The vegetation of the Roodeplaat Dam Nature Reserve. III. Phenological observations

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The phenology of a number of phanerophytes, chamaephytes, hemi-cryptophytes, cryptophytes and therophytes was studied over a three-year period and it was found that certain phanerophytes exhibited activity as early as the second half of July. Most other species commence growing and/or flowering only in September, while the flowering phase of a number of species commences only in late summer or early winter.
S. Afr. J. Bot. 1986, 52: 153 – 158

Die fenologie van 'n aantal fanerofiete, chamefiete, hemikriptofiete, kriptofiete en terofiete is oor 'n drie-jaar-periode ondersoek en daar is gevind dat sekere fanerofiete reeds in die tweede helfte van Julie aktiwiteit begin toon. Die meeste ander spesies begin eers in September groei en/of blom terwyl die blomfase van 'n aantal spesies eers in die laat somer of winter 'n aanvang neem.
S.-Afr. Tydskr. Plantk. 1986, 52: 153 – 158

Keywords: Flowering phase, periodicity, phanerophytes, phenology, shoot growth

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Accepted 12 September 1985

Introduction

The first two papers in this series on the vegetation of the Roodeplaat Dam Nature Reserve included a check list of the plant species, short descriptions of the climate and geology and a phytosociological classification of the different plant communities (Van Rooyen 1983a; 1983b).

A study was also undertaken of the qualitative and quantitative phenology of certain trees, shrubs and herbs over a three-year period (Van Rooyen 1984). Phenology can be described as the study of the timing of recurring biological events, the causes of their periodicity with regard to biotic and abiotic factors and the inter-relationship among phases of the same or different species (Lieth 1974). Phenological changes do not involve only the leaf emergence, flowering, fruiting and leaf fall on trees or other perennials, but also the periodic appearance and disappearance of geophytes and therophytes in a community. Such changes in species and number of individuals are not only of seasonal occurrence, but they also vary from year to year (Müller-Dombois & Ellenberg 1974). The aim of this paper is to give some insight into the phenology of the savanna vegetation of the Roodeplaat Dam Nature Reserve.

Methods

The species that were used for the phenological study were either conspicuous or occurred in large numbers or were differential species for the different plant communities. Ten individuals of each of 31 phanerophyte and two chamaephyte species were randomly selected and permanently marked. For a period of three consecutive years detailed qualitative observations were made of their different phenophases. The phenological variables that were monitored comprise vegetative and/or flower bud swelling, shoot growth rate, leaf expansion rate, number of immature and mature leaves, leaf fall stage, leaf senescence stage, number of flower buds, open flowers, withered flowers and unripe fruit, fruit maturation stage, fruit discolouration stage, number of ripe fruit, dissemination rate of fruit and/or seeds and the stage of dissemination.

The intervals between observations differed from two to four weeks depending on the time of the year and the activity of the plant species.

The phenophases were recorded as follows on a six-point scale (0, 1, 2, 3, 4, 5):

Rate: A high growth rate, for example shoot growth, was awarded a high value and vice versa.

Number: A large number of flowers for example, was awarded a high value and vice versa.

Stage: A high degree of leaf or fruit senescence for example, was given a high value and vice versa.

When one of the 10 marked individuals of a species displayed a certain phenophase it was regarded as the starting point for that phenophase for that particular species. For each observation date the mean data for the 10 individuals of a species were used to indicate the average stage of development for each species. This information on each of the phenological variables was then displayed in the form of a phenogram for each species for the three-year study period (Van Rooyen 1984). The detailed information contained in these phenograms was then summarized and presented in Figure 2. The leaf phase commences with vegetative bud swelling and concludes with the leaf fall stage. The flowering stage commences with flower bud swelling and concludes with the withered flower stage. The fruiting phase commences with the presence of unripe fruit and concludes when dissemination terminates. The observations on merely the presence or absence of leaves, flowers and fruit were also conducted on a number of unmarked shrubs and herbaceous species (chamaephytes, hemicryptophytes, cryptophytes and therophytes) and the results are presented in Figures 4 & 5. The authors of the different species mentioned in the text are given in Van Rooyen (1983a).

