

STEYN, HESTER MARIA

**NAMAQUALAND EPHEMERALS: PHENOLOGY
AND THERMAL UNITS**

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**NAMAQUALAND EPHEMERALS: PHENOLOGY AND
THERMAL UNITS**

by

HESTER MARIA STEYN

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in the Faculty of Science
(Department of Botany)
University of Pretoria
Pretoria

Supervisor: Dr. N. van Rooyen

Co-supervisors: Dr. M.W. van Rooyen

Prof. G.K. Theron

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**DEDICATED TO MY PARENTS, AND MY FRIENDS (RIAAN, MAGDA AND MARIETTE) WHO
MADE THE FIELDWORK AN UNFORGETTABLE EXPERIENCE**

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ABSTRACT

NAMAQUALAND EPHEMERALS: PHENOLOGY AND
THERMAL UNITS

by

HESTER MARIA STEYN

Supervisor: Dr. N. van Rooyen

Co-supervisors: Dr. M.W. van Rooyen

Prof. G.K. Theron

DEPARTMENT OF BOTANY
MAGISTER SCIENTIAE

The effect of different variables i.e. temperature, sowing date, water stress and achene age, on the phenology and the prediction of phenological stages of five Namaqualand ephemeral plant species were investigated. The species examined were *Dimorphotheca sinuata*, *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* and *Ursinia cakilefolia*.

Later sowing dates and water stress resulted in smaller plants with relatively few open inflorescences at peak flowering and therefore a less spectacular flowering display. There were some differences in the phenology of plants derived from achenes collected at different times.

The use of thermal units resulted in fairly accurate predictions of the timing of phenological stages such as peak flowering or even a spectacular flowering display for tourists. While cold units should be used until flower/inflorescence initiation, the combined use of cold and heat units are recommended in the prediction of later phenological stages.

UITTREKSEL
NAMAKWALANDSE EFEMERE: FENOLOGIE EN
TERMIESE EENHEDE

deur

HESTER MARIA STEYN

Leier: Dr. N. van Rooyen

Mede-leiers: Dr. M.W. van Rooyen

Prof. G.K. Theron

DEPARTEMENT PLANTKUNDE
MAGISTER SCIENTIAE

Die invloed van temperatuur, saai tyd, waterstremming en ageen-ouderdom op die fenologie en die voorspelling van fenologiese stadiums, is vir vyf Namakwalandse efemeerspesies ondersoek. Die spesies wat ondersoek is, is *Dimorphotheca sinuata*, *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* en *Ursinia cakilefolia*.

Latere saai tyd en waterstremming het gelei tot kleiner plante met relatief min oop bloeiwyses tydens piekblom tyd en sodoende 'n minder aanskoulike blommeskouspel. Daar was verskille in die fenologie van plante verkry vanuit agene van verskillende ouderdomme.

Die gebruik van termiese-eenhede het gelei tot redelik akkurate voorspellings van die tydsberekening van fenologiese stadia soos piekblom tyd of 'n aanskoulike blomvertoning vir toeriste. Alhoewel koue-eenhede gebruik moet word tot en met blom/bloeiwyse inisiasie, word die gekombineerde gebruik van koue- en hitte-eenhede aanbeveel vir die voorspelling van latere fenologiese stadia.

CHAPTER 1

INTRODUCTION

Phenology is defined by Lieth (1974) as the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species. While plant phenological stages such as germination, leaf development, flowering time, fruiting time, seed dispersal, senescence and leaf-fall are determined genetically, the onset of a phase is often controlled by some environmental factor (Daubenmire 1959, in Taylor 1969).

As the science of biological events relating to climate, and other environmental factors, phenology is useful at all levels of education to make relevant the complexity of organisms and environmental interactions. Specific plants and selected phenological events might be useful as indicators to key major land management practices and productivity studies (Lieth 1974).

A hypothesis was formulated that a plant species needs a constant thermal unit sum to reach a certain stage of development (Lettau 1965). This amount of heat and/or cold that a specific plant needs to reach a certain phenological stage can be quantified by using thermal units. The Heat Unit Approach measures the quantity of thermal or solar thermal units a plant receives through its life cycle until flowering or any other phenological stage. According to Wang (1960) the Heat Unit Approach has been widely adopted because of its value in satisfying practical needs, rather than for its accuracy or its theoretical soundness.

Covering an area of approximately 55 000 km², Namaqualand lies in the north-western arid corner of the Republic of South Africa (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992). The unpredictable nature of the rainfall in Namaqualand has been an important selective force determining the life history characteristics of ephemeral species indigenous to this region. As a result of the unpredictability of the rainfall, germination

of seeds can occur over a long period in time and this in turn determines the length of the growing period. The reaction of the ephemerals to this unpredictability is manifested in plastic responses in life span, size and biomass allocation (Van Rooyen *et al.* 1992).

Namaqualand owes its fame mainly to the mass display of wild flowers, which transforms the normally barren landscape into a land of colour for a few weeks in the spring following a good winter rainy season (Van Rooyen *et al.* 1992). This annual wild flower display attracts thousands of tourists. Yet many of them return home disappointed because their visit was either too early or too late to experience the full splendour of the wild flowers.

According to the Chief Directorate: Nature and Environmental Conservation (undated), the best flower displays usually occur from early August to mid-September. Weather patterns, particularly hot berg winds, determine the duration of the flower season, and accurate predictions are therefore difficult to make.

Although studies on the phenology of Namaqualand ephemerals were done by Van Rooyen, Grobbelaar & Theron (1979) and Van Rooyen, Theron & Grobbelaar (1979), no previous work has been done to predict the timing of phenological stages and in particular the timing of peak flowering.

The aim of this study was to investigate the effect of different environmental conditions i.e. temperature, sowing date, water stress and achene age, on the phenology of Namaqualand ephemerals and to determine whether the widely used Heat Unit Approach could be applied to predict the phenological development of the ephemerals of Namaqualand.

The thesis is presented in the form of papers. These papers are to be submitted for publication in various international scientific journals. Except for the papers, a general introduction, a literature review on thermal units, an overview of methods, a general conclusion and a comprehensive list of references are also included.

CHAPTER 2

LITERATURE REVIEW ON THERMAL UNITS

Knowledge of phenological development in crops as a function of environmental variables can be useful in crop improvement (Seddigh, Jolliff & Orf 1989); the scheduling of spraying programmes to control insects, disease or weeds and the selection of suitable farming areas and of appropriate crop varieties for these areas (Wang 1960).

The influence of temperature on plant phenology has long been recognized. As early as 1730 De Reamur found that the sum of the mean daily air temperature, until a certain stage of plant development was reached, remained more or less constant over several years. He assumed that this thermometric constant represented the amount of heat (heat units) required for a plant species to reach a given stage of maturity (Mederski, Miller & Weaver 1973). Since then, many different formulae have been used to calculate thermal units to predict a certain phenological stage in a wide spectrum of plant species.

The earliest attempts at predicting phenological development were based on temperature records only, while subsequent improvements included the use of other variables e.g. photoperiod (Nuttonson 1955), radiation (Caprio 1974) and stress (Idso, Jackson & Reginato 1978).

METHODS USING TEMPERATURE ONLY

a) Heat units

Adanson (1750, in Dijkhuis 1971) reasoned that a base temperature has to be subtracted from the mean daily air temperature, as growth does not persist below this critical temperature. He suggested the following formula:

$$EHU = [(T_x + T_n)/2] - T_b$$

EHU - effective heat units per day

T_x - maximum temperature

T_n - minimum temperature

T_b - base temperature

The above mentioned formula is commonly used in the United States and Canada (Dijkhuis 1971) and has also been used by several authors as a base to develop more accurate formulae (Gilmore & Rogers 1958; Arnold 1960; Bunting 1976). Newman, Blair, Dale, Smith, Stirm & Schaal (1968) also used Adanson's formula but called the accumulated heat units, growing degree days (GDD).

However, the base temperature is not a constant temperature throughout the growing period of a specific plant (Iwata 1975, in Eicker 1979), but varies with external conditions and plant age and should be adapted accordingly.

The formula used by Livingstone (1916, in Eicker 1979) is based on the summation of the effectivity of a mean daily temperature:

$$u = 2^{(0.1T - 4.44)}$$

u - daily effectivity of the mean daily temperature

T - mean daily temperature

The base temperature was taken as 4.44°C with an effectivity of 1; at 14.44°C the effectivity would have doubled. According to Iwata (1975, in Eicker 1979) this formula is not an improvement on that of Adanson (1750, in Dijkhuis 1971).

Lindsey & Newman (1956) found that temperature summations based upon daily means were inadequate as the daily mean failed to take into account the duration of the various temperature levels during the daylight and night hours. Their method of temperature summation was based on the diurnal course of temperature and was designed to reflect the approximate durations of different temperature levels during the day:

$$DH = 12(h - t)^2 / (h - w)$$

DH - degree hours per day

h - daily maximum temperature
w - daily minimum temperature
t - base temperature

In their calculation of heat units Gilmore & Rogers (1958) used a base temperature as well as a maximum temperature. The maximum temperature was defined as the temperature above which no growth was assumed to take place. They demonstrated the successful use of their formula to determine the number of heat units required by *Zea mays* from planting date until flowering. Their formula is as follows:

$$EHU = [(T_x + T_n)/2] - 10$$

EHU - effective heat units per day

T_x - maximum temperature if $T_x \leq 30^\circ\text{C}$ or $[30^\circ\text{C} - (T_x - 30^\circ\text{C})]$ if $T_x > 30^\circ\text{C}$;

T_n - minimum temperature if $T_n \geq 10^\circ\text{C}$ or 10°C if $T_n < 10^\circ\text{C}$.

Holmes & Robertson (1959, in Wang 1960) introduced a generalized formula for the computation of degree days:

$$DD = N[(t - b) + L\sigma/N]$$

DD - degree days per month

N - number of days in a month

t - monthly mean temperature

b - base temperature

L - proportionality coefficient obtained from a table

σ - standard deviation of monthly mean temperature

The estimation of heat units by measuring the area under a sine curve, the amplitude of which has been adjusted to the daily maximum and minimum temperatures, was proposed by Arnold (1960), and has proved an efficient tool of considerable value to plant ecologists. The area below a temperature curve for a specific time span, can be measured directly by the use of a planimeter, or indirectly, through the measurement of the mean temperature for the day (Arnold 1960). The precision of the estimate is not affected by the introduction of upper temperature thresholds and is well within the

limitations set by the ability of the ecologist to make biological interpretations of the data.

Although ecologists often use heat units above a given threshold or base temperature to measure or predict the effect of temperature on biological processes (Baskerville & Emin 1969), Arnold (1960) cautioned that heat unit accumulations did not give exact answers to practical problems, even if they were based on accurate temperature measurements. This could be the result of one or more of the following:

- it is usually assumed that the relationship between temperature and the rate of plant development is linear while it is undoubtedly curvilinear;
- other environmental factors besides temperature, i.e. daylength and irradiance, affect the rate of plant development;
- temperature measured at a single location is used as a basis for predictions and the variations in microclimate are ignored; and
- the use of a fixed threshold or base temperature throughout the life span of a plant species does not take into account that the base temperature varies with external conditions and plant age (Wang 1960).

According to Lettau (1965) the use of air temperature alone was not satisfactory with regard to the prediction of flowering time of lady's slippers (*Cypripedium acaule*). She investigated the combined use of soil and air temperature to predict flowering time in this species. The daily mean soil temperature above a base temperature was accumulated until a certain value was achieved, whereafter the daily mean air temperature above the same base temperature was accumulated. With the combination of soil and air temperature, Lettau (1965) could predict flowering time of *C. acaule* with an accuracy of three days.

In 1969 Abrami modified the formula of Lindsey & Newman (1956) by using two

temperature thresholds:

$$A = 12(b - c) [(2a - b - c)/a - d]$$

A - area contained above a threshold temperature and under the trace on a thermograph chart (degree hours per day)

a - larger of either maximum temperature or upper threshold

b - lesser of either maximum temperature or upper threshold

c - lower threshold

d - lesser of either minimum temperature or lower threshold

If the daily temperature remains below the minimum threshold, the area is defined as zero, which means that on such a day, the effects of temperature on growth cannot be estimated (Abrami 1969). Abrami (1969) found it necessary to consider a possible different lower as well as upper threshold temperature for every 24 hour growth period. These two points (upper and lower thresholds) delimit the range within which growth appears to be influenced in a measurable way by temperature changes.

Temperatures above an optimum and below a base temperature were ignored by Iwata & Okubo (1969, in Eicker 1979) by taking temperatures above the optimum as equal to the optimum and below the base as equal to the base. Their formula was found by Eicker (1979) to give the best prediction of the date of 50% flowering in *Zea mays*, grown in the western Transvaal, South Africa.

In a study by Baskerville & Emin (1969) a FORTRAN program was written which calculates heat accumulation using: a) the lower threshold only; b) an upper threshold with a horizontal cut-off; and c) an upper threshold with a vertical cut-off. The input consists of a serial listing of daily maximum and minimum temperatures. The output is a 12 (month) x 31 (day) matrix giving the total accumulated heat units at the end of each day.

Heat units can also be expressed in growing hour units, if continuous temperature data is available (Lowry 1970):

$$GHU = \sum_n (T - T_t)$$

GHU - growing hour units if $T > T_t$

n - number of hours

T - hourly temperature

T_t - base temperature

In 1976 Bunting tried to improve the formula of Adanson with the following:

$EHU = [(T_x - 10)/2] - [(10 - T_n)/4]$ if the mean daily temperature is above 10°C;

$EHU = [(T_x - 10)/4] - [(10 - T_n)/4]$ if the mean daily temperature is below 10°C.

EHU - effective heat units per day

T_x - maximum temperature

T_n - minimum temperature

10°C was taken as the base temperature

The heat unit formula of Bunting (1976) is not widely used as it is, according to Eicker (1979), based on the Adanson formula which he regards as useless.

Brown's (1978) formula makes provision for a curvilinear relationship between day temperature and plant development, while the relationship between night temperature and plant development is linear:

$$HU = Y_1 + Y_2$$

HU - heat units per day

$$Y_1 = 3.33 (T_x - 10^\circ\text{C}) - 0.0842 (T_x - 10^\circ\text{C})^2$$

$$Y_2 = 1.8 (T_n - 4.4^\circ\text{C})$$

T_x - maximum temperature

T_n - minimum temperature

10°C was taken as the base temperature during the day;

4.4°C was taken as the base temperature during the night.

A pre-condition for the use of this formula is to allocate a value of zero to Y_1 and/or Y_2 if the maximum temperature of a certain day is below 10°C or the minimum night temperature drops below 4.4°C respectively. This formula was successfully used in the

prediction of the date of 50% flowering in *Zea mays* grown in Canada (Brown 1978).

McGiffen & Masiunas (1992) improved the accuracy of the calculated degree days by transforming the daily minimum-maximum air temperatures into continuous data using a sine wave approximation of the diurnal rise and fall of temperature.

b) Cold units

Another approach was proposed by Richardson, Seeley & Walker (1974) who used the accumulation of cold units to predict the breaking of dormancy in deciduous fruit trees. He accumulated the hours with favourable temperatures, but ascribed more value to temperatures which were efficient to break winter dormancy. A negative value was given to high temperatures, as they had a negative effect on the breaking of dormancy.

Richardson's formula is the following:

$$CU = \sum_{i=1}^n \sum_{j=1}^7 (a_j P_{ij})$$

n = number of days per month

$$a_1 = 0$$

$$a_2 = 0.5$$

$$a_3 = 1.0$$

$$a_4 = 0.5$$

$$a_5 = 0$$

$$a_6 = -0.5$$

$$a_7 = -1.0$$

P_{i1} = number of hours during day i with a mean temperature below 1.4°C

P_{i2} = number of hours during day i with a mean temperature from 1.4°C to < 2.5°C

P_{i3} = number of hours during day i with a mean temperature from 2.5°C to < 9.3°C

P_{i4} = number of hours during day i with a mean temperature from 9.3°C to < 12.5°C

P_{i5} = number of hours during day i with a mean temperature from 12.5°C to < 15.9°C

P_{i6} = number of hours during day i with a mean temperature from 15.9°C to 18.0°C

P_{i7} = number of hours during day i with a mean temperature above 18°C

Richardson's formula was successfully applied by Anderson (1974) and Matthee (1982) to predict the breaking of dormancy in deciduous fruit trees in the western Cape Province, South Africa.

In 1990 Craigon, Atherton & Basher calculated vernalizing degree days in carrot (*Daucus* sp.) by using daily mean air temperatures. For days when the mean air temperature lay between the base and optimum temperature, the vernalizing day degrees were taken as the mean temperature minus the base temperature. For days when the mean temperature lay between the optimum and maximum vernalizing temperatures, that temperature was converted to its equivalent 'effective' temperature in the sub-optimum range and degree days calculated as before.

METHODS USING TEMPERATURE AND PHOTOPERIOD

According to Wang (1960), Fritsch is known as the first person (1861) who used the product of photoperiod and temperature to express the climatological needs of 889 plant species from flowering until ripening of the seeds. He calculated photothermal units per day (PT) as follows:

$$PT = T \times L$$

T - mean daily temperature

L - daylength in hours

Nuttonson (1955) found that the use of photothermal units resulted in a more constant number of units needed to attain certain phenological stages than heat units alone. He used the following formula, which included the use of a base temperature:

$$PTU = \sum_{i=Dp}^{Dm} (T - T_c)t_s$$

PTU - photothermal units

Dp - planting date
 Dm - date of maturity
 T - mean daily temperature
 Tc - base temperature
 t_s - daylength in hours

According to Eicker (1979) photothermal units can also be calculated by the following formula:

$$PTU = 2ht \times \text{Daylength} / 12$$

PTU - photothermal units per day

2ht - sum of 2-hourly temperatures

In 1980 Maas & Arkin (in Perry, Siddique & Wallace 1987) used a 'rate-duration' method to simulate phenological development in crop growth models. The model may be evaluated using daily mean temperature and photoperiod to give a rate of development (day⁻¹) for a single day. By evaluating the model for successive days and summing the resultant rates, it is possible to monitor progress through a development stage to the point where the stage is completed when the sum of the daily development rates equals 1.0. That is

$$\sum_{i=1}^n DDR = 1.0$$

DDR - daily development rate

n - number of days required to complete the development phase

Perry *et al.* (1987) developed the following model to predict flowering times of wheat in Australia:

$$1/D = b_0 + b_1(T_m) + b_2(P_m)$$

D - duration from sowing to flowering

T_m & P_m - the average daily mean temperature and photoperiod during the phase

b₀, b₁ & b₂ are fitted regression parameters which characterize each cultivar

According to Loss, Perry & Anderson (1990) the above mentioned model offered a simple method of predicting flowering times of Australian wheat. The predicted flowering times for cultivars with vernalization requirements were as accurate as those for other cultivars, despite the model not accounting explicitly for vernalization.

METHODS USING IRRADIATION

A study of Clausen, Keck & Hiesey (1940, in Caprio 1974) suggested that the number of solar thermal units required to bring ecotypes of the same species into bloom, appeared to be in some way directly related to the total solar thermal units available for the entire growing season.

Caprio (1974) found that an area such as Seattle, U.S.A., where more degree days are required to induce flowering than in Glasgow, Scotland, are characterized by less sunshine in the spring and he included irradiation in his formula:

$$\text{STU} = [\text{cal}(0.3 - 4 \text{ micron})/\text{cm}^2 \text{ per day}][(\text{T}_m + \text{T}_n)/2] - \text{T}_b]$$

STU - solar thermal units per day

T_m - maximum temperature

T_n - minimum temperature

T_b - base temperature

According to this solar thermal unit theory the number of degree days required to bring lilacs (*Syringa vulgaris*) to bloom, is inversely related to the amount of solar irradiation received (Caprio 1974).

Bates (1976) summed the amount of irradiation (MJ/m² per day) from sowing until harvest. The accumulation of the daily irradiation was successfully used in the case of citrus trees in the United States and Israel (Newman *et al.* 1968).

STRESS UNITS

According to Idso *et al.* (1978), water stress is often a factor in shortening a plant's life span and it should be included in any model that attempts to determine rates of phenological development. The formula they used is:

$$SSD = (T_c - T_a)_{PM}$$

SSD = standard stress degree days

$(T_c - T_a)$ = canopy - air temperature differential existing at 14:00 on a given day.

Based on their findings Idso *et al.* (1978) proposed that the utility of the traditional degree day concept of plant phenology determination, could be significantly enhanced by combining it with the stress degree day concept. According to them, the results illustrated the general principle that degree days alone could not reflect the lengths of a plant's various stages of growth, but rather some combination of those degree days and the stress degree days concurrently accumulated. Their combined approach integrated the soil environment with the standard climatic representation provided by the traditional degree day concept.

In spite of all the criticism against the use of effective heat units or growing degree days (GDD) (Adanson 1750, in Dijkhuis 1971) and the development of new formulae, it seems as if GDD is still the most popular formula in the computing of thermal units (Katz 1952; Robinson 1971; Doyle 1975; Goyne, Woodruff & Churchett 1977; Peng, Krieg & Hicks 1989; Sparks 1989; McGiffen & Masiunas 1992). Growing degree days is a simple yet effective method to calculate the number of required heat units. Pettitt, Allen & Barfield (1991) used degree days in studying the phenology of vegetable leafminer (Diptera: Agromyzidae).

