacity for growth during more than one season, the second season usually in early/midwinter, clearly gives these species a competitive advantage in the winter rainfall region. C3 species are well adapted to the winter rainfall area, shown by their predominance in the south western Cape (Vogel et al. 1978), because they require lower temperatures associated with periods of low water stress (Boutton et al. 1980; Ellis et al. 1980). Our study confirms a cool, wet growth season for C3 species in our area.

The study area in the south eastern Cape has equal numbers of species of C3 and C4 grasses (Cowling 1983b) which suggests that this region of non-seasonal rainfall, lying between the winter rainfall area to the west and the summer rainfall region to the east, is the overlap area for the C3 and C4 photosynthetic modes (see also Vogel et al. 1978). However, in terms of cover abundance, C4 species (particularly T. triandra and other species capable of cool season growth) predominate over C3 species in the study area (Cowling 1983b). We suggest that this high cover abundance is largely the result of the competitive advantage of the C4 grass species with more than one growth season per year, in a region of mild temperatures and non-seasonal rainfall.

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

Succulents

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

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

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

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

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

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

Summer growth by the ericoid shrubs, Metalesia muricata and Elytroappendix rhinoceros is more easily explained by their extensive root systems. The depth of the tap root alone of E. rhinoceros has been measured as 6.06 m and the laterals spread to a diameter of 4 – 5 m (Scott & van Breda 1937); the latter are probably effective exploiters of chance summer rains. In the renosterveld community, the roots of these species easily reached the pedocutanic horizon, 0.65 m deep, which was moist even in midsummer when the upper layers (0.3 – 0.6 m deep) lacked moisture.

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

Large leaved (sclerophyll) shrubs

Thicket Species. No obvious pattern of growth emerged from studies of the large leaved sclerophyll shrubs in both the dune and Krom River thickets, though there was a strong tendency for growth to cease for a short period in midsummer and all leaf fall occurred in summer (Appendices 1 and 5). In the dune thicket, new leaves and shoots were produced in spring (e.g. Cussonia thysiflora); winter, spring and autumn (e.g. Raphanea giliiana) and throughout most of the year (e.g. Olea exasperata) (Appendix 1). In the Krom River thicket, spring and summer growth was most common although Rhus incisa and R. longispina grew in autumn and R. glauca grew mostly from spring through the autumn but ceased growth in December (Appendix 5). The ‘generalist’ strategy of continuous carbon fixation and growth whenever conditions are suitable is best explained by deep rooted, large leaved sclerophyllous shrubs of Californian chaparral (Morrow & Mooney 1974; Mooney et al. 1975; Mooney et al. 1974; Mooney 1983). This description may fit the behaviour in our area of some deep rooted thicket species with relatively long lived leaves (more than 1½ years, pers. obs.).

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

Cowling (1983c) has argued that subtropical thicket species would have migrated into the Cape Region from the north east with the onset of warmer, wetter Holocene conditions after ± 12 000 B.P. Only those species with wide phenological flexibility would have been able to penetrate the non-seasonal rainfall area as insufficient summer rainfall would severely restrict summer growing and winter deciduous thicket species (e.g. Acacia caffra and A. schweinfurthii). We suggest that flexibility in the growth phenophases of deep rooted, ‘high cost-low profit’ (Orians & Solbrig 1977) sclerophyll shrubs would pre-adapt them for penetration of the non-seasonal and winter rainfall regions of the Cape. The ability to exploit bimodal and winter rains has led to the successful penetration of the southern and south western Cape by two thicket species in particular, Sideroxydon inerme which gains importance as a dune thicket element further westwards of our area as far as the Cape Peninsula and Pierocelastrus tricuspidatus penetrates the dry (150mm y−1) Mediterranean climate area of the Cape west coast as far as Elands Bay, where summer rain is less than 20% of the total. Flowering and fruiting patterns of thicket species were ir-
regular. However, when all species were considered, there were reproductive peaks in spring and autumn (Appendices 1 and 5; Liversidge 1972; Siegfried 1982; Pierce 1983; K.L. Tinley pers. comm.). Individuals within a species flower and fruit at different times of the year and also show variability in the quantity of their reproductive output (this study; Liversidge 1972; Frost 1976; K.L. Tinley pers. comm.). Of the nine species monitored both in this study and in Liversidge’s (1972) study of dune thicket near Port Elizabeth, seven species showed marked differences in flowering and fruiting phenophases between the two study areas.