Results and Discussion

The climate diagram of the study area for the study period as well as the phenograms of the different plant species that were studied are shown in Figures 1, 2, 3, 4 and 5.

According to the phenophases of the plant species, the year can be divided into six seasons. Spring is divided into early spring (mid-July until the end of August), and late spring (September until the end of October). Summer is divided into early summer (November until the end of December) and late summer (January until the middle of March). Autumn is from mid-March until mid-May, while winter is from mid-May until mid-July.

The phenodynamic aspects of the selected plant species are discussed briefly under the following headings:

Activity during spring before rain;
Vegetative activity;
Reproductive activity;
Senescence;
Evergreenness.

Activity during spring before rain

Some species commence growing or flowering in the dry period preceding the first spring rain e.g. *Acacia caffra, A. robusta, Boscia albitrunca, Dombeya rotundifolia* and *Ximenia caffra.*

During the early stages of a dry period the water lost by a tree through transpiration exceeds the water absorbed through the roots. The water potential of the tree declines and causes water stress, leaf senescence and leaf abscission (Reich & Borchert 1982). Since the absorption of the residual soil moisture continues to take place at a low rate, this results in a slow increase in the water potential of the tree due to the virtual absence of transpiration. When the water potential exceeds a certain threshold value, growth may resume, even before the first rains fall.

Vegetative activity

Concurrent shoot growth and leaf expansion

This occurs during spring (mid-July to October) and was recorded for species such as *Acacia caffra, A. robusta, Boscia albitrunca, Combretum molle, Euclea undulata, Mundulea sericea, Ochna pulchra, Olea europaea* subsp. *africana, Pappea capensis* and *Rhus leptodictya* (Figure 2). According to Larcher (1980) the onset of vegetative activity in the first half of the growth season depends on certain air and soil temperature thresholds that must be exceeded.