CHAPTER 3

METHODS

This chapter summarizes the methods used in this study. For a more detailed description of the methods employed, the reader is referred to the relevant articles of Steyn *et al.* (In prep. a - e)(see Chapters 4 - 8).

Seeds/achenes of five ephemeral plant species were collected in the Goegap Nature Reserve approximately 12km east of Springbok (29°41'S, 17°55'E) in Namaqualand. According to Acocks (1988), the area is part of the Namaqualand Broken Veld and the climate of the area is characterized by warm, dry summers and cold, moist winters. All the plants for the various experiments were grown outside or under controlled conditions at the University of Pretoria.

PLANT SPECIES USED IN THIS STUDY

a) *Dimorphotheca sinuata* DC.

Dimorphotheca sinuata is so spectacular and common in Namaqualand, that it has become known as the Namaqualand Daisy. *Dimorphotheca sinuata* is an ephemeral forb of the Asteraceae that forms a bushy plant, growing 100 - 300mm high with flower-heads about 80mm in diameter. The inflorescences are composed of a single row of oblong florets that are greenish-purple at the base, forming a ring around an orange centre (Eliovson 1972) (Figure 1a). The leaves of this species are usually shallowly-lobed (Le Roux & Schelpe 1988).

b) *Foveolina albida* (DC.) Kallersjo

An ephemeral of the Asteraceae, branching mainly from the base. The leaves are silvery-haired and doubly-lobed and up to 20mm long. The flower-heads have only yellow disc-florets (Figure 1b), are almost round, 50 - 70mm in diameter, single and borne on long slender flower-head stalks (Le Roux & Schelpe 1988).

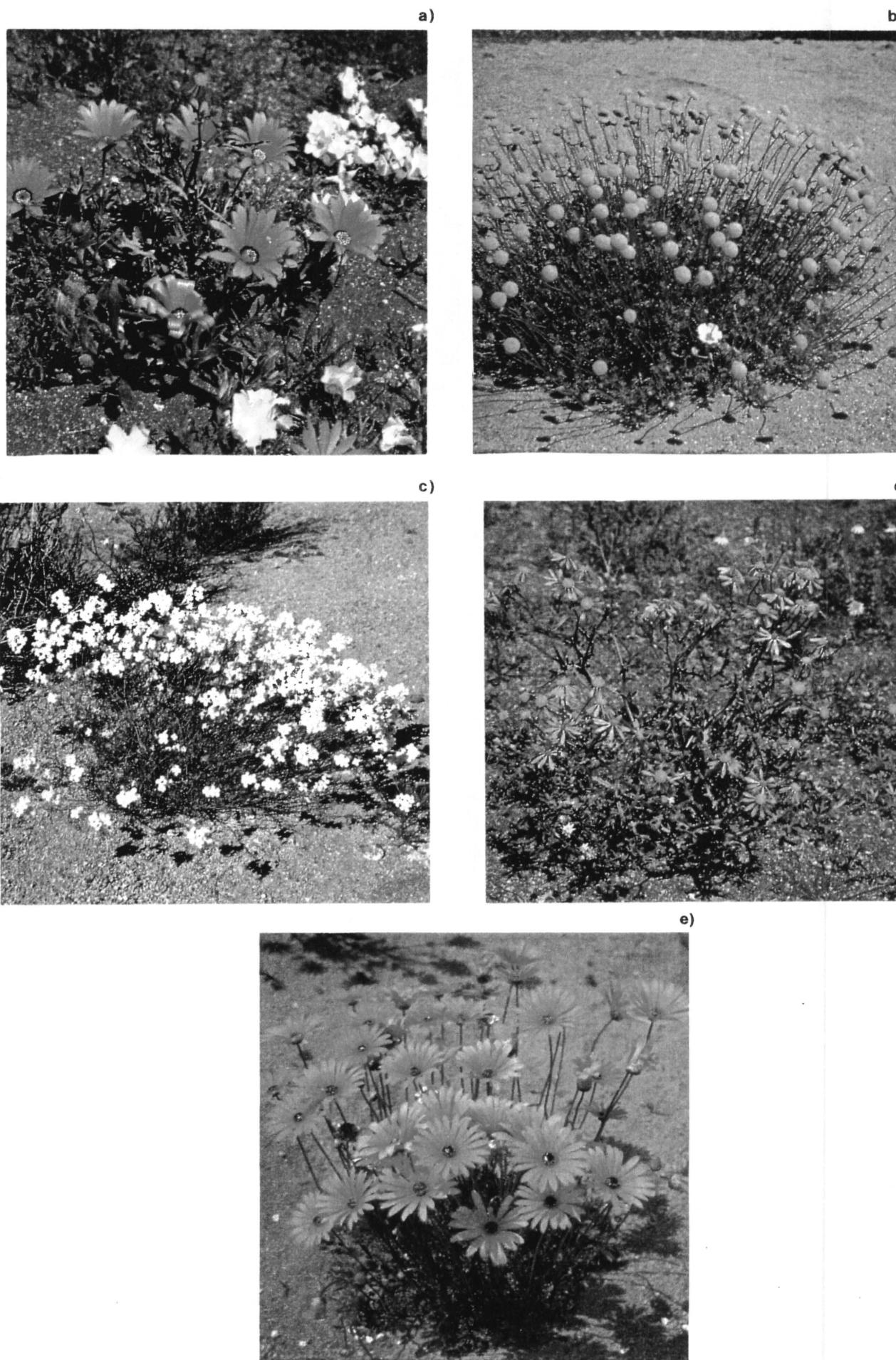


Figure 1. Namaqualand ephemeral species used in this study; a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and e) *Ursinia cakilefolia*.

c) *Heliophila seselifolia* Burch. ex DC. var. *seselifolia*

In this erect, much-branched ephemeral of the Brassicaceae, from 7 to 11 stems branch out at ground level and grow to a height of 350mm. The leaves are up to 70mm long and lobed into 3 - 7 very narrow, entire segments. The masses white flowers are loosely clustered at the ends of the branches (Figure 1c). The fruits are about 30mm broad and slightly beaded (Le Roux & Schelpe 1988).

d) *Senecio arenarius* Thunb.

Senecio arenarius is an ephemeral of the Asteraceae growing up to 400mm high. The leaves are bright green, up to 80mm long, hairy and lobed to doubly-lobed into toothed segments, being smaller near the top of the plant. This species usually bears clusters of small daisies that are grouped together in a broad compact head that is showy in mass (Eliovson 1972). The flower-heads are about 25mm in diameter with magenta-pink ray-florets and yellow disc-florets (Figure 1d). The involucral bracts are free in a single row (Le Roux & Schelpe 1988).

e) *Ursinia cakilefolia* DC.

An ephemeral of the Asteraceae, growing up to 250mm high. The light green feathery leaves are up to 60mm long, toothed and doubly-lobed into very narrow segments. The flower-heads are borne singly on slender stalks that stand well above the foliage and the drooping buds straighten up as they come into flower (Eliovson 1972). The flower-heads are 25 - 35mm in diameter with orange ray-florets and black disc-florets (Figure 1e). The involucral bracts are in many rows and the innermost bracts are the largest with a conspicuous transparent tip (Le Roux & Schelpe 1988).

To study the effect of various factors on the phenology of these five ephemeral species, the following experiments were carried out:

THE EFFECT OF CONTROLLED TEMPERATURE AND SOWING DATE

Disc flower achenes of *Dimorphotheca sinuata* and *Ursinia cakilefolia* were sown in a

temperature controlled glass house on the fifth of April and the fourth of June 1991. Ten replicates were used. Twenty eight days after sowing, the plants were subjected to one of five temperature treatments (Steyn *et al.* In prep. a)(see Chapter 4):

- 1) control: remained at 22°C/16°C (9 hours/15 hours);
- 2) cold treatment: 14 days at 22°C (9 hours) and 3°C (15 hours);
- 3) heat treatment; 14 days at 25°C for 24 hours;
- 4) cold/heat treatment: 14 days at 22°C (9 hours) and 3°C (15 hours) and four weeks later, a heat treatment for 14 days at 25°C; and
- 5) heat/cold treatment: 14 days at 25°C for 24 hours and four weeks later, a cold treatment for 14 days at 22°C (9 hours) and 3°C (15 hours).

While not undergoing a heat or cold treatment, plants were placed in a control room (22°C/16°C) and grown at prevailing daylengths.

Phenological data were collected weekly from 28 days after sowing. From flower bud initiation, all plants were examined phenologically, twice a week. The phenological stages which were distinguished were inflorescence initiation, anthesis, 50% flowering and peak flowering.

THE EFFECT OF SOWING DATE

Potting trials

Seeds/achenes of *Dimorphotheca sinuata* (disc flower achenes), *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* and *Ursinia cakilefolia* were sown on four different dates: the fifth of April, the second of May, the fourth of June and the second of July. Ten replicates were used for each species (Steyn *et al.* In prep. b) (see Chapter 5).

Phenological data were collected weekly from 28 days after sowing. From the initiation of flowers/inflorescences, all plants were examined phenologically, twice a week. The following phenological stages and the number of days since sowing on which each stage was reached, was noted for each plant: flower/inflorescence initiation, first flower/inflorescence at anthesis and peak flowering time.

Field observations

During August and September 1991 phenological data on the same five species were recorded in the Springbok area, Namaqualand. The height, number of open flowers/inflorescences, number of floral buds as well as the flowering stage were determined randomly for each of 20 plants at a locality on a particular date (Steyn *et al.* In prep. b)(see Chapter 5).

THE EFFECT OF WATER STRESS

Seeds/achenes of *Dimorphotheca sinuata* (disc flower achenes), *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* and *Ursinia cakilefolia* were sown on four dates: the fifth of April, the second of May, the fourth of June and the second of July. Ten replicates were used. Control plants were watered daily, while plants subjected to water stress, were watered only once a week (Steyn *et al.* In prep. c)(see Chapter 6).

Twenty eight days after sowing the weekly recording of phenological data started. The following phenological stages were distinguished and the number of days from the sowing date on which each stage was reached, was noted for each plant: flower/inflorescence initiation, first flower/inflorescence at anthesis and peak flowering.

THE EFFECT OF ACHENE AGE

Disc flower achenes of *Dimorphotheca sinuata* were collected in the spring of 1989, 1990 and 1991 in the Goegap Nature Reserve.

In 1991 the achenes collected in 1989 and 1990 were sown on four dates as in the case of the sowing date experiment. In April 1992 the experiment was repeated with achenes collected in all three years (Steyn *et al.* In prep. d)(see Chapter 7).

All plants were examined phenologically twice a week from the initiation of inflorescences. The following phenological stages were distinguished: inflorescence initiation, first inflorescence at anthesis and peak flowering.

THERMAL UNITS

Results from the sowing date experiment (Steyn *et al.* In prep. b)(see Chapter 5) were used to determine the time needed until a certain phenological stage was reached. Thermal unit indices were used to calculate the amount of thermal units required by a species to reach a certain phenological stage (Steyn *et al.* In prep. e)(see Chapter 8).

The air temperature (°C) and the relative air humidity (%) were registered continuously at the experimental site. The daily maximum and minimum temperatures, the daylengths as well as the irradiation at Pretoria (25°24'S, 28°10'E) and Springbok (29°41'S, 17°55'E) for the timespan April until September 1991 were obtained from the Weather Bureau in Pretoria.

For more information on the accumulation of thermal units and the statistical criteria used, the reader is referred to Steyn *et al.* (In prep. e)(see Chapter 8).

STATISTICAL ANALYSIS

An analysis of variance (ANOVA), was used to test for statistical differences at $\alpha = 0.05$. Scheffé's test and the LSD test (Least Significant Difference) were used for paired comparisons between species and between treatments within each species. Differences in plant height data were analyzed statistically at 40, 80 and 120 days after sowing.

Where applicable a multifactor analysis of variance was used to test for significant differences. All the data were analyzed with the use of the Statgraphics 5.0 computer program (1989, STSC, Inc., 2115 East Jefferson Street, Rockville, Maryland 20852, U.S.A.).

CHAPTER 4
**THE INFLUENCE OF TEMPERATURE AND SOWING DATE ON
THE PHENOLOGY OF TWO NAMAQUALAND EPHEMERAL
SPECIES UNDER CONTROLLED CONDITIONS**

H.M. STEYN, N. VAN ROOYEN, M.W. VAN ROOYEN & G.K. THERON

(Department of Botany, University of Pretoria, Pretoria 0002)

ABSTRACT

The phenology of two Namaqualand ephemerals, *Dimorphotheca sinuata* DC. and *Ursinia cakilefolia* DC., was studied under different controlled temperatures at two sowing dates.

In both species, different temperature treatments and sowing dates had no significant effect on the maximum plant height that was attained, although plants from the June (winter) sowing, started rapid stem elongation sooner than those of the April sowing (autumn) and heat treated plants tended to be taller in the case of *U. cakilefolia*. In both species, a cold treatment early in the life cycle, stimulated inflorescence initiation and anthesis.

Plants sown in June produced more inflorescences at peak flowering, than those sown in April. It appeared that plants established in June had a longer and more spectacular flowering period.

The distinct differences in phenology displayed by plants of the two sowing dates can probably be attributed to the differences in daylength experienced by April and June plants.

KEY WORDS: *Dimorphotheca sinuata*, ephemerals, phenology, sowing date, temperature, *Ursinia cakilefolia*

INTRODUCTION

Namaqualand is an arid region in the north-western corner of the Republic of South Africa. The climate of Namaqualand can be described as a warm, dry desert climate, characterized by sparse, irregular winter rainfall and large daily and seasonal temperature fluctuations (Schulze 1965).

This area supports an abundant flora of annual plants which transform this barren area during spring into a showy floral display (Le Roux & Schelpe 1988). Due to the unpredictable nature of the rainfall, germination of seeds of ephemeral species can occur anytime from autumn to mid-winter, depending on the timing of the first good rains (Van Rooyen, Grobbelaar & Theron 1979). The growth period of these ephemerals can last six to eight months when the rainy season starts early (March), or the growth period may only last two to three months if the rain comes in mid-winter (July) (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992).

Many studies have been carried out to determine the effect of environmental factors on the growth rate of plants (Wilson 1967; Constable & Rose 1988; Roberts & Menary 1989; Seddigh, Jolliff & Orf 1989; Mortensen 1991). The relationship between growth rate and temperature is dynamic, as the inherent growth rhythm of the plant has a strong effect on its response to temperature (Hari, Kellomaki & Vuokko 1977). Temperature plays a dual role in growth as it strongly affects the daily increments and determines the rate of maturation (Hari *et al.* 1977). The effect of temperature on flower initiation is also two-fold: firstly it modifies the photoperiodic requirement for initiation, and secondly it directly affects flower development (Roberts & Menary 1989).

The aim of this study was to determine the effect of different controlled temperature treatments and sowing dates on the phenological development of two Namaqualand ephemeral species, and thereby to test the hypothesis that low temperatures promote flower bud initiation of winter annuals (Mott & McComb 1975; Van Rooyen *et al.* 1992) and anthesis in some annual species (Baskin & Baskin 1974). This paper forms part of a study (Steyn 1993) on the influence of environmental variables (temperature and water

stress), sowing date and achene age on the phenology of selected Namaqualand ephemerals, with the prediction of peak flowering time as the ultimate goal (Steyn, Van Rooyen, Van Rooyen & Theron In prep. a)(see Chapter 8).

METHODS

Disc flower achenes of *Dimorphotheca sinuata* DC. and *Ursinia cakilefolia* DC. were collected in 1990 from plants growing in the Goegap Nature Reserve (between longitude 17°55' and 18°08' and latitude 29°34' and 29°43') close to Springbok, Namaqualand. The experiments were conducted at the University of Pretoria in a temperature controlled glass house at temperatures of 22°C/16°C (day/night) and prevailing daylengths. In all five treatments, the "daytime" temperature conditions extended from 8:00 - 17:00 and "night" temperatures from 17:00 - 8:00. The achenes were sown in pots with a volume of 1 000 cm³, filled with quartz sand, on two sowing dates, viz. the fifth of April 1991 (April plants) and the fourth of June 1991 (June plants). Two weeks after sowing the seedlings were thinned to one per pot. Ten replicates were used per treatment and all the values in Tables and Figures are the mean except where stated otherwise.

Temperatures were recorded continuously by means of a thermohygrograph and corrected with minimum and maximum thermometers. Daylengths were obtained from the Weather Bureau in Pretoria.

Twenty eight days after sowing, the plants were subjected to one of the following five treatments:

- a) control: remained at 22°C/16°C (9 hours /15 hours)
- b) cold treatment: 14 days at 22°C (9 hours) and 3°C (15 hours);
- c) heat treatment: 14 days at 25°C for 24 hours;
- d) cold/heat treatment: 14 days at 22°C (9 hours) and 3°C (15 hours) and four weeks later, a heat treatment for 14 days at 25°C; and

e) heat/cold treatment: 14 days at 25°C for 24 hours and four weeks later, a cold treatment for 14 days at 22°C (9 hours) and 3°C (15 hours).

While not undergoing cold and/or heat treatments, plants were kept in the control room (22°C/16°C) and grown at prevailing daylengths.

All plants were watered daily to field capacity with tap water that was kept at room temperature and once a week, Arnon & Hoagland's complete nutrient solution (Hewitt 1952) was applied. All plants were examined phenologically, twice a week and the height or length of each plant was measured weekly. Both species belong to the family Asteraceae, and the individual flowers were not counted, but an inflorescence was considered as an unit. The following phenological stages were distinguished: inflorescence initiation, anthesis, 50% flowering and peak flowering. The date on which the stage was reached, was noted for each plant and the number of days from sowing until a specific phenological stage had been reached, was calculated. The terms peak or peak flowering are used throughout this paper to indicate the date on which the highest number of open inflorescences over the entire flowering period, occurred. In contrast, a flowering peak refers to any significant culminating point in the flowering curve - not necessarily the highest peak. The date on which the number of open inflorescences was 50% of the number at peak flowering, was termed the date of 50% flowering.

An one-way analysis of variance (ANOVA), was used to test for a statistically significant difference at $\alpha = 0.05$. Scheffé's test of the Statgraphics 5.0 computer program (1989, STSC, Inc., U.S.A.) was used for paired comparisons between species and between treatments within each species. Differences in plant height data between treatments were analyzed statistically at 40, 80 and 120 days from sowing. A multifactor analysis of variance was used to test for significant differences in the total number of inflorescences produced at different treatments.

RESULTS AND DISCUSSION

Plant height

Dimorphotheca sinuata

No significant difference in the maximum height attained by plants subjected to different temperature and sowing date treatments could be demonstrated (Figure 1a & b). This is contrary to the findings of Van Rooyen (1988) and Steyn, Van Rooyen, Van Rooyen & Theron (In prep. b)(see Chapter 5), who found that plants sown in April were significantly taller than those sown in June when grown out of doors under naturally varying winter temperatures and prevailing daylength.

Plants of the five temperature treatments sown in June (June plants), elongated sooner and at an age of 40 and 80 days they were significantly taller than plants of the April sowing (April plants) of the same age (Figure 1a & b). Height differences between April and June plants disappeared from 100 days after sowing. Plants sown in April reached their maximum height at an age of approximately 120 days, while the maximum height of June plants was reached at approximately 80 days (Figure 1a & b). Since the temperature treatments remained the same these differences between April and June plants could probably be attributed to differences in daylength between the sowing dates (Table 1). Daylength decreased for the first 77 days in the case of the April plants, while daylength started to increase 18 days after the sowing of June plants. Although the daylength experienced by April plants decreased for the first 11 weeks, they nevertheless developed under longer daylengths than June plants for the first 40 days. The difference in plant height between April and June plants became more apparent between 40 and 100 days after sowing, when the daylengths experienced by June plants were longer than those experienced by April plants. This response of *D. sinuata* to daylength confirms the statement of Sharma and Nanda (in Salisbury 1981) that the most common vegetative growth response to photoperiod in the annual *Eschscholtzia californica*, is an increased rate of stem elongation under long days.

Table 1. Daylength at Pretoria for the period 4 April until 30 July. (Sowing dates were 5 April and 4 June)

Date	Daylength (hours)	Date	Daylength (hours)
4 April	11.76	4 June	10.62
11 April	11.61	11 June	10.56
18 April	11.43	18 June	10.55
25 April	11.28	25 June	10.56
2 May	11.11	2 July	10.58
9 May	10.98	9 July	10.63
16 May	10.86	16 July	10.72
23 May	10.75	23 July	10.80
30 May	10.67	30 July	10.92

Ursinia cakilefolia

As in the case of *D. sinuata*, plants of *U. cakilefolia* of both sowing dates reached more or less the same maximum height after 140 - 155 days. The June plants of all temperature treatments elongated sooner than April plants (Figure 1c & d) and at an age of 40 and 80 days, June plants were significantly taller than April plants.

Plants sown in April elongated until they were harvested at an age of 150 days. The height curve of April plants subjected to a cold/heat treatment, levelled off after 76 days, but two weeks later elongation recurred (Figure 1c). The other four treatments produced sigmoid growth curves (Figure 1c). June plants, on the other hand, reached their maximum height at approximately 100 days. In the case of the cold treatment the growth curve levelled off after 60 - 70 days. June plants subjected to a heat treatment showed the longest period of increasing height (Figure 1d).