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

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

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

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

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

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

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

**Concluding Remarks**

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

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Appendix 1 Phenograms of species in dune fynbos and thicket

Key:
- Ripen fruit/seed
- Unripe fruit/seed
- Pre-flower
- Active growth
- Slighted growth
- No growth
- Leaf loss
- Leaf death
- Start of sampling

Species:
- Ficinia ramosissima Kunth
- Euclera racemosa Murray
- Rhus crenata Thunb.
- Putterickia pyracantha (L.) Szyzys.
- Cassine aethiopica (Thunb.)
- Agathosma stenophleba Steud.
- Polycia echinata (Thunb.) Nees
- Anthospermum aethiopicum L.
- Olia exasperata Jacq.
- Rhus schlechteri Diels
- Caespa flabellata Diels
- Calotropis procera L.
- Crassula expansa Ait. ssp. filicaulis (Haw) Toekl.
- Muraltia squarrosa (Thunb.) DC.
- Sutherlandia fruticosa L.f.
- Physcia littoralis D.Dietr.
- Disparagia procoides Gaertn.
- Elytrigia albida L.
- Wachendorfia thyrsiflora L.
- Leucadendron rheni (L.) B.Dietr.
- Leucadendron hookerianum (Thunb.) B.Dietr.
- Leucadendron capense (B.Linn. ex Pers.) B.Dietr.
- Cussonia thyrsiflora Thunb.
- Raphanea pallida (Somd.) Meisn.
- JFMAW
- JASONDJFMA
Appendix 2 Phenodiagrams of species in dune grassland. Key: see Appendix 1

Cerastium capense Bond. = Medicago hispida Gaertn =
Tetragonia africana Spreng. = Sebaea minutiflora Schinz.
Satyrium princeps Bolus = Ixia orientalis Ker.
Romulea atrandra Lewis = Oxalis smithiana E.& Z.

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

Diheteropogon filiformis (Nees) Clayton
Tetraria involucrata (Rottb.) C.B.Ci.
Metalasia muricata (L.) Less.
Stoebe plumosa Thunb.

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

Cliffortia ferruginea L.f.
Scirpus antarcticus L.
Cerastium capense Bond.
Drosera alciace Hamet
Briza maxima
Briza minor
Elionurus multiflorus (Spreng.) Kunth
Bulbostylias collina Kunth
Gynodon dactylin (L.) Pers.
Eragrostis capensis (Thunb.) Trin.
Sporobolus africanus (Poir.) Robyns & Tournay
Thamnochortus fruticosus Berg.
Gazania linearis (Thunb.) Druce
Hesperantha radicata L.

Aspalathus angustifolia (Lam.) R. Dahlg. ssp. angustifolia
Aspalathus spinosa L. ssp. spinosa
Commelina africana L.
Spiloxene ? atelligata
Micranthus plantagineus Eckl.
Monadonia bracteata (Sw.) Dru
Babiana patersoniae L.
Hesperantha falcatula (L.f.) Ker.
Oxalis sp.
Romulea dichotoma (Thunb.) Baker
Arctopus echinatus L.
Oxalis polyphylla Jacq.
Hypoxis sp.
Wachendorfia paniculata L.
Appendix 5 Phenodigrams of species in Kromme River thicket. Key: see Appendix 1

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

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

Appendix 8 Classification of species into growth form classes (see Table 2). Phenophases are given in appendices and figures where indicated
Cassine aethiopica Thunb.
Olea exasperata Jacq.
Rhus schlechteri Diels
Cassonia thrysiflora Thunb.
Rapanea giliana (Sond.) Mez.
Sideroxylon inerme L. (Figure II)
Pterocelastrus tricuspidatus (Lam.) Sond. (Figure II)

Dune grassland (see Appendix 2)

Annuals
Cerastium capense (Thunb.) Pers.
Medicago hispida Gaertn
Torilis africana Spreng
Sebaea minutiflora Schinz.

Geophytes
Satureyri princeps Bolus
Ixia orientalis Ker.
Romuela attandra Lewis
Oxalis smithiana E. & Z.

Non-geophytic forbs
Cerastium capense Sond.

Grasses

Grassy fynbos (see Appendix 3)

Grasses
C4 Diheteropogon filifolius (Nees) Clayton
Restioids
Restio triticeus Rottb. (Figure 3).
Cyperoids
Tetragonia involucrata (Rottb.) C.B.Cl.
Small leaved shrubs
Metalasia muricata (L.) Less.
Stoebe plumosa Thunb.
Helichrysum cymosum (L.) Less.
Helichrysum terebilium (L.) Less.
Selago glomerata Thunb.
Carpocece vaginellata Salter
Erica diaphana Spreng. (Figure 9)
Erica pectinifolia Salisb. (Figure 9)
Large leaved shrubs
Proteoids
Leucospermum cuneiforme (Burm. f.) Rourke (Figure 9)
Leucadendron salignum Berg. (Figure 9).