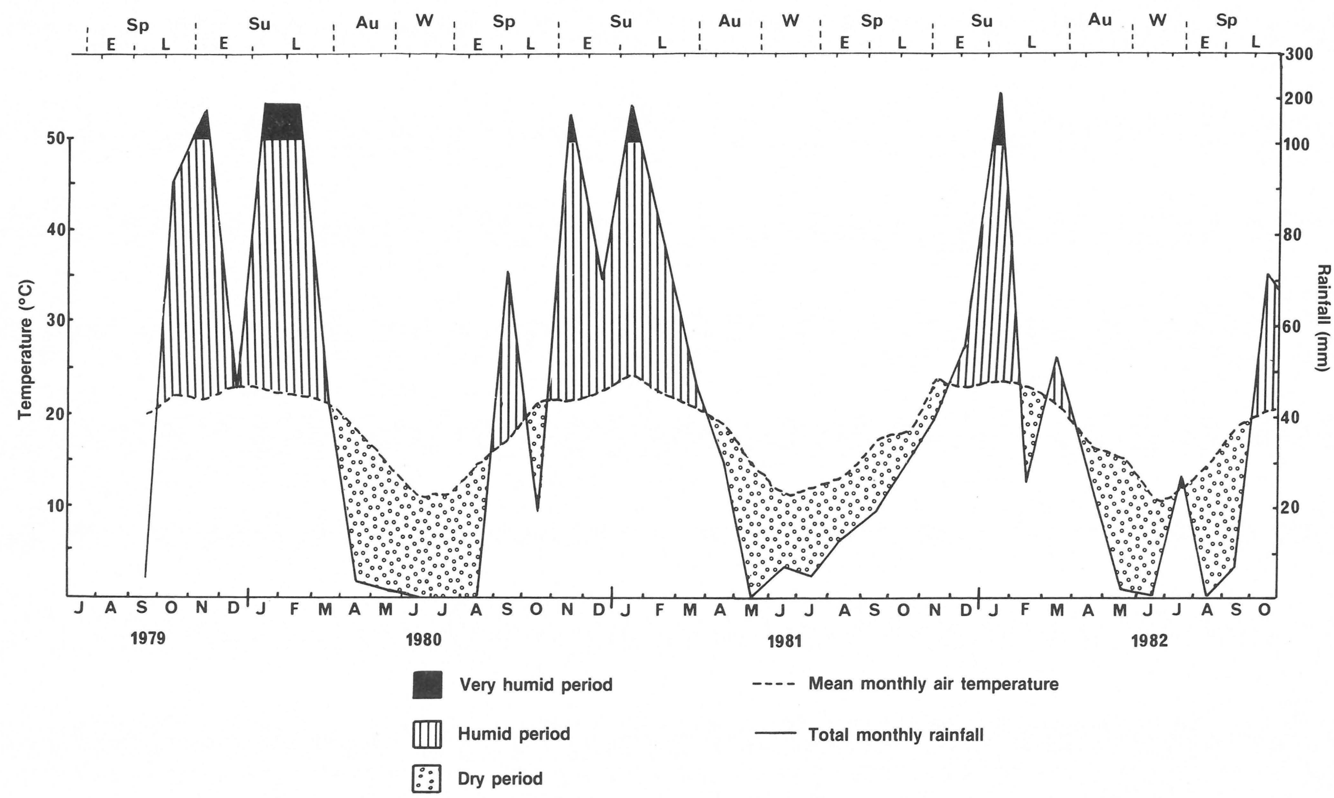

Figure 1 Climate diagram for the Roodeplaat Dam Nature Reserve for the period 1979 to 1982. Sp — spring; Su — summer; Au — autumn; W — winter; E — early; L — late.