The plants of both sowing dates, subjected to a heat treatment produced the tallest plants (Figure 1c & d) although this difference was not significant at $\alpha = 0.05$. A cold/heat treatment and a cold treatment retarded the growth of April and June plants respectively. These results indicate that high temperatures enhance height growth in *U. cakilefolia* irrespective of the sowing date.

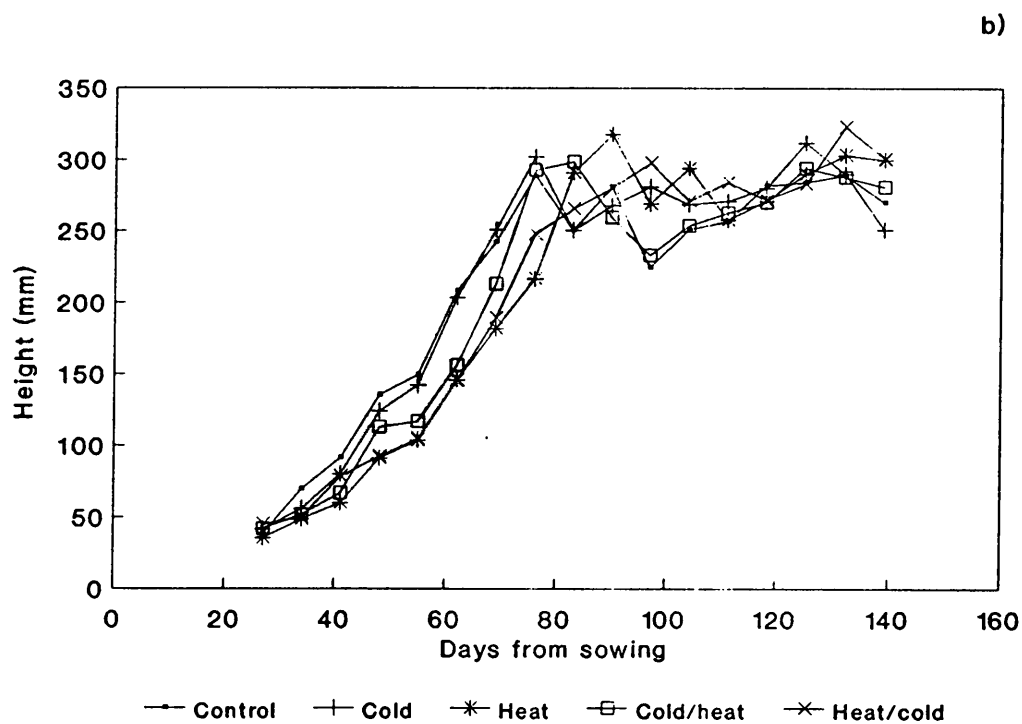
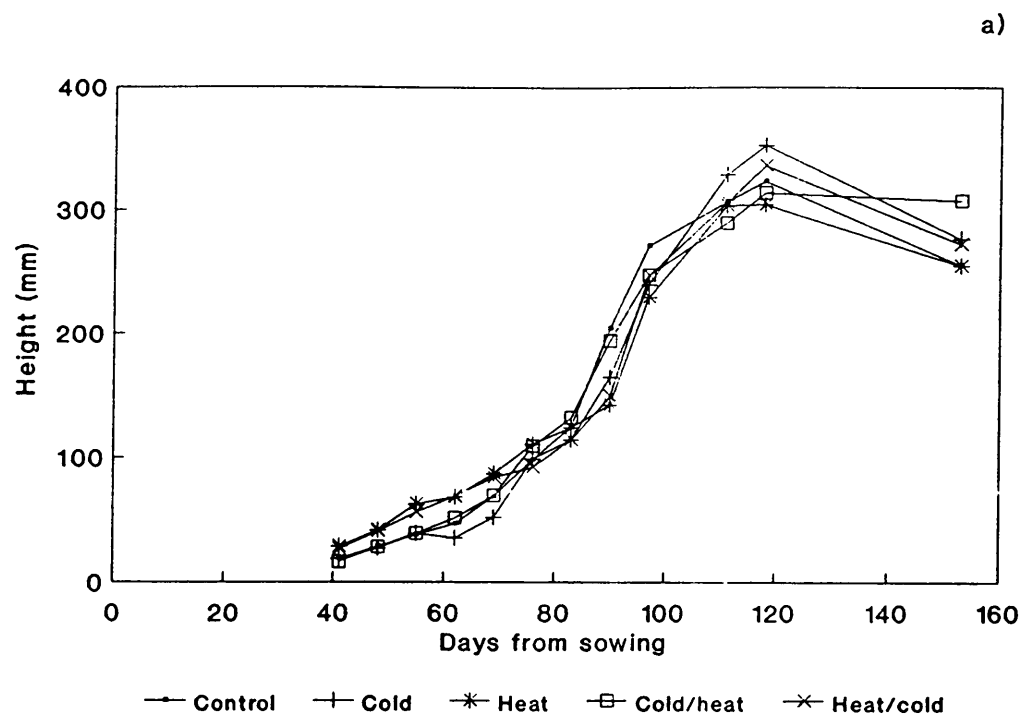


Figure 1. The height of plants grown under different temperature treatments. *Dimorphotheca sinuata* plants sown in a) April and b) June, and *Ursinia cakilefolia* plants sown in c) April and d) June.

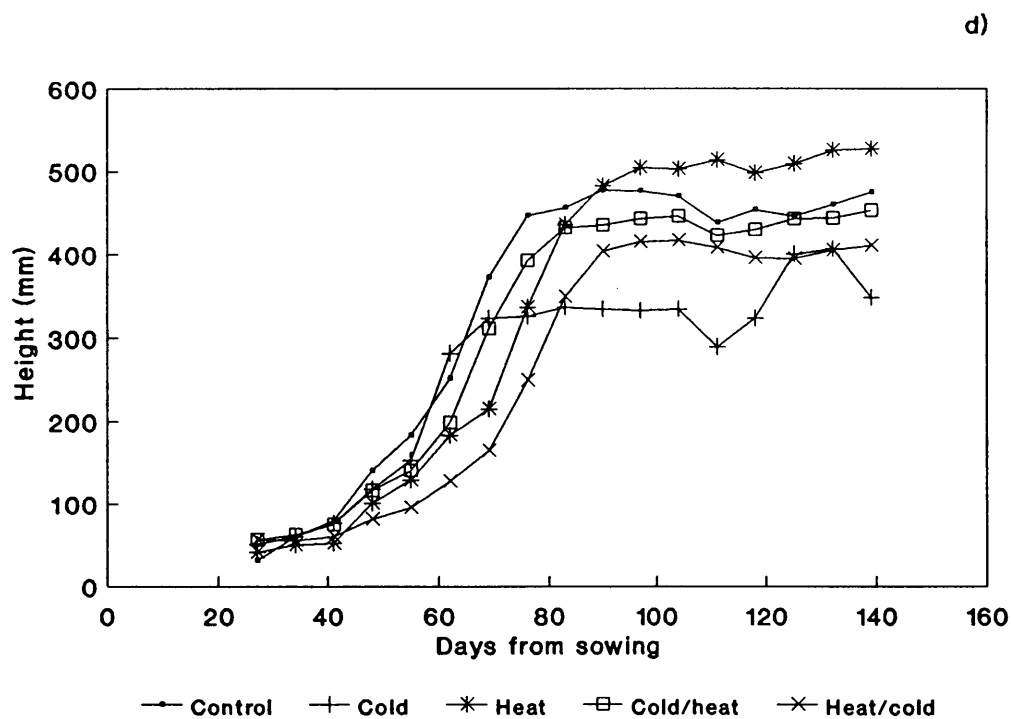
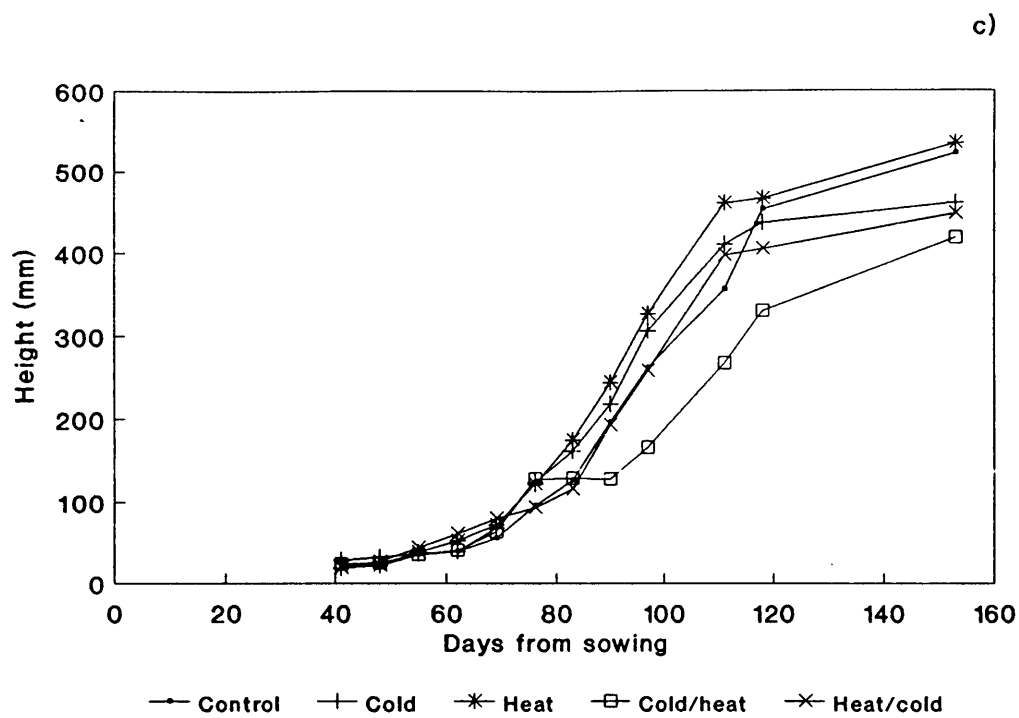


Figure 1. Continued.

Number of leaves on the main stem at inflorescence initiation

Dimorphotheca sinuata

During the initial rosette phase of *D. sinuata*, leaves were produced only on the main stem. The apical meristem of the main stem also produced the first floral primordium. Therefore, the number of leaves produced on the main stem was determined by factors controlling flower initiation (Van Rooyen *et al.* 1992).

April plants subjected to a cold and cold/heat treatment, had significantly less leaves on the main stem at inflorescence initiation than those of the two heat treatments (Figure 2a). These results confirm those of Mott & McComb (1975) and Van Rooyen (1988), and imply that these plants are developmentally younger at inflorescence initiation than the plants of the other treatments. In the case of June plants there was a significant difference in number of leaves on the main stem between plants of the cold/heat and heat/cold treatments (Figure 2b). For both sowing dates, therefore plants subjected to high temperatures (heat and heat/cold treatments) produced more leaves on the main stem than the other treatments. These results are also supported by the findings of Elphinstone & Rees (1990) who found that the final number of leaves initiated in *Iris x hollandica* before flowering, increased with increasing temperature.

Ursinia cakilefolia

April plants subjected to a cold and cold/heat treatment, had significantly less leaves on the main stem (Figure 2c) than those of the heat/cold treatment, while plants of the cold/heat treatment also had significantly less leaves than plants of the heat treatment. There was no significant difference in number of leaves on the main stem between June plants (Figure 2d).

Production of inflorescences

In the case of *D. sinuata*, the average time from sowing to inflorescence initiation of April plants, was shorter when cold or cold/heat treated than with any of the other treatments (Table 2). Inflorescence initiation started first in the control and cold/heat

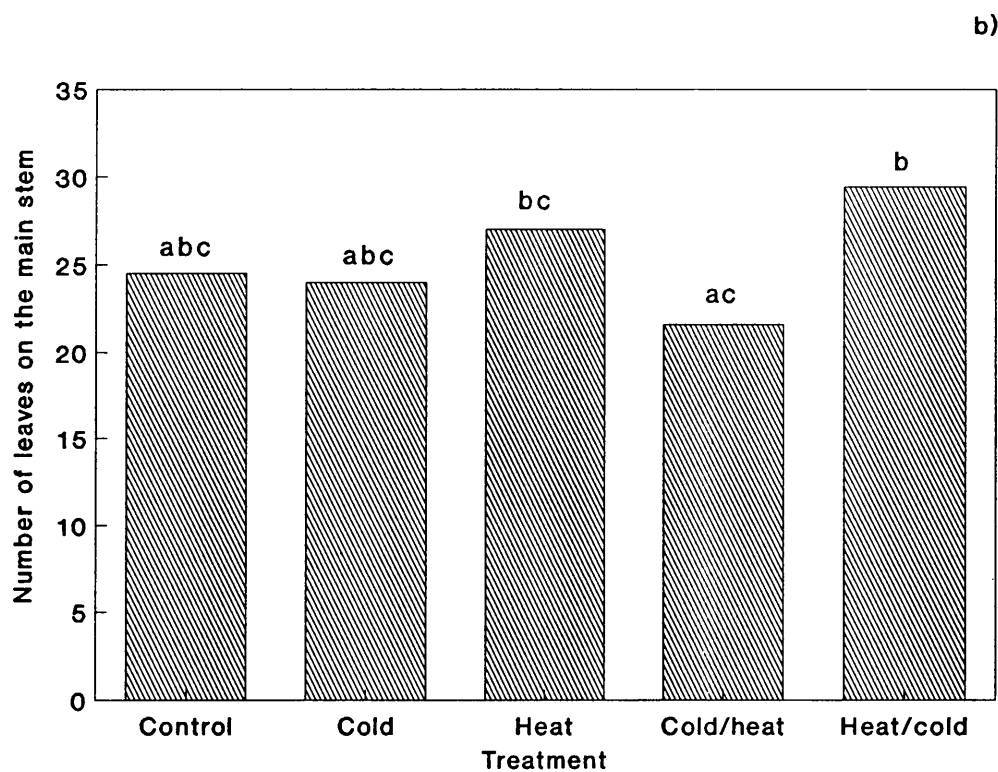
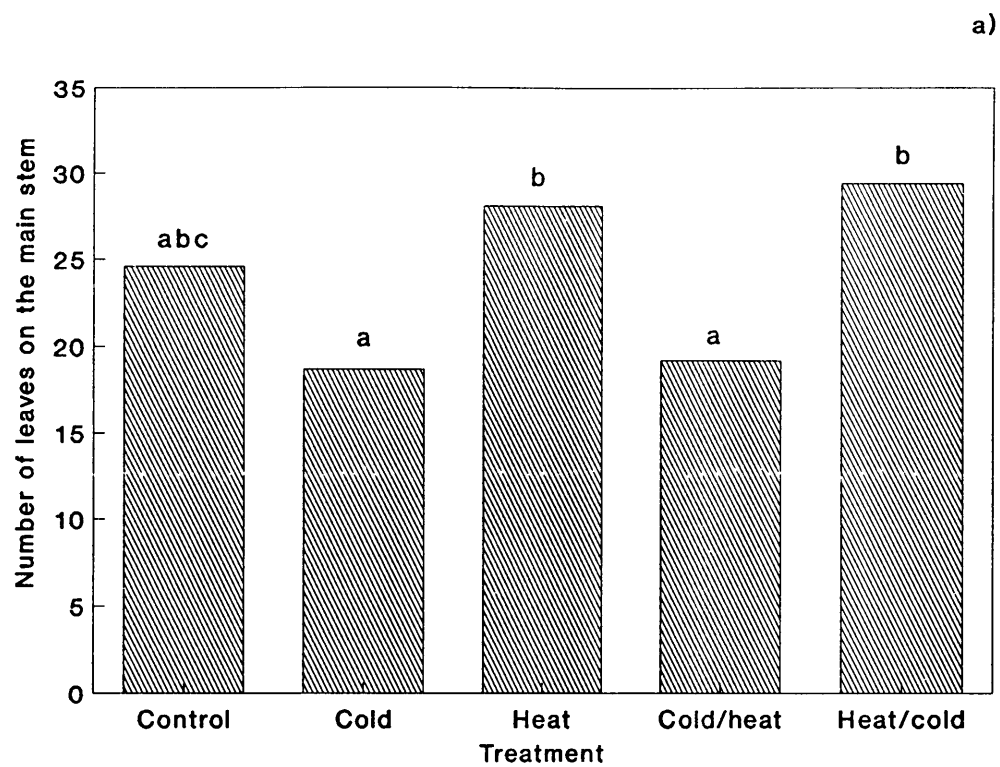


Figure 2. The average number of leaves on the main stem at inflorescence initiation of plants grown under different temperature treatments; *Dimorphotheca sinuata* plants sown in a) April and b) June, and *Ursinia cakilefolia* plants sown in c) April and d) June. Bars with the same letter do not differ significantly at $\alpha = 0.05$.

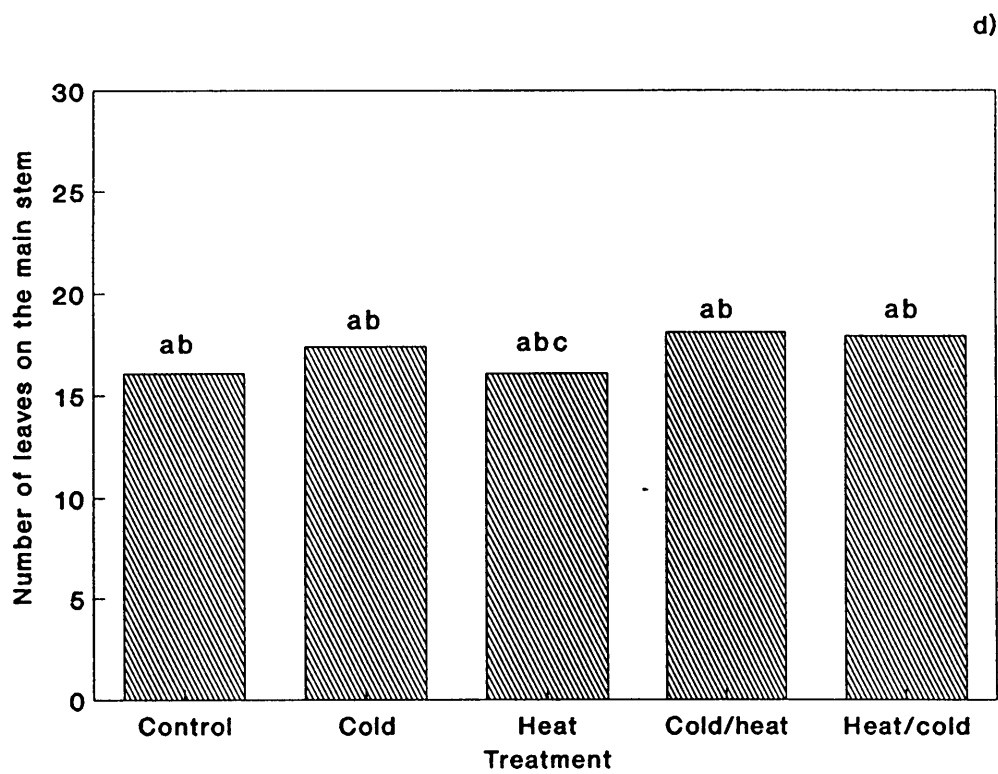
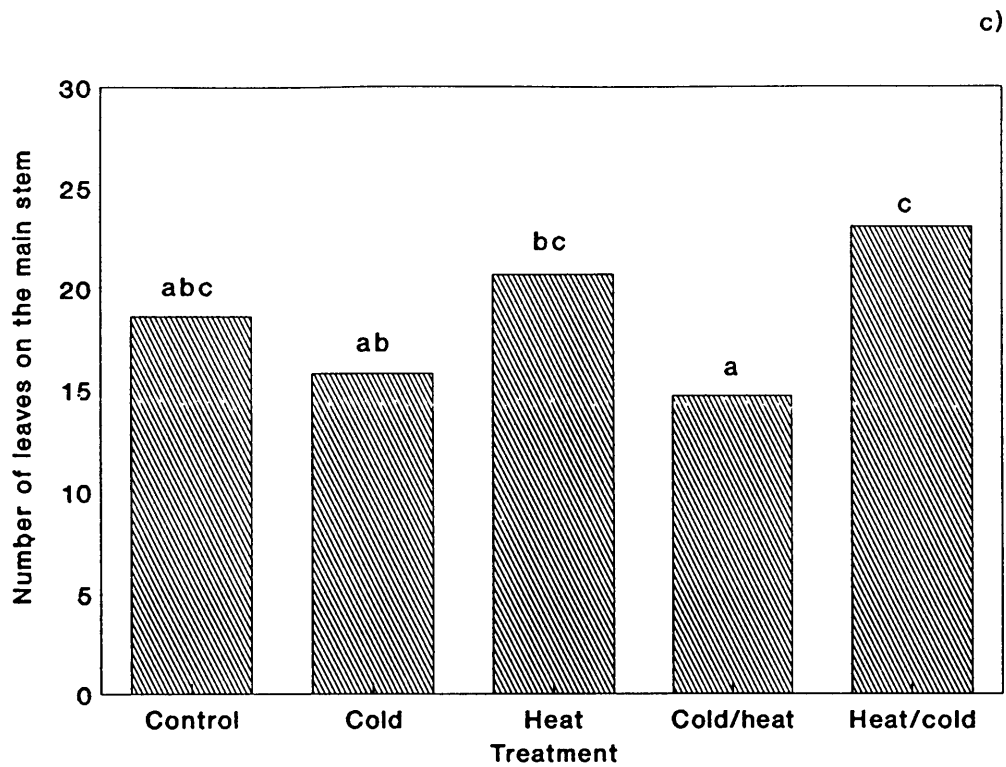


Figure 2. Continued.