Restioid grassland (see Appendix 4)

Annuals
Scirpus antarcticus L.
Ceratium capense Sond.
Drosera aliae Hamet
Briza maxima L.
Briza minor L.

Geophytes
Monadenia bracteata (Sw.) Dru.
Spiloxene? stellata
Miconanthus planagineus Eckl.
Babiana paterosiae L.
Hesperantha falcata (L.f.) Ker.
Oxalis sp.
Romulea dichotoma (Thunb.) Baker
Arctopus echinatus L.
Oxalis polyphylla Jacq.
Hypoxis sp.
Wachendorfia pariculata L.

Non-geophytic forbs
Gazania linearis (Thunb.) Druce
Hypochoeris radicata L.
Commelina africana L.
Grasses
C3 Elionurus muticus (Spreng.) Kunth
Cynodon dactylon (L.) Pers.
Arangrostis capensis (Thunb.) Trin.
Sporobolus africanus (Poir.) Robyns & Tournay
Themeda triandra Forsk. (Figure 4)
Tristachya leucothrix Nees (Figure 5)

Restioids
Thamnochortus fruticosus Berg.

Cyperoids
Bu Bolsystis collina Kunth
Small leaved shrubs
Clifforia furgiciana L.f.
Aspalathus angustifolia (Lam.) R.Dahlgr. ssp. angustifolia
Aspalathus spinosa L.

Kromme River thicket (see Appendix 5)

Succulents
Sarcostemma vimalale (L.) R.Br.
Crassula cultrata L.
Large leaved shrubs
Thicket species
Cassine tetragona (L.f.) Loes
Rhus laevigata L.

Renosterveld (see Appendix 6)

Annuals
Briza maxima L.
Lobelia erinus L.
Sebaea aurea (L.f.) Roem. & Schult.

Geophytes
Hesperantha falcata Ker.
Moraea bellendini N.E.Br.
Thunbergiella filifolius (Lam.) Wolff.
Miceranthus plantagineus Eckl.
Ornithogalum subsulatum Bak.
Homalium sp.
Moraea algoensis Goldbl.
Romulea longipes Schltr.
Isia orientalis Ker.
Satyriona membranaceum Sw.
Bulbine narcissifolia Salm-Dyck
Oxalis sp. 1
Babiana patersoniae L.
Oxalis sp. 2.
Oxalis polyphylla Jacq.
Spiroæne minuta (L.) Fourc.
Ornithogalum minusulatum Jacq.

Non-geophytic forbs
Pelargonium dichondraefolium DC
Cotula turbinata L.

Succulents
Ruschia tenella (Haw.) Schw.

Small leaved shrubs
Aspalathus spinosa L.
Cliffortia linearifolia E. & Z.
Metalasia muricata (L.) Less (Figure 10)
Elytrotopappus rhinocerotis (L.f.) Less (Figure 10)
Helichrysum terefolium (L.) Less
Helichrysum anomalum (Sch. Bip.) Less
Chrysocoma tenifolia Berg.
Selago corymbosa L.
Graptophyllum repens L.
Lobostemon argenteus Buek.
Indigofera denudata Thunb.

Large leaved shrubs

Thicket species
Eucla crispa (Thunb.) Gürke

Shale grassland (see Appendix 7)

Annuals
Senecio erubescens Ait.
Drosera cistiflora L.
Sebaea aurea (L.f.) Roem. & Schult.

Geophytes
Moraea sp.
Oxalis purpurea L.
Galdionus longicollis Bak.
Piloselloides hirsuta (Forsk.) Jeffrey
Bulbine narcissifolia Salm-Dyck
Aristea pusilla (Thunb.) Ker
Isia orientalis Ker
Babiana patersoniae L.
Arctopus echinatus L.

Non-geophytic forbs
Pelargonium dichondraefolium DC
Tephrosia capensis (Thunb.) Pers.

Grasses
C3 Helictotrichon hirtulum (Steud) Schweickerdt
C4 Cynodon dactylon (L.) Pers.

Restioids
Restio sieberi Kunth.

Cyperoids
Ficinia tristachya (Rottb.) Nees
Tetraria cuspidata (Rottb.) C.B.CI.

Succulent
Crassula ciliata Thunb.

Small leaved shrubs
Passerina rubra C.H.Wr.
Asparagus capensis L.
Helichrysum odoratissimum (L.) Less