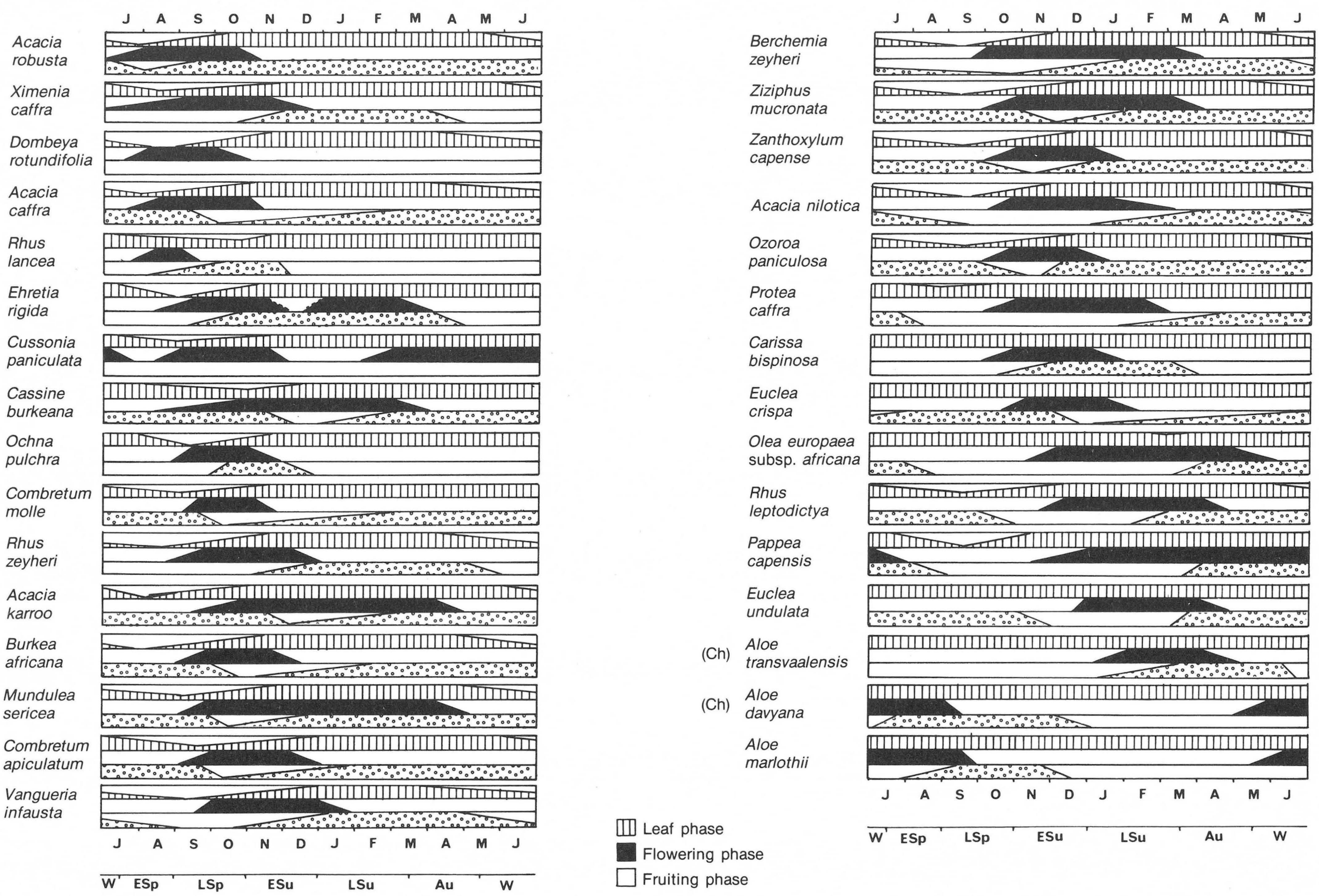

Figure 2 Phenograms of a number of phanerophyte and chamaephyte species on the Roodeplaat Dam Nature Reserve. Ch — chamaephyte species; ESp — early spring; LSp — late spring; ESu — early summer; LSu — late summer; Au — autumn; W — winter.

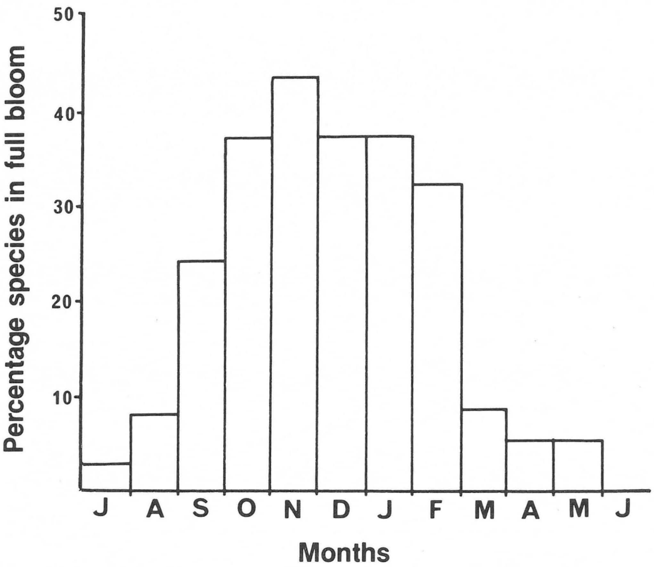

Figure 3 Peak flowering period for phanerophyte species (percentage of 34 species in full bloom).

Initiation of shoot growth after leaf expansion

A lag phase between leaf expansion and shoot elongation was recorded for a number of species. This lag can vary from one to six weeks (value indicated in brackets): *Acacia karroo* (1 – 2), *Berchemia zeyheri* (2), *Ehretia rigida* (2 – 6), *Protea caffra* (3 – 5) and *Ximenia caffra* (2 – 3).

Number of growth peaks

In a single growth season periods of growth can alternate with periods without active growth. Up to three peaks were recorded. These peaks include shoot growth as well as leaf expansion and were exhibited by *Berchemia zeyheri, Dombeya rotundifolia* and *Olea europaea* subsp. *africana*. Under relative normal climatic conditions (Figure 1: 1979/80), most of the species can be expected to show two growth peaks. In other words, growth peaks usually occur after peaks in rainfall, although this is not always the rule. However, when a dry spring or early summer is experienced (1981), only one peak in late summer usually occurs. A bimodal growth pattern can be attributed to a number of possible causes, for example a dry midsummer period (Rogers & Westman 1981), insect defoliation in the growth season (Guy *et al.* 1979), or to the early production of high concentrations of abscisic acid in mature leaves which temporarily inhibits growth (Huxley & Van Eck 1974). When the latter limiting factor is removed under conditions that are still favourable for growth, for example by defoliation, growth may resume.