Table 2. Days from sowing until inflorescence initiation, 50% flowering and peak flowering stage as well as the number of open inflorescences at peak flowering and the total number of reproductive organs produced during the flowering period of two ephemeral species that were subjected to various temperature and sowing date treatments

Species (Sowing date)	Treatment	Number of days to:			Number of open inflorescences per plant	Total number of reproductive organs per plant
		Inflorescence initiation	50% flowering	Peak flowering		
<i>Dimorphotheca sinuata</i>						
(April)	Control	74	125	136/143	14.2	59
	Cold	68	129	136	21.4	84
	Heat	75	125	143	15.9	65
	Cold/heat	69	122	143	20.5	95
	Heat/cold	79	122	136	17.4	75
(June)	Control	50	111	156	21.6	124
	Cold	58	114	132	16.6	128
	Heat	61	111	153	21.1	119
	Cold/heat	53	125	156	24.2	156
	Heat/cold	61	114	142	24.4	172
<i>Ursinia cakilefolia</i>						
(April)	Control	69	115	136	4.7	19
	Cold	65	111	136	4.2	22
	Heat	69	97	136	4.8	19
	Cold/heat	64	115	132	5.5	24
	Heat/cold	72	109	136	6.2	22
(June)	Control	41	86	132	5.4	26
	Cold	52	114	125	5.7	24
	Heat	58	79	118	3.4	18
	Cold/heat	49	76	142	5.3	31
	Heat/cold	40	90	125	7.6	35

treated June plants. A cold treatment apparently shortened the period until inflorescence initiation in the case of April plants of *D. sinuata* and *U. cakilefolia*. Mott & McComb (1975) observed that lower temperatures lead to a decrease in the time to flower initiation and the number of nodes to first flowering in the winter annual *Helipterum craspedioides*. In the case of *Boronia megastigma*, a woody, under-story shrub, Roberts & Menary (1989) found that the initiation of flower buds under low temperatures occurred more rapidly and to a much greater extent than under moderate temperatures. In the case of June plants of *U. cakilefolia* however, the heat/cold treated plants reached the stage of inflorescence initiation first, followed by the control.

Anthesis

Dimorphotheca sinuata

The onset of anthesis (first open inflorescence in treatment) in April plants occurred 80 - 92 days after sowing (Figure 3a & b), while anthesis in June plants started 55 - 65 days after sowing (Figure 4a & b). Although June plants started to flower earlier than April plants, peak flowering of June plants was 1 - 2 weeks later than that of April plants (Figure 3 & 4). The cold treatment being an exception, as the June plants reached peak flowering somewhat earlier than the same treatment of the April sowing.

Plants sown in April produced a flowering curve with one or two peaks (Figure 3a & b), while June plants produced three or more flowering peaks (Figure 4a & b). The number of open inflorescences at peak flowering of the cold treated April plants was the highest (Table 2), this may be the result of the stimulation of inflorescence initiation by low temperatures. June plants subjected to a cold treatment reached peak flowering first (132 days) although a heat/cold treatment produced the first distinct flowering peak after 100 days (Figure 4). The heat/cold and cold/heat treatments resulted in the highest number of open inflorescences in June plants of *D. sinuata*.

With the exception of the cold treated plants, the number of open inflorescences per plant at peak flowering time of April plants was lower than that of June plants (Table 2).

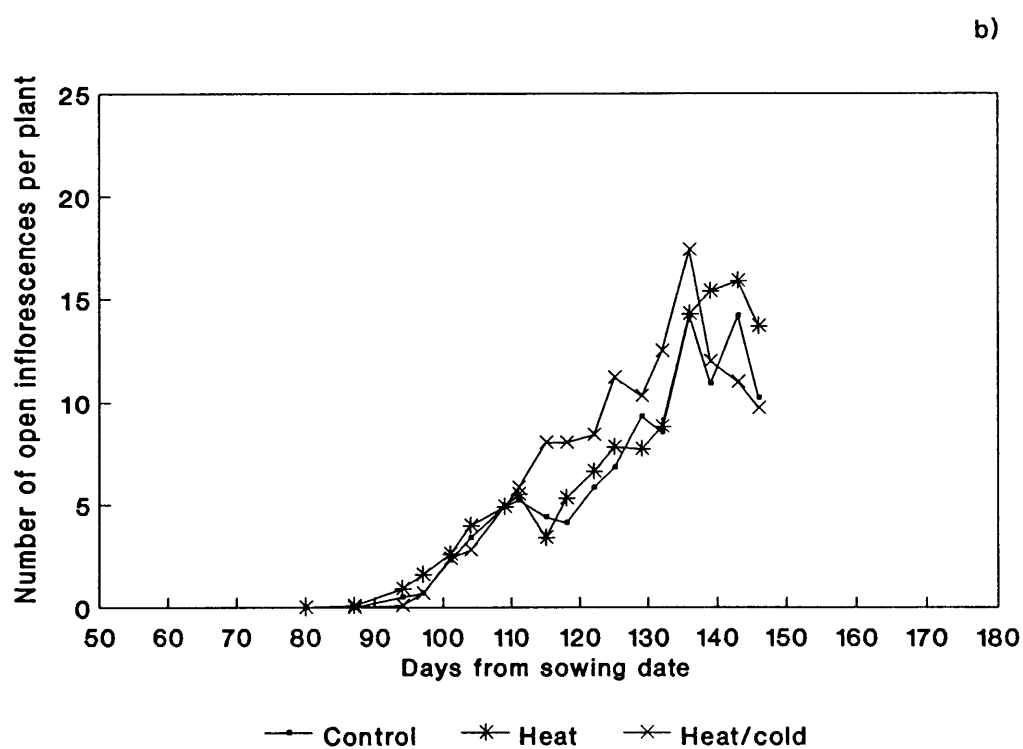
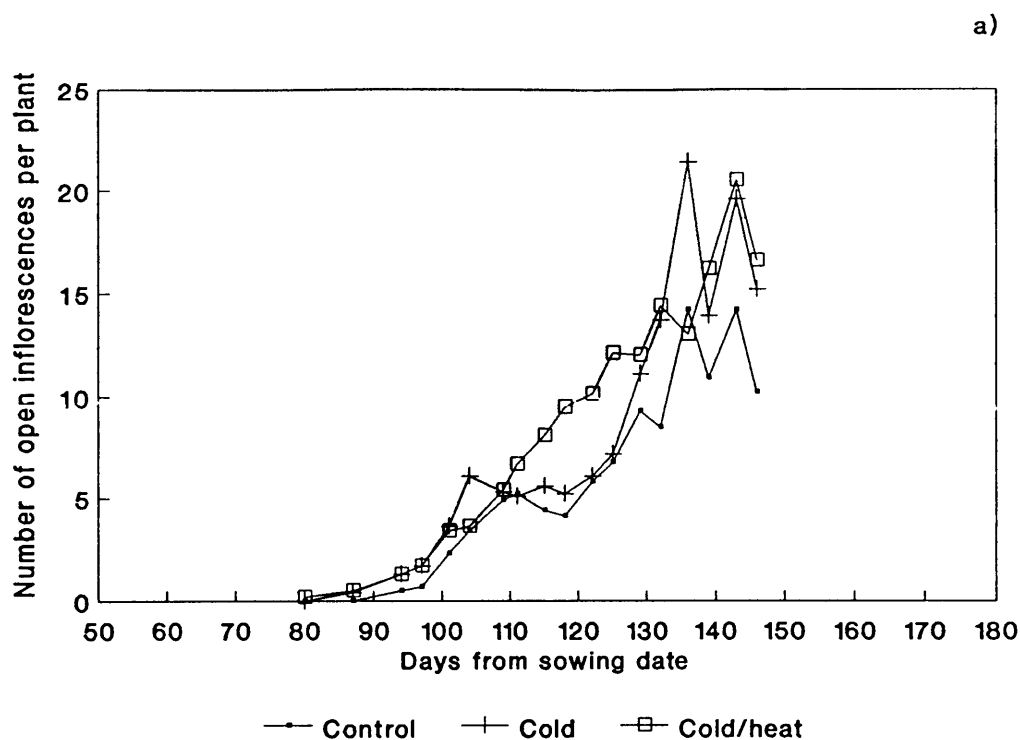


Figure 3. The number of open inflorescences per plant of *Dimorphotheca sinuata* sown in April.

a) Control, cold and cold/heat treatments, and b) control, heat and heat/cold treatments.

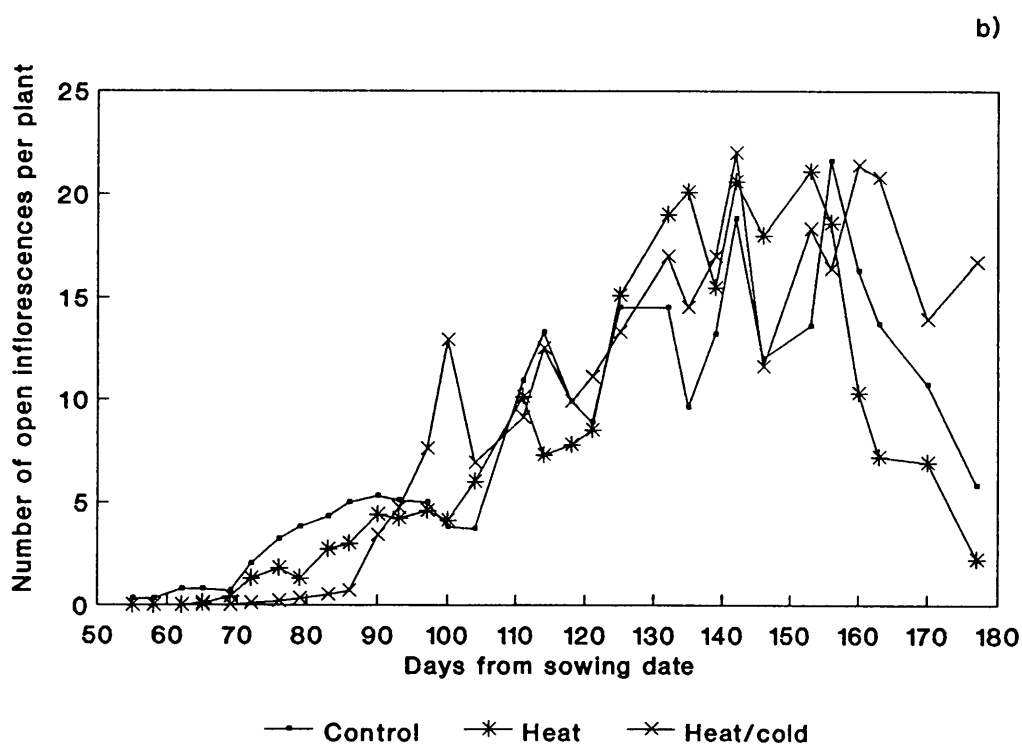
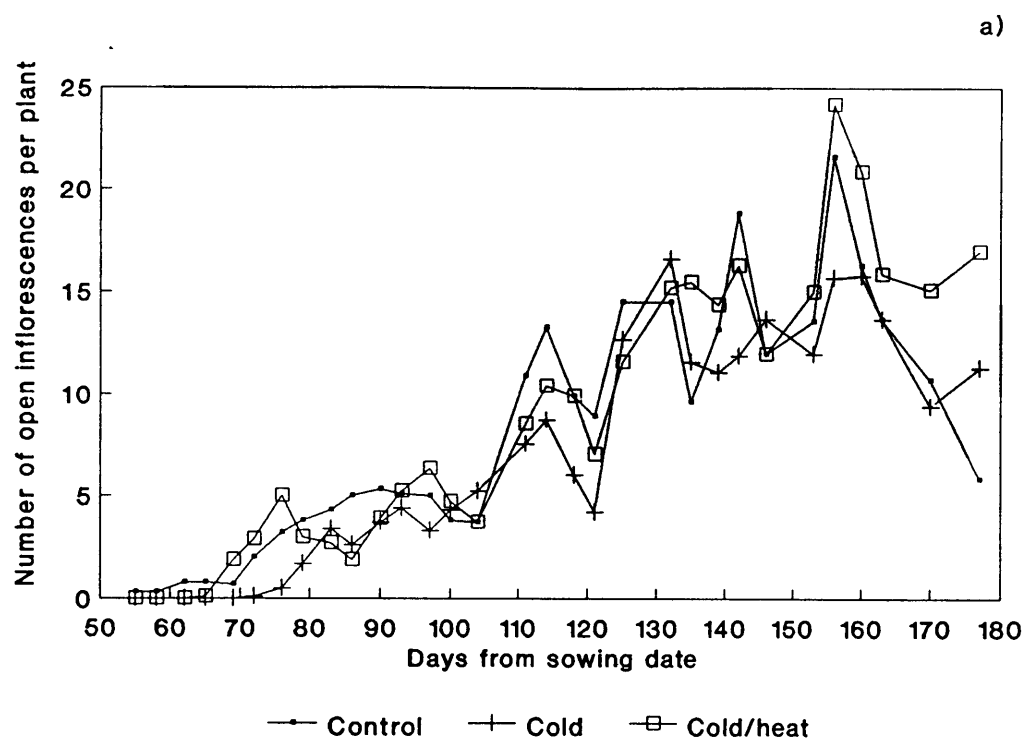


Figure 4. The number of open inflorescences per plant of *Dimorphotheca sinuata* sown in June.

a) Control, cold and cold/heat treatments, and b) control, heat and heat/cold treatments.

In both species studied, June plants at all five treatments, had a longer flowering period than April sown plants (Figures 3 - 6).

Ursinia cakilefolia

The onset of anthesis in April plants started 69 - 88 days after sowing, while anthesis of the June plants started 55 - 65 days after sowing (Figures 5 & 6). As in the case of *D. sinuata* the June plants started to flower sooner after sowing and the period between anthesis and peak flowering was longer than that of the April plants, with the exception of the cold treatment. *Ursinia cakilefolia* differed from *D. sinuata* in that June plants with the exception of the cold/heat treatment, reached peak flowering sooner than April plants (Table 2).

Regardless of the temperature treatment, all April plants of *U. cakilefolia* reached peak flowering at nearly the same time (132 - 136 days after sowing). Heat treated June plants reached peak flowering first (118 days), while cold/heat treated plants were the last to reach peak flowering (142 days). However, the later plants had already produced a smaller flowering peak at 75 days after sowing (Figure 6). The highest number of open inflorescences per plant at peak flowering of both April and June sowings was found on heat/cold treated plants (Table 2, Figures 5 & 6).

As in the case of *D. sinuata*, April plants of *U. cakilefolia* produced less inflorescences at peak flowering than June plants, with the exception of the heat and the cold/heat treatments (Table 2). Generally it seemed as if plants established in June, had a longer and more spectacular flowering period (Figures 5 & 6).

The total number of reproductive organs produced throughout the life span of *D. sinuata* and *U. cakilefolia* plants are shown in Table 2.

In contrast to miniature roses, where the number of flowers per plant shows an almost linear decrease with an increase in temperature (Mortensen 1991), the multifactor ANOVA indicated no significant effect of temperature or sowing date on the total

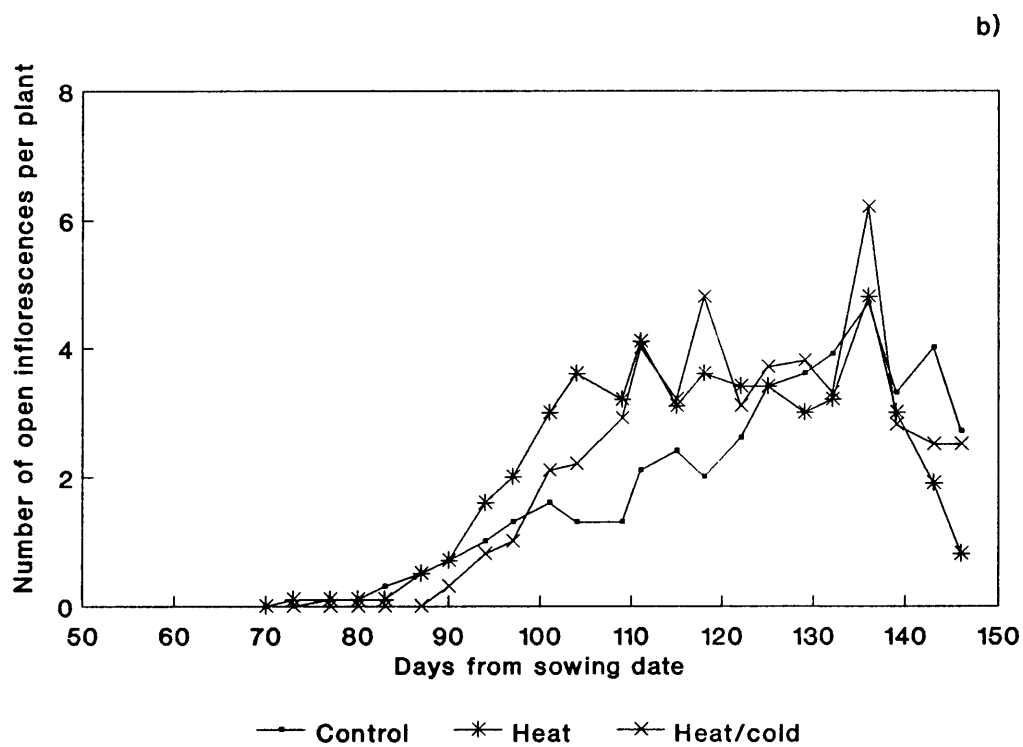
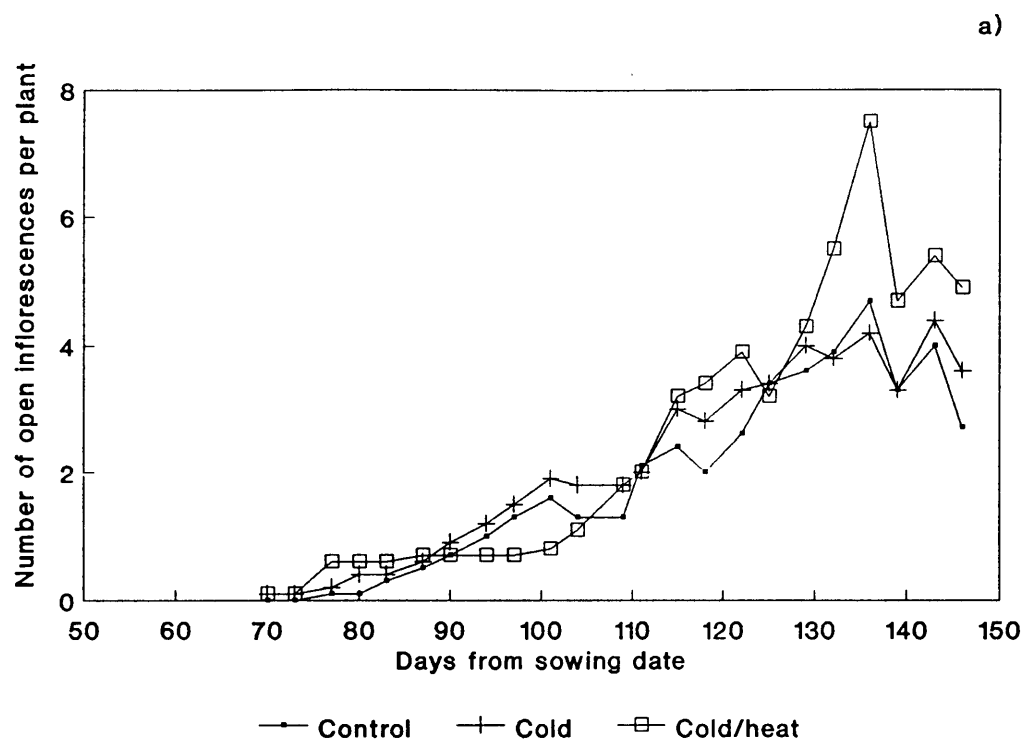


Figure 5. The number of open inflorescences per plant of *Ursinia cakilefolia* sown in April.

a) Control, cold and cold/heat treatments, and b) control, heat and heat/cold treatments.