Reproductive activity

Flowering before vegetative growth

This was recorded only for *Dombeya rotundifolia, Combretum molle*, and once for *Boscia albitrunca*. Huxley & Van Eck (1974) attribute this phenomenon to flower bud initiation during the end of the preceding season.

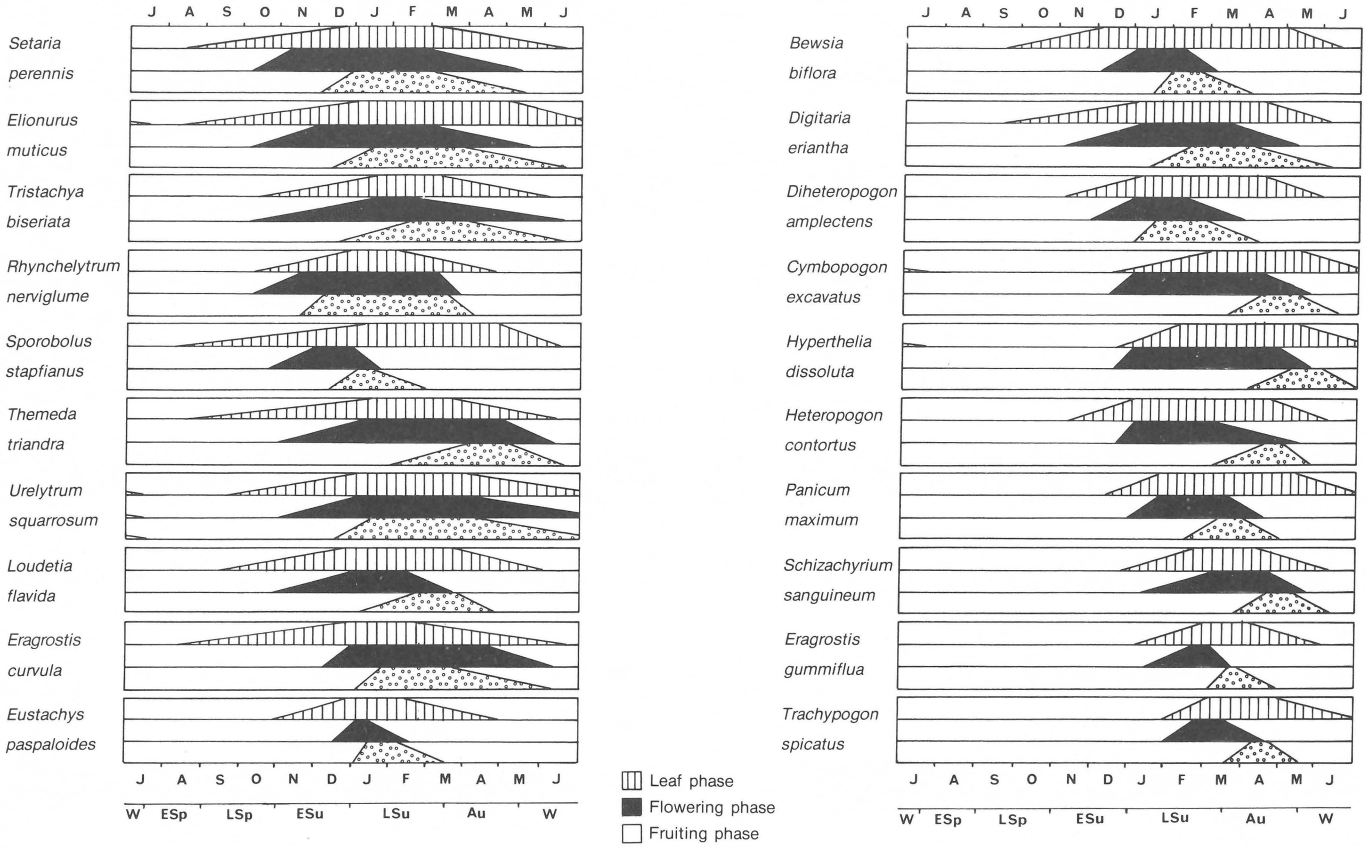

Figure 4 Phenograms of a number of hemi-cryptophyte species on the Roodeplaat Dam Nature Reserve. ESp — early spring; LSp — late spring; ESu — early summer; LSu — late summer; Au — autumn; W — winter.

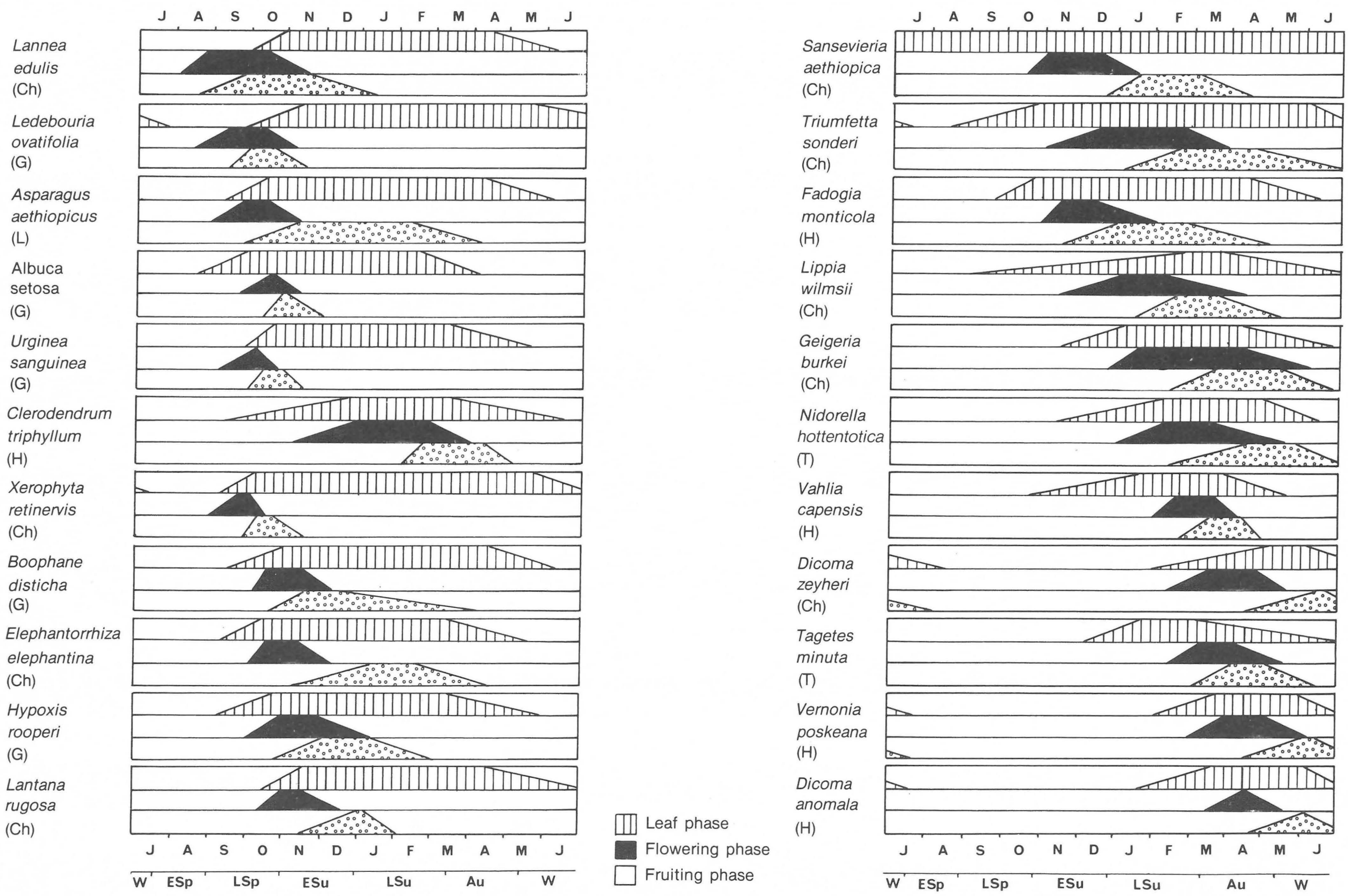

Figure 5 Phenograms of a number of plant species on the Roodeplaat Dam Nature Reserve. Ch — chamaephyte species; H — hemi-cryptophyte species; G — cryptophyte species; T — therophyte species; L — climber; ESp — early spring; LSp — late spring; ESu — early summer; LSu — late summer; Au — autumn; W — winter.

Variation in the date of anthesis

Some species have a relatively constant period in which anthesis commences (two-week variation) regardless of the variation in climatic conditions from year to year. Species belonging to this category include *Acacia robusta, Combretum apiculatum, C. molle, Mundulea sericea* and *Rhus zeyheri*. Other species vary up to eight weeks before anthesis starts, for example *Ehretia rigida, Zanthoxylum capense* and *Euclea undulata.*

According to Alvim & Alvim (1978), the close synchronization of growth patterns among mature trees can possibly be attributed to the influence of an external factor, for example a period of moisture stress. Species that flower on more or less the same date each year, show little or no reaction to variation in rainfall from year to year. It is possible that the flowering strategy of these species is strongly influenced by environmental variables such as photoperiod of which the annual variation is never erratic (Alvim & Alvim 1978). Opler *et al.* (1976) attribute the above-mentioned phenomenon in some tropical species to an endogenous rhythm.

Peaks in the flowering period

Most of the phanerophyte species flowered mainly during the period September to February with a peak in November (Figure 3). This corresponds with the flowering patterns of woody species in Botswana (Miller 1949), Tanzania (Scott 1934) and savanna trees in Malawi (Hall-Martin & Fuller 1975).

Duration of flowering period

Species with a flowering period of less than four weeks (17,6% of the phanerophyte species) include for example *Acacia caffra, Boscia albitrunca, Euclea undulata, Ochna pulchra, Vangueria infausta* and *Zanthoxylum capense*. However, most of the phanerophyte species flowered for one to three months. Those with a flowering period of more than three months (17,6% of the phanerophyte species) are for example *Acacia karroo, A. nilotica, Cassine burkeana, Mundulea sericea Pappea capensis* and *Ziziphus mucronata*.