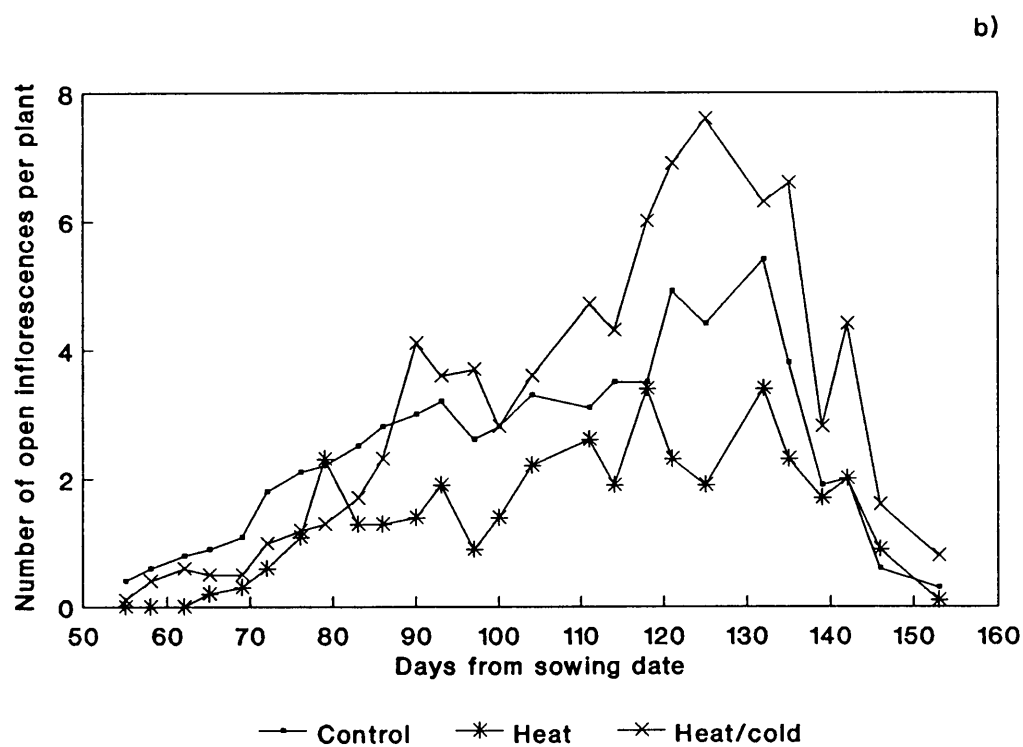
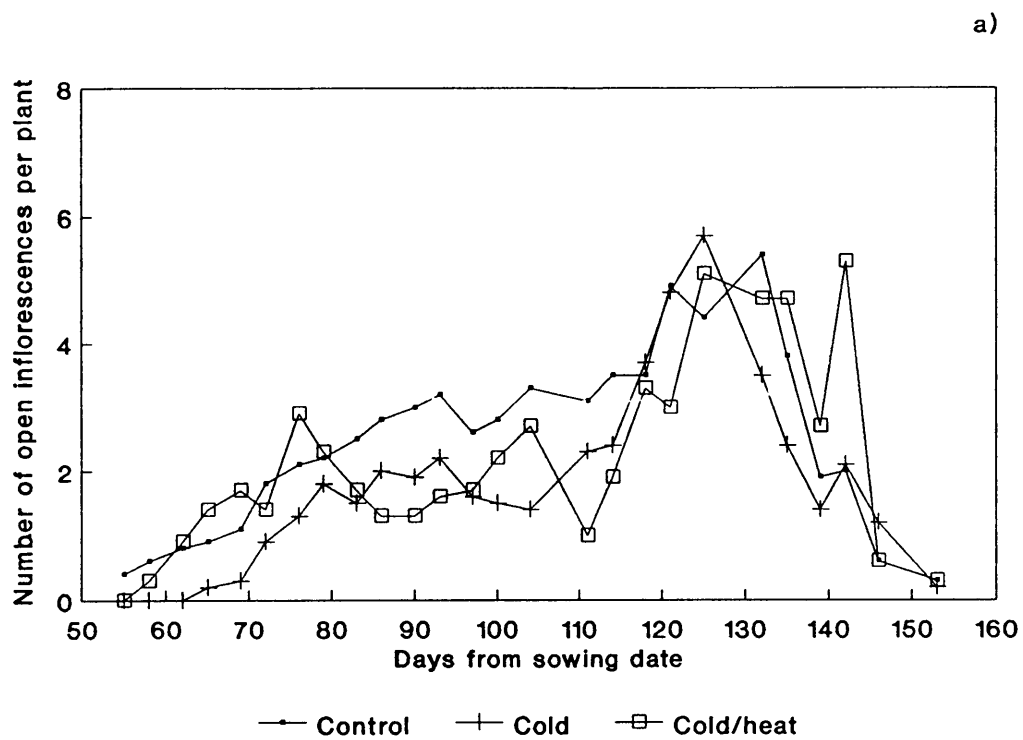


Figure 6. The number of open inflorescences per plant of *Ursinia cakilefolia* sown in June.

a) Control, cold and cold/heat treatments, and b) control, heat and heat/cold treatments. 38

number of reproductive organs produced by *U. cakilefolia*. In the case of *D. sinuata* the multifactor analysis of variance (Scheffé's test) showed a significant difference between temperature treatments and sowing dates. The interaction between temperature and daylength could be the cause of the higher number of reproductive organs produced by plants of the June sowing.

In a study on three winter annuals from Ireland, Clark (1969) found that daylength had no effect on the number of flower buds produced. Lewis & Went (1946) found a quantitative longday response in seven winter ephemerals from a Californian desert, while Evenari & Gutterman (1985) obtained similar results with 21 species of the Negev desert in Israel. Seventeen of those species showed a quantitative reaction, while the rest reacted as long day plants under glass house conditions, but day neutral in the field.

CONCLUDING REMARKS

Different temperature and sowing date treatments had no significant effect on the maximum height attained by *D. sinuata* and *U. cakilefolia* plants, however, higher temperatures tend to stimulate growth in the case of *U. cakilefolia* plants. In both species, June plants elongated sooner than April plants and at an age of 40 and 80 days June plants were significantly taller than April plants of the same age.

In both species, a cold treatment early in the growing season, accelerated inflorescence initiation in April plants. However this response was not found in the case of June plants. Therefore, the hypothesis that low temperatures promote the initiation of inflorescences in annual plants cannot fully explain the observed results. The plant's response to temperature is apparently modified by the prevailing photoperiod, although it may also be due to an endogenous rhythm. As a result of these interactions inflorescence initiation occurred sooner in June plants than in April plants, which can possibly be regarded as an adaptation to ensure spring flowering in these species.

Although the flowering curves differed between *U. cakilefolia* plants of different

treatments, the total number of reproductive organs produced was not affected significantly by temperature or sowing date. June sowing in the case of *D. sinuata* however, resulted in the production of more reproductive organs during the flowering period. In both species, the response of April and June plants to the temperature treatments were not similar.

Plants sown in June, produced more inflorescences at their peak and had a longer flowering period than plants sown in April.

ACKNOWLEDGEMENTS

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REFERENCES

- BASKIN, J.M. & BASKIN, C.C. 1974. Effect of vernalization on flowering of the winter annual *Alyssum alyssoides*. **Bulletin of the Torrey Botanical Club**, 101: 210 - 213.
- CLARK, S.C. 1969. Some effects of temperature and photoperiod on growth and floral development in three winter annuals. **New Phytologist**, 68: 1137 - 1144.
- CONSTABLE, G.A. & ROSE, I.A. 1988. Variability of soybean phenology response to temperature, daylength and rate of change in daylength. **Field Crops Research**, 18: 57 - 69.
- ELPHINSTONE, E.D. & REES, A.R. 1990. Temperature and development in *Iris x hollandica* during pre-planting storage. II. Floral initiation. **Journal of Horticultural Science**, 65: 185 - 192.
- EVENARI, M. & GUTTERMAN, Y. 1985. Desert plants. In: HALEVY, A.H. (ed.) **CRC Handbook of Flowering**. Vol. 1. CRC Press, Florida. pp. 41 - 59.

- HARI, P., KELLOMAKI, S. & VUOKKO, R. 1977. A dynamic approach to the analysis of daily height growth of plants. *Oikos*, 28: 234- 241.
- HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- LE ROUX, A. & SCHELPE, E.A.C.L.E. 1988. Namakwaland. Veldblomgids van Suid-Afrika 1. Revised edition. Botanical Society of South Africa, Cape Town.
- LEWIS, H. & WENT, F.W. 1946. Plant growth under controlled conditions. 4. Response of California annuals to photoperiod and temperature. *American Journal of Botany*, 32: 1 - 12.
- MORTENSEN, L.M. 1991. Effects of temperature, light and CO₂ level on growth and flowering of miniature roses. *Norwegian Journal of Agricultural Sciences*, 5: 295-300.
- MOTT, J.J. & McCOMB, A.J. 1975. The role of photoperiod and temperature in controlling the phenology of three annual species from an arid region in Western Australia. *Journal of Ecology*, 63: 633 -641.
- ROBERTS, N.J. & MENARY, R.C. 1989. Environmental interaction between daylength, night temperature, and photon flux density on growth and flowering in *Boronia megastigma* Nees.. *Journal of Horticultural Science*, 64: 597-604.
- SALISBURY, F.B. 1981. Responses to Photoperiod. In: LANGE, O.L., NOBEL, P.S., OSMOND, C.B. & ZIEGLER, H. (eds.) *Physiological Plant Ecology 1. Responses to the physical environment*. Springer- Verlag, New York. pp. 135 - 167.
- SCHULZE, B.R. 1965. Climate of South Africa. Part 8. WB 28. Government Printer, Pretoria.
- SEDDIGH, M., JOLLIFF, G.D. & ORF, J.H. 1989. Night temperature effects on soybean phenology. *Crop Science*, 29: 400-406.
- STEYN, H.M. 1993. Namaqualand ephemerals: phenology and thermal units. M.Sc. dissertation. University of Pretoria, Pretoria.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. a). The prediction of phenological stages in five Namaqualand ephemeral species using thermal unit indices.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In

prep. b). The influence of sowing date on the phenology of five Namaqualand ephemeral species.

VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis. University of Pretoria, Pretoria.

VAN ROOYEN, M.W., GROBBELAAR, N. & THERON, G.K. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. 2. The therophyte population. *Journal of South African Botany*, 45: 433 - 452.

VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1992. The ephemerals of Namaqualand: effect of germination date on development of three species. *Journal of Arid Environments*, 22: 51 - 66.

WILSON, J.W. 1967. Effects of seasonal variation in radiation and temperature on net assimilation and growth rates in an arid climate. *Annals of Botany*, 31: 41-57.

CHAPTER 5

THE INFLUENCE OF SOWING DATE ON THE PHENOLOGY OF FIVE NAMAQUALAND EPHEMERAL SPECIES

H.M. STEYN, N. VAN ROOYEN, M.W. VAN ROOYEN & G.K. THERON

(Department of Botany, University of Pretoria, Pretoria, 0002)

ABSTRACT

Seeds/achenes of five Namaqualand ephemeral species were sown on four dates (April, May, June and July) to determine the effect of sowing date on the phenology of these species.

In all five species, seeds sown in autumn (April) produced the tallest plants. Sowing in July caused more rapid stem elongation and plants reached their maximum height over a shorter period than those of the earlier sowing dates.

The number of leaves on the main stem at the initiation of flowers/inflorescences, tended to decrease the later the sowing date. In all five species examined, the time to the onset of anthesis decreased, the later the seeds were sown.

Plants from the early sowing (April) produced more open inflorescences per plant at peak flowering than those of the later sowing dates. However, plants derived from seed sown in May and June, produced more inflorescences during their entire life span.

It is therefore concluded that early rain (autumn/April) will result in the establishment of plants which will take a long time to reach anthesis and peak flowering, but at their peak these plants will be taller and produce more open inflorescences and consequently a more spectacular show than plants which established later in the season.

KEY WORDS: *Dimorphotheca sinuata*, ephemerals, *Foveolina albida*, flowering, *Heliophila seselifolia*, Namaqualand, phenology, *Senecio arenarius*, sowing date, *Ursinia cakilefolia*

INTRODUCTION

Namaqualand, in the north-western arid corner of the Republic of South Africa, owes its fame mainly to the display of wild flowers following a good winter rainy season (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992). The climate of the region is characterised by a hot, dry summer and sparse and erratic winter rainfall, falling mainly in the months April to July (Schulze 1965). Depending on the timing and amount of the rainfall, germination of seeds can occur at different times during autumn and winter. The length of the favourable growth period therefore depends on the timing of the first seasonal rain which is sufficient for germination. Van Rooyen *et al.* (1992) found that the survival of seedlings and the subsequent growth and development of the plants are influenced by climatic conditions prevailing during the growing season.

Not only do the ephemeral populations vary considerably in species composition and abundance between seasons and localities within a single year, but also from one year to another (Van Rooyen, Grobbelaar & Theron 1979). It has been suggested that the temperatures prevailing at the time of the infrequent rainfall, determine which species will germinate (Went 1949; Went & Westergaard 1949; Tevis 1958) as each species has its own and often very narrow requirements for germination (Visser 1993).

Arid and semi-arid regions characteristically support an abundant flora of annual plants which complete their life-cycles in short periods following substantial rainfall (Bowers 1987). Differences in the time of germination will cause plants to experience different regimes of temperature and photoperiod during their development (Pilbeam, Hebblethwaite, Ricketts & Hassan 1990). Annual plants may exercise considerable flexibility in their response to environmental variables, such as temperature and daylength, that are necessary to induce flowering (Primack 1979).

The aim of this study was to investigate the effect of sowing date on the growth and phenology of five ephemeral plant species. This paper forms part of a study (Steyn 1993) on the influence of environmental conditions and sowing date on the phenology of selected Namaqualand ephemerals, with the prediction of peak flowering time as the

ultimate goal.

METHODS

Potting trial

Seeds/achenes of *Dimorphotheca sinuata* DC. (disc flower achenes), *Foveolina albida* (DC.) Kallersjo, *Heliophila seselifolia* Burch. ex DC. var. *seselifolia*, *Senecio arenarius* Thunb. and *Ursinia cakilefolia* DC. were collected in 1990 in the Goegap Nature Reserve, near Springbok. The seeds were sown in 1 000 cm³ pots filled with quartz sand, on four different sowing dates from autumn to mid winter: fifth of April (April plants), second of May (May plants), fourth of June (June plants) and the second of July (July plants). Two weeks after emergence, the seedlings were thinned to one individual per pot. The plants were grown out of doors at the University of Pretoria and watered daily to field capacity with tap water. Once a week they received Arnon & Hoagland's complete nutrient solution (Hewitt 1952). Ten replicates were used per treatment and the mean of the replicates was used in all the Tables and Figures except where stated otherwise.

Phenological data were recorded weekly from 28 days after sowing. The height or length of each plant was measured weekly. From the initiation of flowers/inflorescences, all plants were examined phenologically, twice a week. The following phenological stages and the number of days since sowing on which each stage was reached, were noted for each plant: flower/inflorescence initiation, first flower/inflorescence at anthesis and peak flowering time. All the species, except *Heliophila seselifolia* (Brassicaceae), belong to the family Asteraceae, and therefore the individual flowers were not counted but an inflorescence was considered as an unit.

The total number of open inflorescences per sowing date treatment of *Dimorphotheca sinuata*, *Foveolina albida* and *Ursinia cakilefolia* was counted twice a week. The term peak flowering implied the highest mean number of open flowers/inflorescences during the flowering phase. In contrast, a flowering peak refers to any distinct culminating

point in the flowering curve - not necessarily the highest peak.

The air temperature (°C) and relative air humidity (%) were registered continuously by means of a thermohygrograph in a Stevenson screen standing at the same height as the plants. Soil temperature was registered by a soil thermograph of which the probe was inserted into one of the pots which was filled with quartz sand and watered with the plants.

An one-way analysis of variance (ANOVA)(Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) was used to test for statistical significant differences at $\alpha = 0.05$. The LSD test was used for comparisons between treatments within species. Differences in plant height data between treatments were analyzed statistically at 40, 80 and 120 days after sowing.

Field observations

From 18 August to 18 September 1991 phenological data were recorded for *D. sinuata*, *F. albida*, *H. seselifolia*, *S. arenarius* and *U. cakilefolia* growing in the Springbok region, Namaqualand. The height, number of open flowers/inflorescences, number of flower/inflorescence buds as well as the flowering stage e.g. 50% or peak flowering, were determined per plant for 20 plants per species.

RESULTS AND DISCUSSION

Potting trial

Plant height

The maximum height reached by *Dimorphotheca sinuata* plants sown in April was significantly higher than that of the June and July plants (Figure 1a). At their maximum height, April plants were 30 mm taller than May plants, which in turn were 30 mm taller than June and July plants. These results support those of Van Rooyen (1988) who found that the plants sown early in the season (April) were significantly taller (up to 170

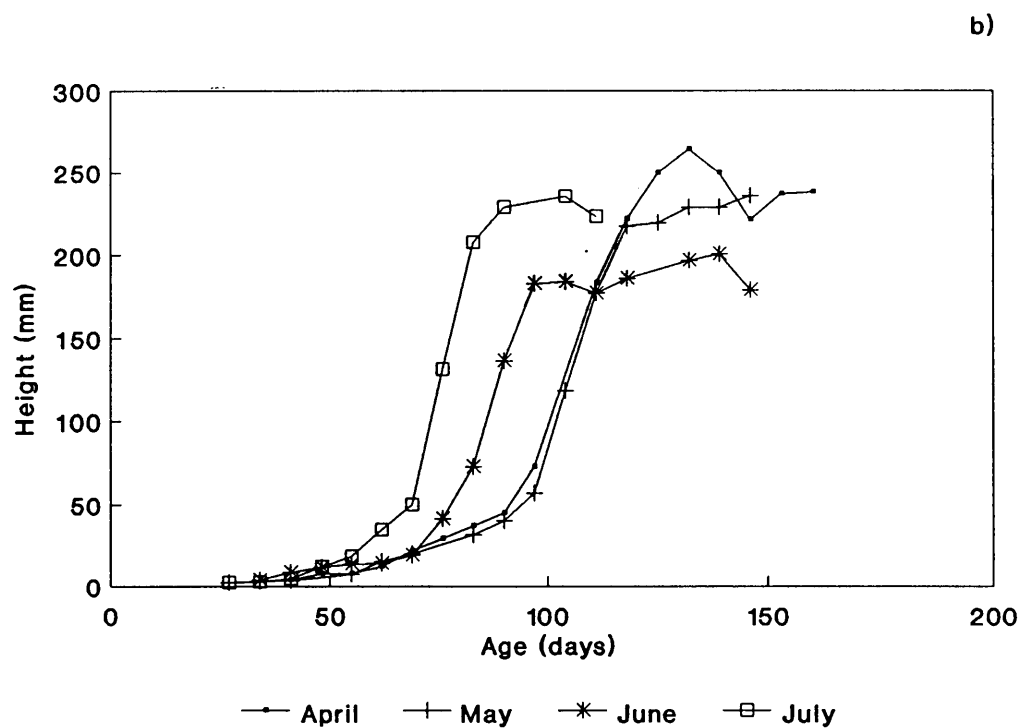
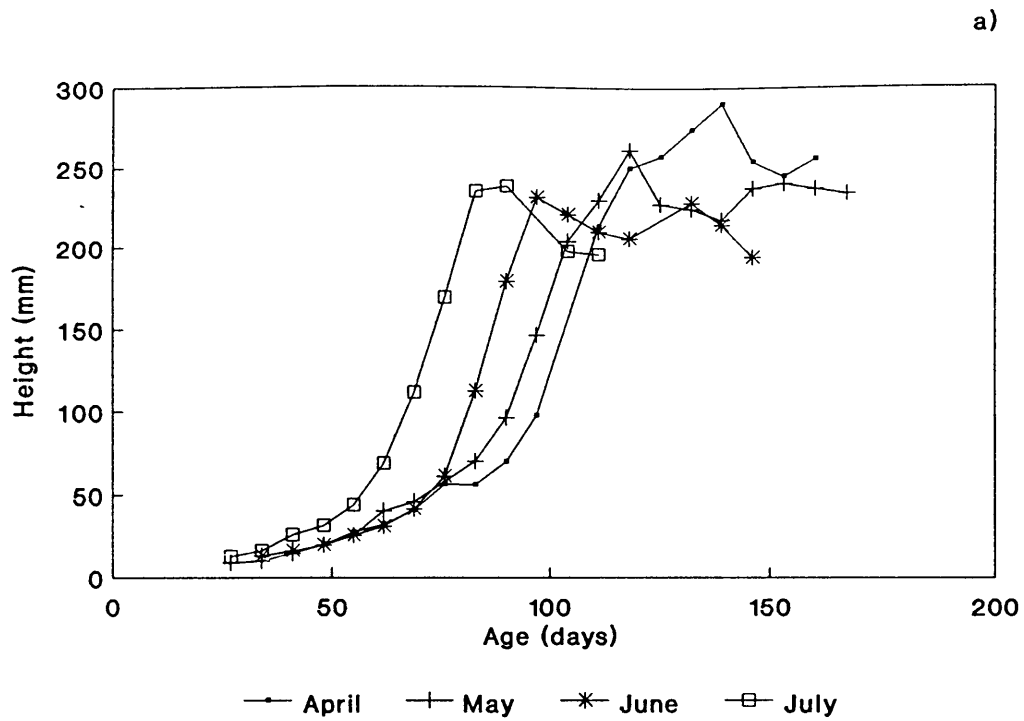


Figure 1. The mean height of plants sown on different sowing dates; a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and e) *Ursinia cakilefolia*. 47

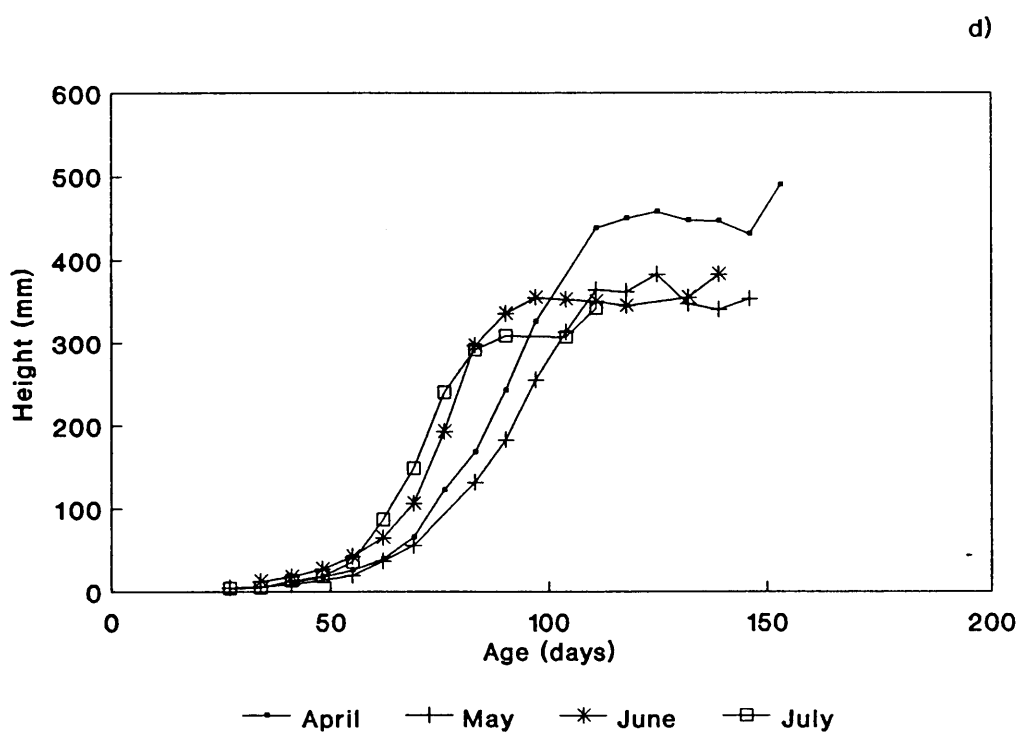
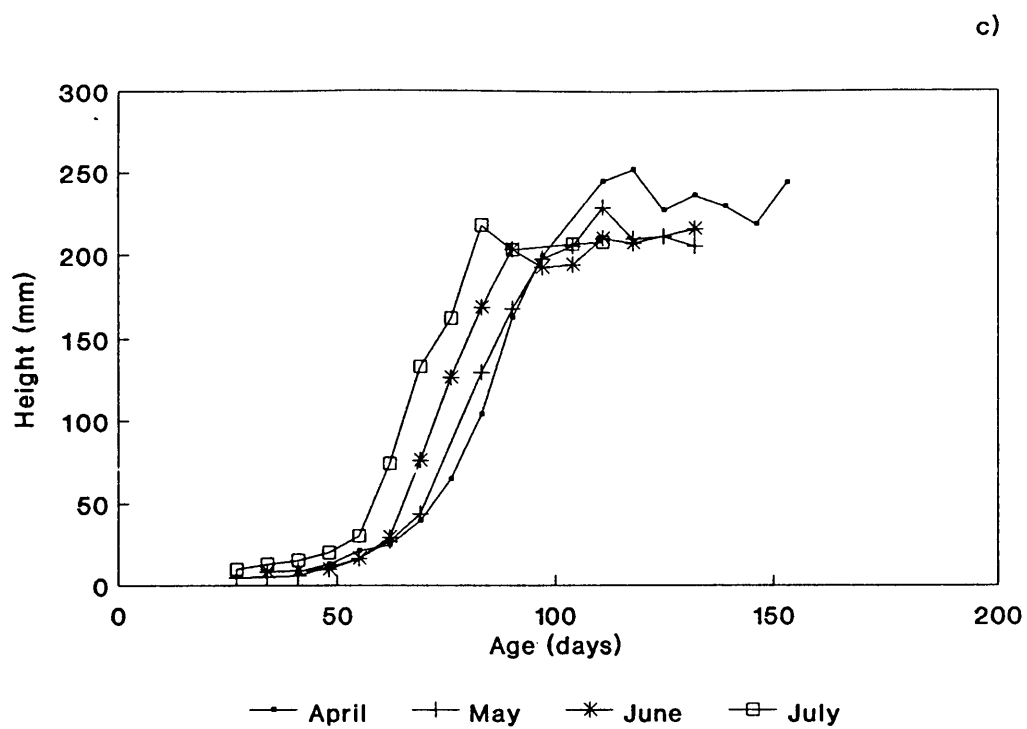


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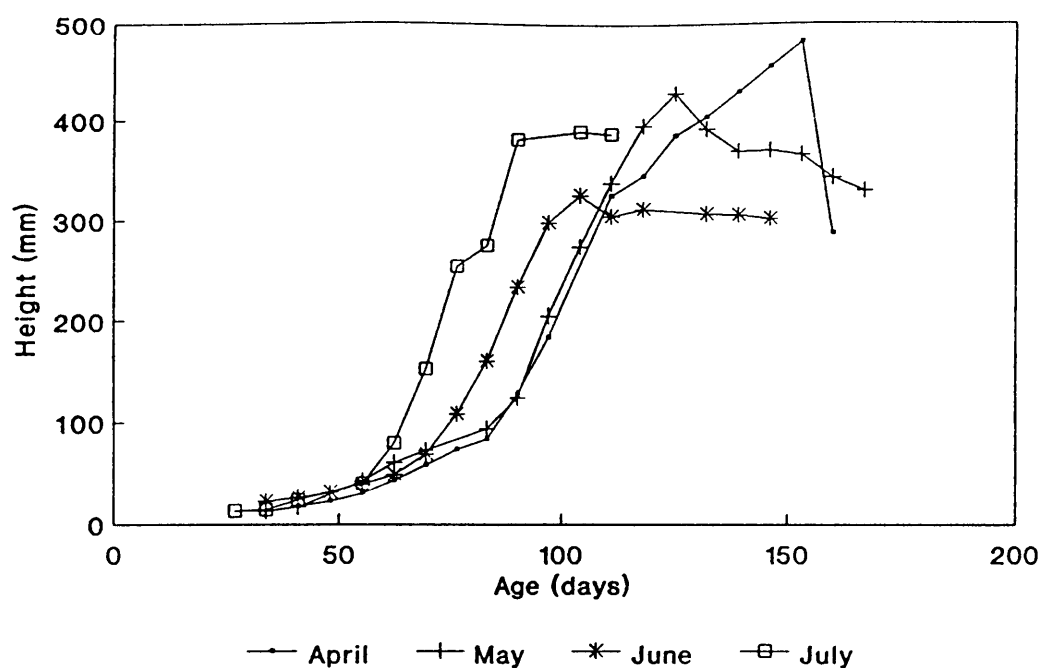


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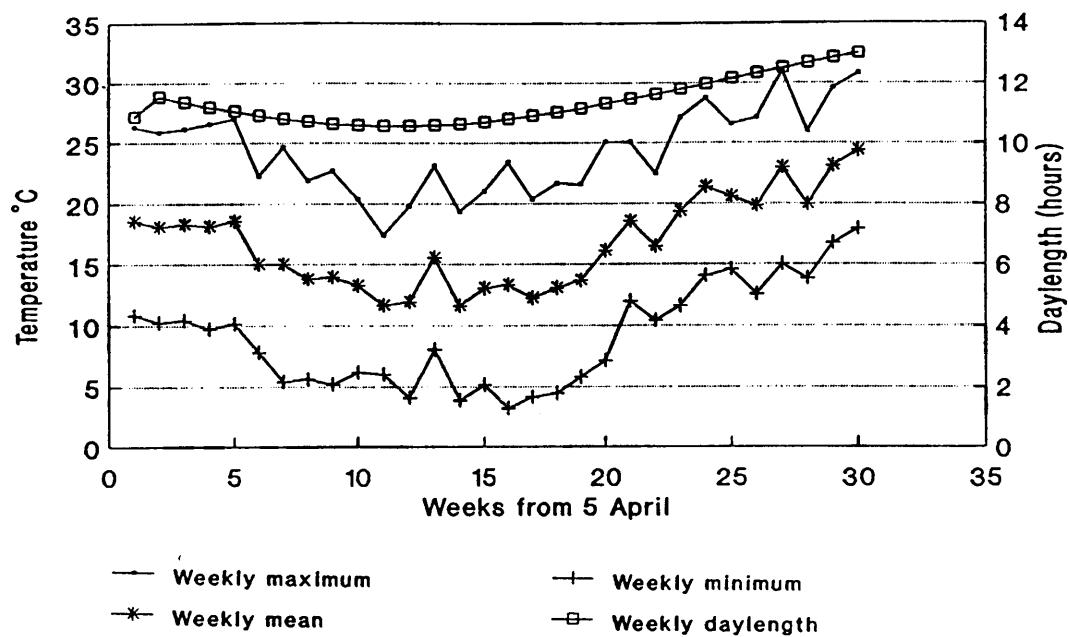


Figure 2. The mean weekly maximum, mean weekly minimum, mean weekly temperature and the mean daylength at Pretoria from April to October 1991.

mm) than plants sown from May to July.

For approximately 80 days, a slow increase in height was recorded for *D. sinuata* plants of the April and May sowing dates and 60 days in the case of June plants (Figure 1a). This lag phase corresponded to the period during which the plants were in a rosette phase, at the end of which the main stem began elongating rapidly. Plants sown in July began to elongate sooner and were significantly taller than plants from other sowing dates at an age of 40 days. At an age of 80 days, June and July plants were significantly taller than the rest, but at an age of 120 days the situation was reversed and April and May plants were significantly taller than June and July plants. The length of the lag phase decreased and plants reached their maximum height sooner the later the sowing date, which corresponds to the findings of Steyn, Van Rooyen, Van Rooyen & Theron (In prep. a) (see Chapter 4), under controlled conditions.

The differences in height between plants of different sowing dates can probably be attributed to differences in the prevailing climatic conditions during each growing period. Mean weekly air temperatures as well as mean weekly maximum and minimum air temperatures from April to October are presented in Figure 2. During the first two months, the mean weekly temperature dropped steadily and the daylength decreased. From the middle of June to the end of July the mean weekly temperature remained more or less constant, with the exception of the first week in July when temperatures were exceptionally high. Daylengths started to increase from the end of June while temperatures started to rise rapidly from the middle of August.

According to Mulroy & Rundel (1977) an initial rosette phase has important ecological implications. They reasoned that this period usually coincides with the coolest part of the year and by adopting this growth habit, plants occupy a micro environment which is warmer diurnally than one further away from the soil surface. As soon as the soil temperatures start to increase, the stems elongate rapidly. The results of this study do not support the hypothesis that stem elongation is a direct result of rising air or soil temperatures, as the stems often started to elongate rapidly during the coldest period - for example in April and May plants.

In the case of *Foveolina albida*, as for *D. sinuata*, a rapid increase in plant height began sooner in the July plants compared to the earlier sowing dates (Figure 1b). The lag phase was more pronounced in April and May plants. April plants were the tallest with a maximum height of 264 mm, while June plants were the shortest with a maximum height of 201 mm. There was a significant difference between the maximum height of April and June plants.

Although April plants of *H. seselifolia* were 20 mm taller than plants of the same species sown on a later date (Figure 1c), these differences were not significant. The onset of rapid stem elongation was earlier, the later the plants were sown.

In general, early sowings of *S. arenarius* and *H. seselifolia* showed a shorter lag phase (62 - 69 days) than *D. sinuata* and *U. cakilefolia*.

In the case of *Senecio arenarius* (Figure 1d), April plants were significantly taller than the rest, while no significant differences in maximum height occurred between plants of the other sowing dates (Figure 1d). In contrast to *D. sinuata*, April plants of *S. arenarius* started to elongate rapidly, earlier than May plants.

Though an initial rosette phase was absent, plants of *Ursinia cakilefolia* showed a similar pattern of plant height increase (Figure 1e) to that of *D. sinuata*. The maximum plant height of April plants (484 mm) was significantly higher than that of June plants (326 mm), while the maximum height of July plants was 390 mm. Once again the later the sowing date, the shorter the lag phase and the sooner maximum height was reached.

In all five species April plants were the tallest while the lag phase in July plants was the shortest, and they reached their maximum height over a shorter growing period.

In all five species tested, June and/or July plants began elongating rapidly sooner, and were significantly taller at an age of 40 days. This is in contrast to Van Rooyen *et al.* (1992), who found that *D. sinuata*, *U. calenduliflora* and *H. pendula* plants that had germinated in the middle of winter, had a more pronounced lag phase possibly due to

the lower temperatures that prevailed in June and July during their study. At an age of 120 days, there was either no significant difference between the height of plants from different sowing dates (*F. albida*, *H. seselifolia* and *U. cakilefolia*) or April plants were significantly taller than those of a later sowing date (*D. sinuata* and *S. arenarius*).

Number of leaves on the main stem at flower/inflorescence initiation

During the initial period of slow growth in all species, leaves were produced on the main stem only. The apical meristem of the main stem also produced the first floral primordium. The number of leaves produced on the main stem was thus determined by factors controlling flower/inflorescence initiation (Van Rooyen *et al.* 1992).

In all five species examined, with the exception of *F. albida*, the number of leaves on the main stem decreased significantly from plants of the early sowing date to those of later sowing dates (Figure 3a-e). This general decrease in number of leaves produced on the main stem from plants sown early in the growth season to those sown in the middle of the season, can be explained by the fact that low temperatures experienced early in the growth period (i.e. plants of the later sowing dates), promote flower/inflorescence initiation and high temperatures promote vegetative growth. Plants subjected to low temperatures, early in their life cycle would therefore have less leaves on the main stem at flower/inflorescence initiation (Mott & McComb 1975; Elphinstone & Rees 1990; Van Rooyen *et al.* 1992; Steyn *et al.* In prep. a)(see Chapter 4). Plants of the late sowing dates were therefore "physiologically" (developmentally) younger at the stage of flower/inflorescence initiation (Krekule & Hajkova 1972).

Production of flowers/inflorescences

The transition from vegetative to reproductive growth is largely genetically controlled but is also influenced by environmental factors, such as temperature and daylength (Evans 1975).

The phenodiagrams in Figure 4 clearly illustrate that the sequence of the different phenological phases is in accordance with the sowing date. However, the intervals between the onset of anthesis as well as the attainment of peak flowering between the

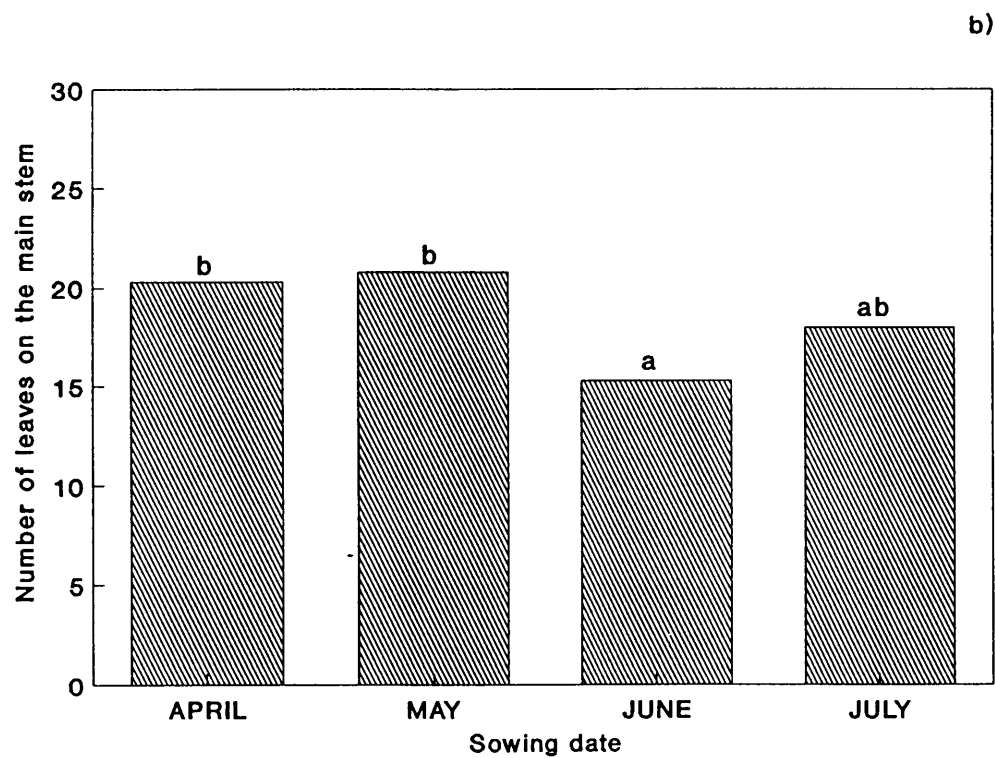
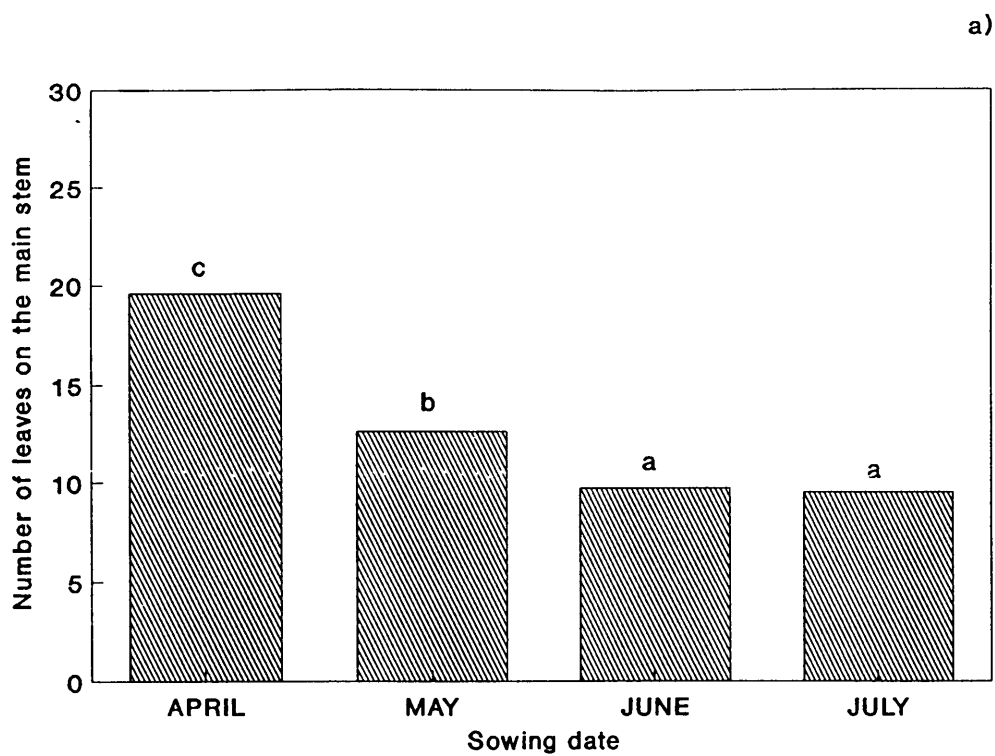


Figure 3. The mean number of leaves on the main stem at flower/inflorescence initiation of
a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and
e) *Ursinia cakilefolia* plants. Bars with the same letter do not differ significantly at $\alpha = 0.05$. 53