Number of flowering phases/peaks

A number of species sometimes exhibited more than one flowering phase during a growth season, for example *Acacia caffra* (2×), *A. robusta* (3×) and *Mundulea sericea* (2×).

Other species have one flowering phase but sometimes more than one flowering peak within that phase, for example *Acacia karroo* (5×) and *Ehretia rigida* (3×).

Multiple flowering phases or peaks were also recorded by Ewusie (1968) in Ghana, Miller (1949) in Botswana, Rutherford (1975) in South West Africa and Opler *et al.* (1980) in Costa Rica.

Species that did not flower at all for at least one year during the study period were for example *Burkea africana, Cussonia paniculata, Dovyalis zeyheri, Euclea crispa, Maytenus heterophylla* and *Rhus lancea*. It has been suggested by Opler *et al.* (1976) that more than one flowering phase in one season or the absence of a flowering phase in a season, can be ascribed to the influence of variations in the rainfall pattern on the initiation of the flowering phase.

The reasons for the absence of flowers for at least one year and in some cases for the three-year study period, are not clear. Rainfall might have some influence as indicated by Opler *et al.* (1976), but it is possible that trees have some difficulty with their energy allocation especially after a year of exceptionally abundant flowering and fruit production (Barbour *et al.* 1980). According to Larcher (1980), seasonal blooming species are found in regions with periodic dry seasons or with a distinct variation in day length.

Peak fruiting period

Ripe fruit occur throughout the year because the fruit of different species mature at different times of the year. Approximately 44% of the selected phanerophyte species have ripe fruit in April, while only 6% have ripe fruit in September (Figure 2).