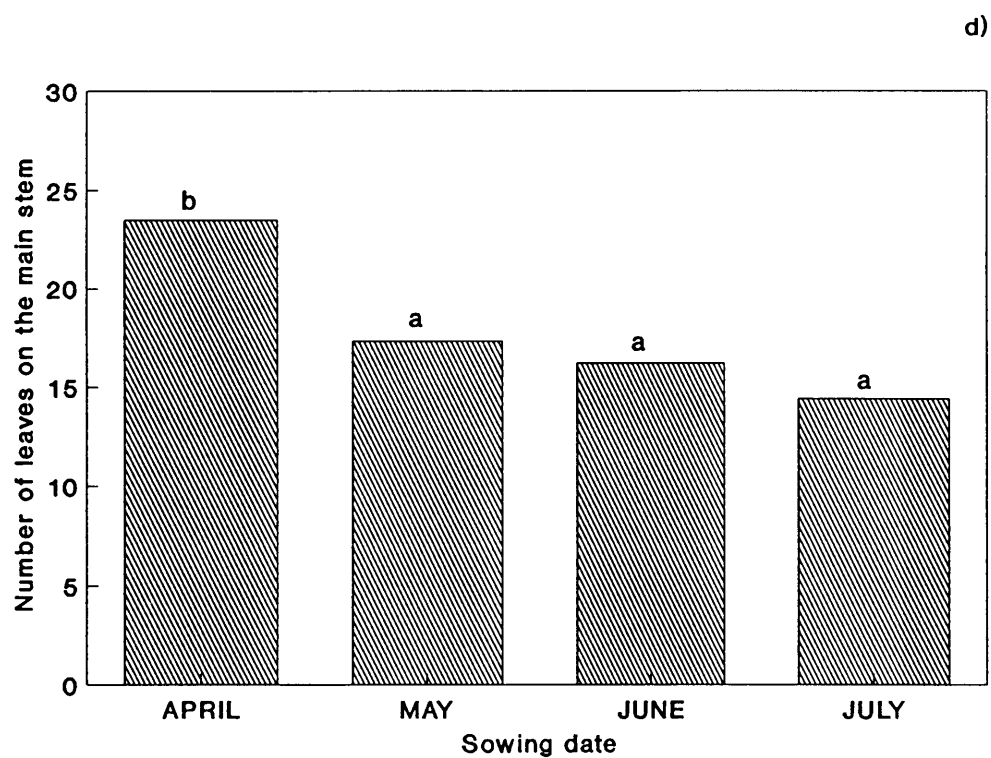
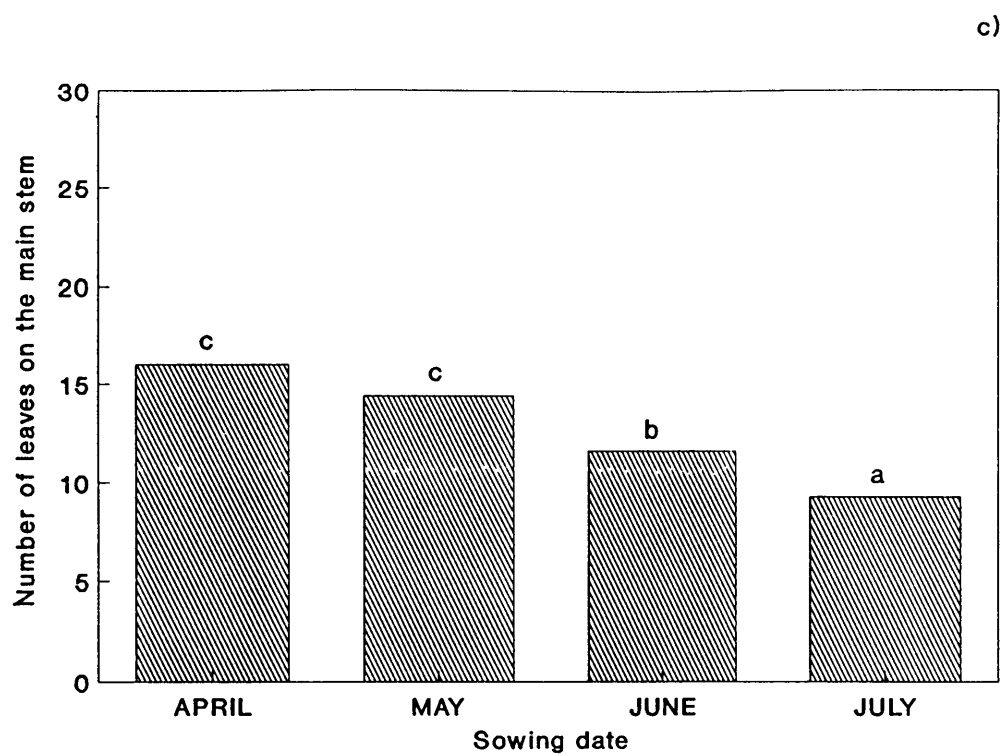


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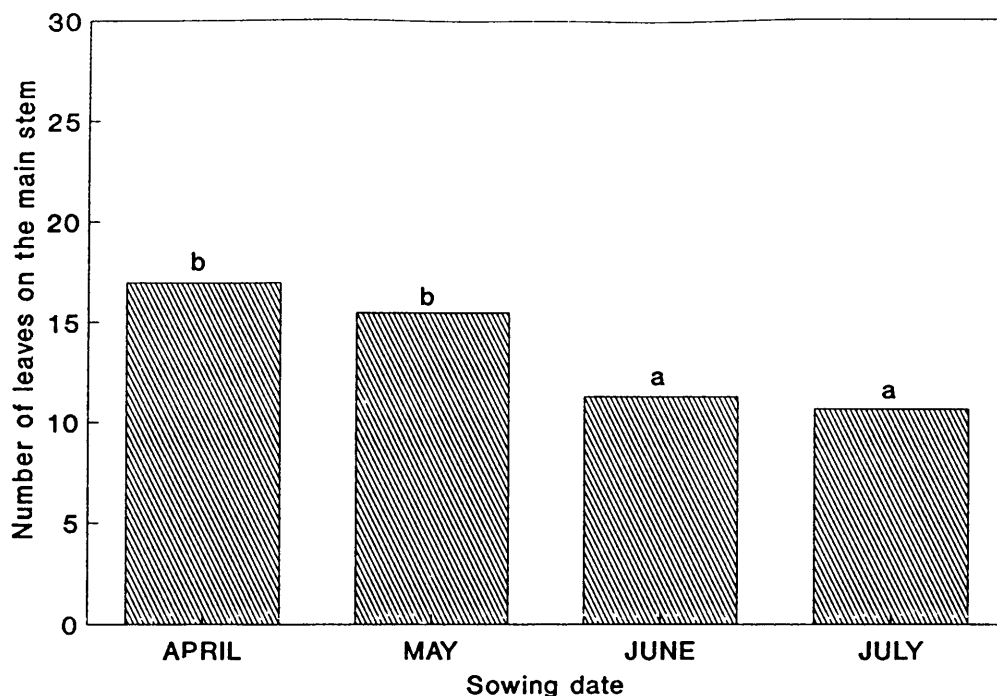


Figure 3. Continued.

different treatments are shorter than the intervals between the sowing dates (Figure 4 & 5).

In all five species studied, the time from sowing to the onset of anthesis decreased, the later the seeds had been sown (Table 1 & Figure 4). This corresponds with the findings of Gutterman (1988), Van Rooyen *et al.* (1992) and Steyn *et al.* (In prep. a) (see Chapter 4). These results are further supported by those of Baskin & Baskin (1974), who found that a low temperature treatment of sufficient length not only shortened the time to flowering in *Alyssum alyssoides* and *Bromus japonicus* (winter annuals), but increased the number of inflorescences produced per plant. Pemadasa & Lovell (1974) on the other hand, found that three dune annuals required low temperatures for floral induction but high temperatures and long days for efficient flower production. Van Rooyen *et al.* (1992) also found that the time to anthesis of several Namaqualand ephemerals would be shortened by high temperatures once floral primordia had been initiated.

In all treatments, *Heliophila seselifolia* reached anthesis first, followed by *U. cakilefolia*, *D. sinuata*, *S. arenarius* and *F. albida* (Table 1). Le Roux (pers. comm.¹), also observed

¹ Le Roux, A. Cape Nature Conservation and Museums, Private Bag 5014, Stellenbosch, 7600, R.S.A.

Table 1. The number of days until anthesis and peak flowering, as well as the number of open inflorescences per plant at peak flowering and the total number of reproductive organs per plant produced during the life span of five ephemeral species sown on four dates

Sowing date	Number of days until:		Number of open inflorescences at peak	Total number of reproductive organs
	Anthesis	Peak flowering		
<i>Dimorphotheca sinuata</i>				
April	96	136	15.5	65
May	88	118	14.0	74
June	76	100	11.0	81
July	65	104	11.1	47
<i>Foveolina albida</i>				
April	109	136	33.3	59
May	104	125	25.0	35
June	90	121	14.6	90
July	79	90	18.7	62
<i>Heliophila seselifolia</i>				
April	81	109	Not counted	Not counted
May	71	111	"	"
June	69	100	"	"
July	62	90	"	"
<i>Senecio arenarius</i>				
April	96	122	Not counted	Not counted
May	95	116	"	"
June	79	100	"	"
July	72	90	"	"
<i>Ursinia cakilefolia</i>				
April	87	136	21.9	40
May	82	118	12.6	69
June	72	128	7.5	51
July	69	104	6.0	34

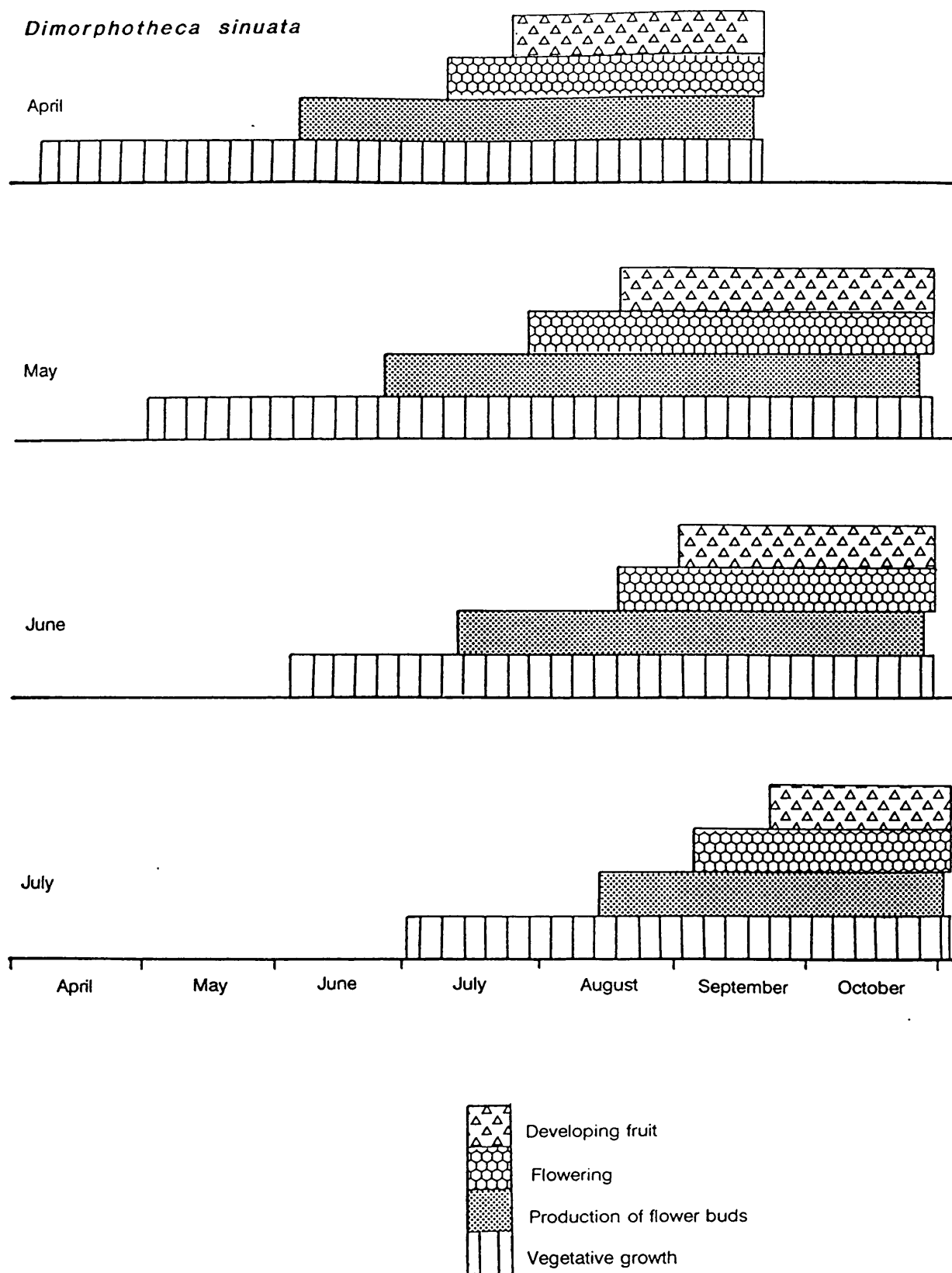


Figure 4. Phenograms of a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and e) *Ursinia cakilefolia* plants from different sowing dates.

b)

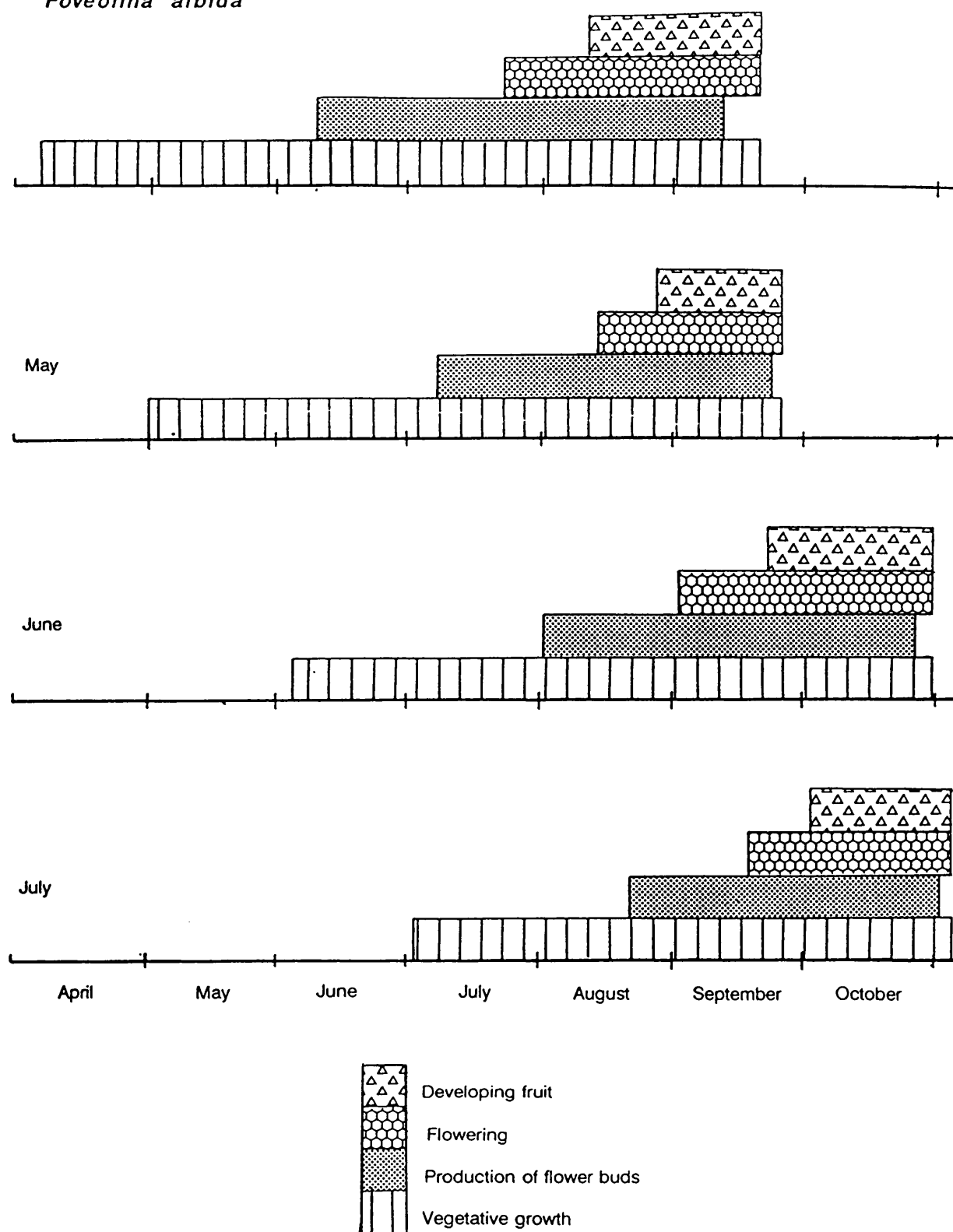
Foveolina albida

Figure 4. Continued.

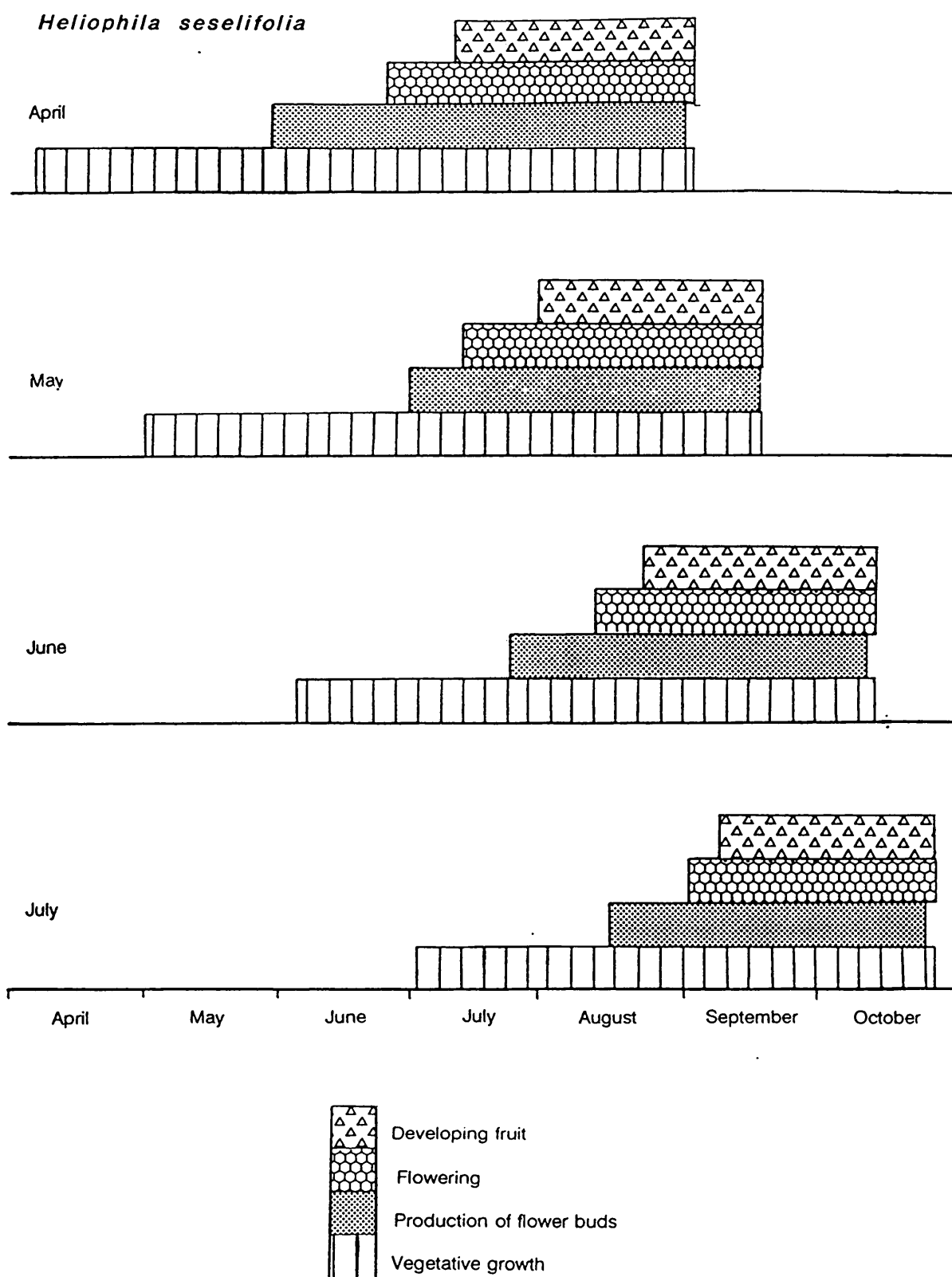


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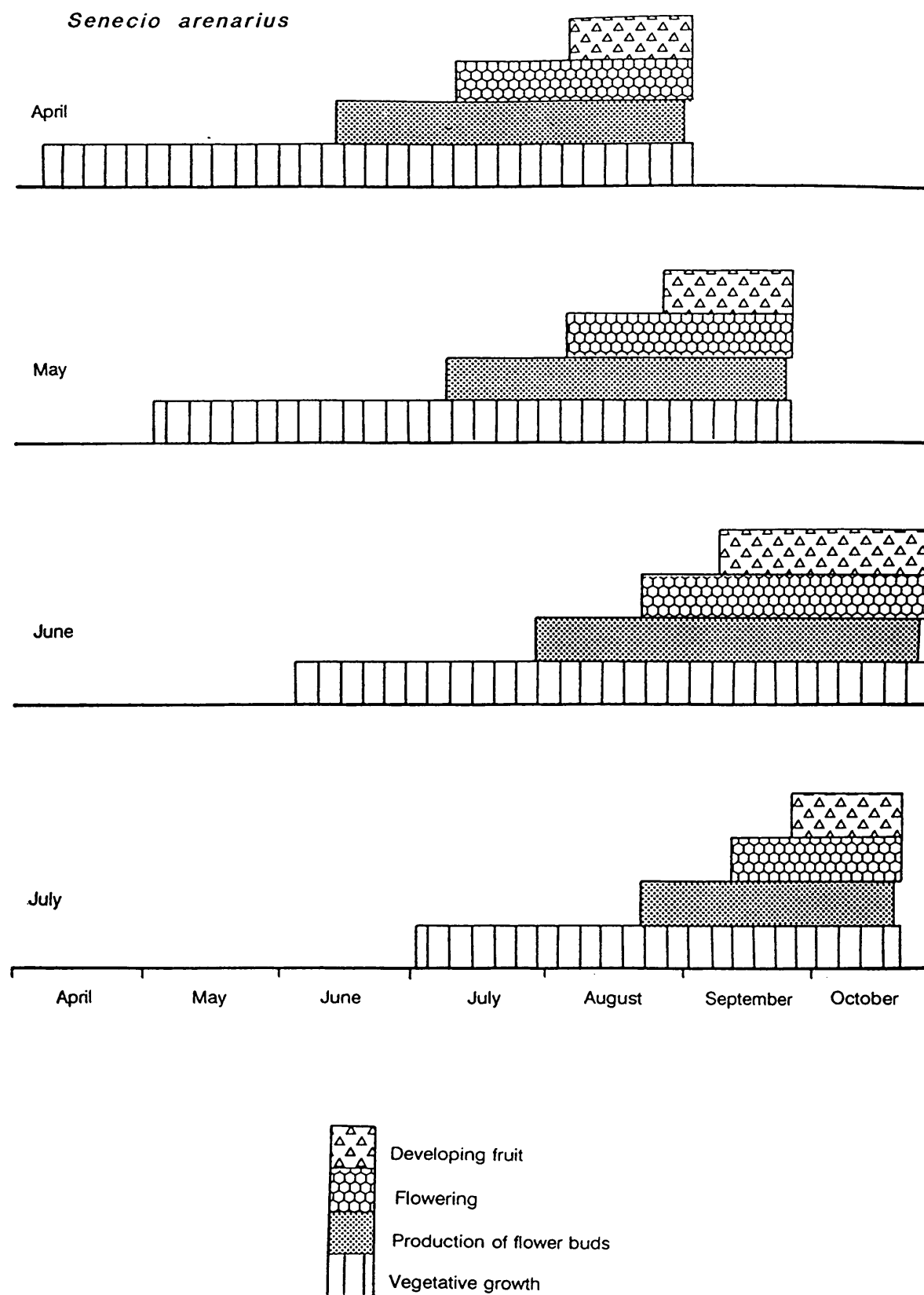


Figure 4. Continued.