Senescence

Leaf senescence and leaf fall

More than 20% of the leaves of a number of species begin to discolour by the second half of March (onset of autumn). This is true for *Acacia caffra, Burkea africana, Berchemia zeyheri, Combretum molle, Dombeya rotundifolia, Rhus leptodictya, Vangueria infausta* and *Ziziphus mucronata*.

The leaf fall of about 47% of the selected phanerophyte species starts in winter. For about 17% it commences in spring, just before or simultaneously with spring growth.

According to Reich & Borchert (1982) the rate of leaf fall of trees in the early dry season is strongly correlated with a decrease in soil moisture and an increase in water stress experienced by the plants. Seasonal droughts, low air humidity, decreasing day lengths and temperature also play an important role in inducing a rest period in tropical trees (Huxley & Van Eck 1974; Alvin & Alvim 1978; Shukla & Ramakrishnan 1982).

Leafless period

Some of the species studied are leafless for a month or more per year, for example *Acacia robusta, Dombeya rotundifolia, Burkea africana, Ziziphus mucronata, Acacia nilotica* and *Zanthoxylum capense.*

Evergreenness

The so-called evergreen species are those of which leaf fall and new growth either occur simultaneously in the active growth season *or* those which still bear more than 50% of the previous season's leaves when the new leaves start unfolding. Examples are *Carissa bispinosa, Cassine burkeana, Euclea crispa, E. undulata, Olea europaea* subsp. *africana* and *Rhus lancea*.

The phenodynamics of the chamaephyte species, hemicryptophyte species, cryptophyte species (geophytes) and therophyte species are shown in Figures 4 & 5. Most of the chamaephytes start to flower during September and October while there is an absence of flowers during March to June.

The flowering phase of most of the hemi-cryptophyte species commences during the period November to March. Some grass species that flower in the late spring (September/October) are *Tristachya biseriata, Rhynchelytrum nerviglume* and *Setaria perennis* while *Schizachyrium sanguineum, Trachypogon spicatus* and *Eragrostis gummiflua* commence flowering only in the late summer (January/February).

The geophytes flower mainly in spring (August to October) as was also found for the geophytes of the south-eastern Cape (Pierce & Cowling 1984). The therophytes flower mainly in late summer (January/February), and can be described as summer annuals. This is in contrast to annuals in the south-eastern Cape which flowered in early autumn, winter and spring i.e. winter annuals (Van Rooyen *et al.* 1979, Pierce & Cowling 1984).

Concluding remarks

The interactions between the phenophases of the species studied and the changes in climatic factors will be discussed in a following paper.

The study of the phenology of woody species in their natural surroundings is complicated by their perennial life cycle, intraspecific genetic variation, interspecific competition, differences in terrain and the mutual influence of climatic factors on the activity of these species (West & Wein 1971).

Another problem is to quantify a phenophase of a tree because the maximum potential of a phenophase has to be estimated in order to calibrate any scale used. From the phenological data that have been presented indicator species can be selected to indicate the start or length of seasons. The onset of spring in the study area is indicated by the emergence of flower buds in *Acacia robusta* or *Dombeya rotundifolia* late in July. On the other hand, the yellowing leaves of *Acacia caffra* and *Dombeya rotundifolia* indicate the onset of autumn late in March.

The length of the growth and reproductive period of woody species extends more or less from the beginning of August until the end of March. The absence of rainfall, and/or extremely low temperatures at the beginning or end of the growth season, will result in a shorter favourable season for growth.

The flowering period of certain species such as *Aloe* spp., is of interest to e.g. bee farmers. The availability of browse in the different seasons is also important information which helps to determine the suitability of a habitat for browsers.

Ecophysiological studies on woody species should explain many of the phenological strategies of these plants, for example why some species flower before vegetative growth commences, the absence of flowering periods in certain years and multiple phases or peaks in vegetative growth and/or flowering in one growth season.

Acknowledgements

We gratefully acknowledge the assistance of the Nature Conservation Division of the Transvaal Provincial Administration, and the financial contributions of the University of Pretoria and the Council for Scientific and Industrial Research.

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