Ursinia cakilefolia

e)

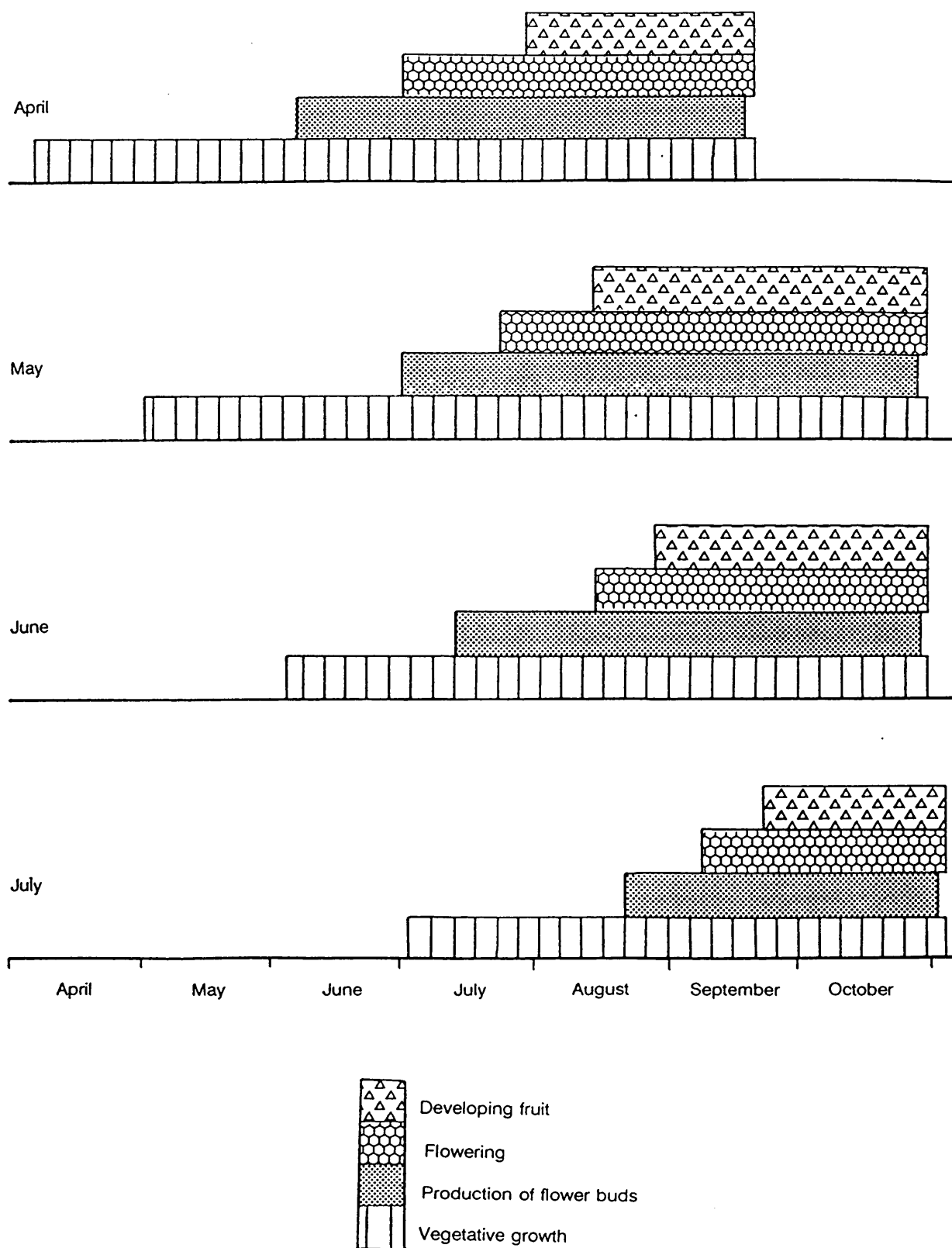


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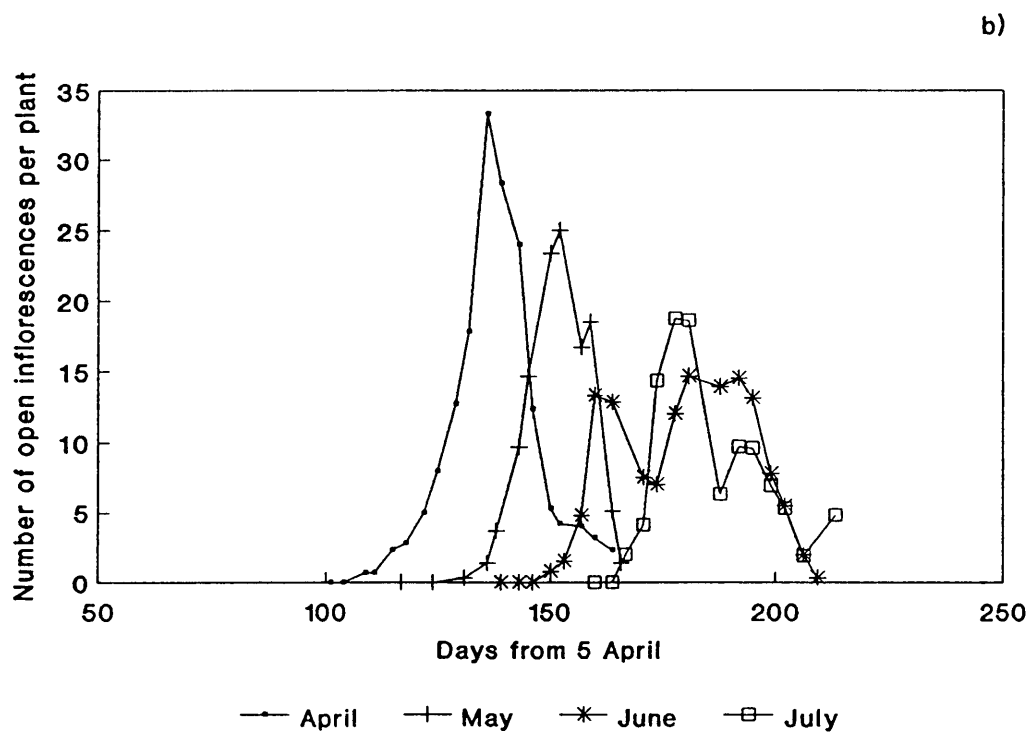
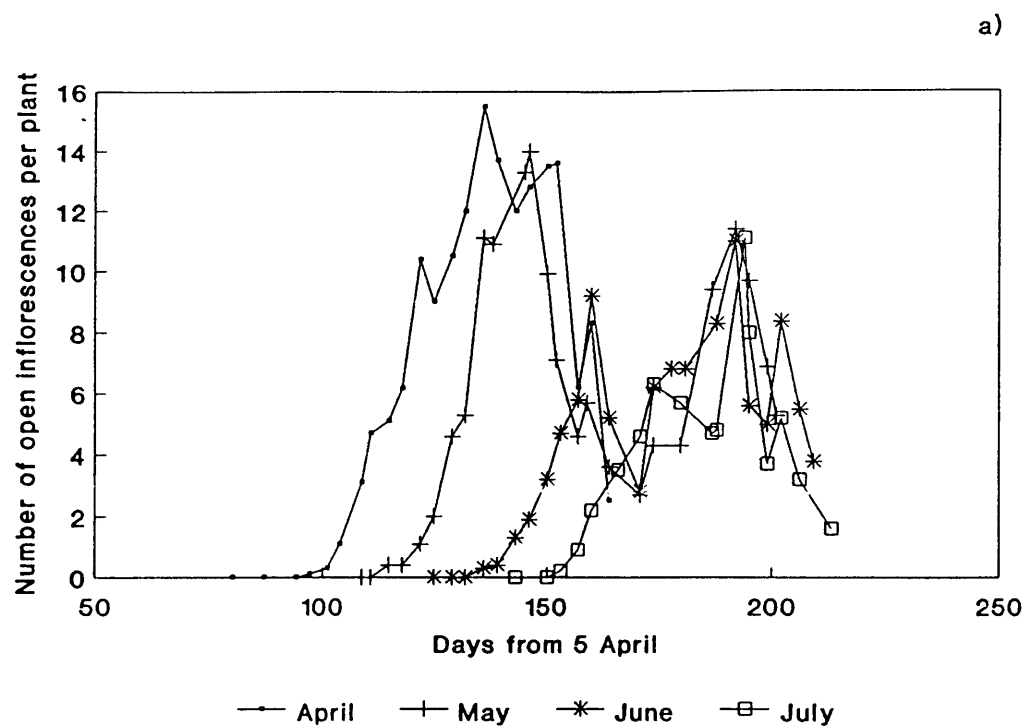


Figure 5. The mean number of open inflorescences per plant of a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Ursinia cakilefolia* plants from different sowing dates.

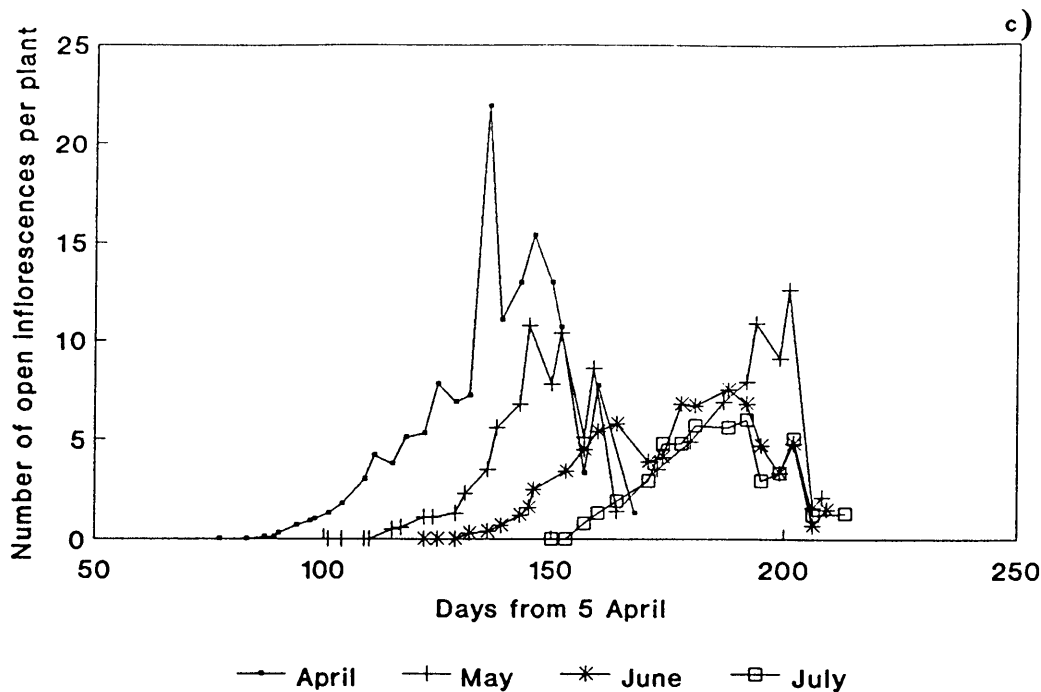


Figure 5. Continued.

that the dominant colour of the Namaqualand flowers changes from white (*H. seselifolia*) through orange to yellow (*F. albida*) during the flowering season.

The flowering curves for *D. sinuata*, *F. albida* and *U. cakilefolia* are presented in Figure 5. April plants produced one (*F. albida*) to three (*D. sinuata* and *U. cakilefolia*) peaks. In the case of *D. sinuata* and *U. cakilefolia*, May plants had two or more flowering peaks. The latest peak was produced at an age when the plants of the other sowing dates were already dead or dying. June plants of all three species, had two or three distinct peaks, while July plants had a short flowering period with two distinct flowering peaks but relatively few open inflorescences at peak flowering.

There was no correlation between successive sowing dates and the duration of the flowering period. May plants had the longest period of flowering in *D. sinuata* and *U. cakilefolia* (Figure 4a & e, Figure 5a & c) while in the case of *F. albida*, *H. seselifolia* and *S. arenarius*, June plants produced a prolonged flowering period. Sowing date however, had a marked effect on the timing of peak flowering of all five species, as there was a distinct tendency towards a decrease in days from sowing until peak flowering the later the sowing date. For example July plants of *F. albida* reached peak flowering when they were 46 days younger than those sown in April (Table 1). Although April plants of *D. sinuata*, *F. albida* and *U. cakilefolia* took longer to reach peak flowering, they had more open inflorescences than plants of any of the other sowing dates (Table 1). The late

peak may have been the result of the delay in inflorescence initiation until low temperatures were experienced during winter (Steyn, Van Rooyen, Van Rooyen & Theron In prep. b)(see Chapter 8). However, as a result of the longer growing period more resources could be accumulated and more flowers/inflorescences were produced at peak flowering time.

In contrast, the lowest peak (least open inflorescences during peak flowering) was associated with plants having a shorter growing period i.e. June and July plants (Table 1). According to Van Rooyen *et al.* (1992) the detrimental effect of a short growing season on reproduction is reduced by the ability of the species to allocate more resources to reproduction under these conditions. Although reproductive output of early sowings exceeds that of late sowings, the opposite is true for reproductive allocation.

The total number of reproductive organs per plant (which includes buds, inflorescences at anthesis, withered inflorescences, developing fruit heads and empty fruit heads) present at the end of the life span for three of the five species, is presented in Table 1. In the case of *D. sinuata* and *F. albida* the total number of reproductive organs was the highest for plants sown in June, while May plants had the highest number of reproductive organs in the case of *U. cakilefolia*. This agrees to a certain extent with the findings of Baskin & Baskin (1974) that low, winter temperatures quantitatively promote flowering in the winter annual *Allysum alyssoides*. Dieringer (1991), however, found that early and middle flowering individuals of *Agalinis strictifolia* (annual herb) flowered longer and produced more flowers and fruit than late flowering individuals.

Field observations

In 1991, the first sufficient rain to trigger germination of ephemerals in the Springbok region occurred when 19.6 mm fell within three days in the beginning of June. Plant height measurements were taken during August and September when the plants were between the stages of 50% flowering to peak flowering, and maximum height is normally almost reached.

Table 2. The mean maximum height of plants, number of open inflorescences per plant at peak flowering as well as the total number of inflorescences produced per plant during the flowering period of five ephemeral species grown in pots (June sowing) and in the field

Species	Maximum height (mm)		Number of open inflorescences (peak)		Total number of inflorescences	
	Pots	Field	Pots	Field	Pots	Field
<i>Dimorphotheca sinuata</i>	232	120	11.0	2.0	81	4.0
<i>Foveolina albida</i>	201	116	14.6	5.4	90	7.1
<i>Heliophila seselifolia</i>	216	153	Not counted	20.4	Not counted	40.1
<i>Senecio arenarius</i>	383	227	Not counted	11.7	Not counted	18.1
<i>Ursinia cakilefolia</i>	326	264	7.5	1.9	51	3.5

The height of *D. sinuata* plants in the Springbok region, ranged from 50 mm to 120 mm; *F. albida* from 59 mm to 116 mm; *H. seselifolia* from 115 mm to 153 mm; *S. arenarius* from 191 mm to 227 mm and *U. cakilefolia* from 115 mm to 264mm. The shorter field plants (Table 2), compared to that of June sown pot plants at the University of Pretoria, could be the result of other environmental variables such as water stress, nutrient deficiency and herbivory.

There was also a significant difference in the mean number of open inflorescences at peak flowering between pot plants of the June sowing date and field plants (Table 2). The relatively fewer inflorescences of the field plants could again be the result of harsher conditions experienced during their growing period. Peak flowering in the field was reached after only 80 days from assumed germination; this is significantly less than the number of days needed by plants grown in Pretoria (Table 1). This difference could, to some extent, be responsible for the difference in the number of inflorescences at peak flowering.

CONCLUDING REMARKS

Different sowing dates had distinct effects on the phenology of the five species studied. Plants derived from seeds sown early in the season, were the tallest and produced more open flowers/inflorescences during peak flowering than those of later sowing dates.

Later sowing resulted in early rapid stem elongation and the initiation of flowers/inflorescences in developmentally younger plants (less leaves on the main stem) and anthesis at a younger age.

It is therefore concluded that early rain (autumn) will result in the establishment of plants which will take a relatively long period to reach anthesis and peak flowering, but at their peak these plants will be taller and produce more open flowers/inflorescences and consequently a more spectacular show than plants that establish later in the season.

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REFERENCES

- BASKIN, J.M. & BASKIN, C.C. 1974. Effect of vernalization on flowering of the winter annual *Alyssum alyssoides*. **Bulletin of the Torrey Botanical Club**, 101: 210 - 213.
- BOWERS, M.A. 1987. Precipitation and the relative abundance of desert winter annuals: a six year study in the northern Mohave desert. **Journal of Arid Environments**, 12: 141 - 149.
- DIERINGER, G. 1991. Variation in individual flowering time and reproductive success of *Agalinis strictifolia* (Scrophulariaceae). **American Journal of Botany**, 78: 497 - 503.
- ELPHINSTONE, E.D. & REES, A.R. 1990. Temperature and development in *Iris x hollandica* during pre-planting storage. II. Floral initiation. **Journal of Horticultural Science**, 62: 185 - 192.

- EVANS, L.T. 1975. The discovery and adaptive role of photoperiodism. In: EMLEU, J.M., EPSTEIN, H.T., HASTINGS, J.W., HOPKINS, J.W. & KLEIN, A.O. (eds.) Daylength and the flowering of plants. Benjamin, Menlo Park. pp. 1 - 14.
- GUTTERMAN, Y. 1988. Day-neutral flowering in some desert *Blepharis* spp.. **Journal of Arid Environments**, 14: 157 - 167.
- HARI, P., KELLOMAKI, S. & VUOKKO, R. 1977. A dynamic approach to the analysis of daily height growth of plants. **Oikos**, 28: 234 - 241.
- HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- KREKULE, J. & HAJKOVA, L. 1972. The developmental pattern in a group of therophytes. II. Vernalization and photoperiodic induction. **Flora**, 161: 121 - 128.
- MOTT, J.J. & McCOMB, A.J. 1975. The role of photoperiod and temperature control in the phenology of three annual species from an arid region of Western Australia. **Journal of Ecology**, 63: 633 - 641.
- MULROY, T.W. & RUNDEL, P.W. 1977. Annual plants: adaptations to desert environments. **BioScience**, 27: 109 - 114.
- PEMADASA, M.A. & LOVELL, P.H. 1974. Factors controlling the flowering time of some dune annuals. **Journal of Ecology**, 62: 869 - 880.
- PILBEAM, C.J., HEBBLETHWAITE, P.D., RICKETTS, H.E. & HASSAN, O.A. 1990. Effects of autumn sowing dates on growth and yield of indeterminate and determinate field beans (*Vicia faba*). **Journal of Agricultural Science**, 114: 339 - 352.
- PRIMACK, R.B. 1979. Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). **American Naturalist**, 114: 51 - 62.
- SCHULZE, B.R. 1965. Climate of South Africa. Part 8. General Survey. WB 28. Government Printer, Pretoria.
- STEYN, H.M. 1993. Namaqualand ephemerals: phenology and thermal units. M.Sc. dissertation. University of Pretoria, Pretoria.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. a). The influence of temperature and sowing date on the phenology of two Namaqualand ephemeral species under controlled conditions.

- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. b). The prediction of phenological stages in five Namaqualand ephemeral species using thermal unit indices.
- TEVIS, L. Jr. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, 39: 681 - 688.
- VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis. University of Pretoria, Pretoria.
- VAN ROOYEN, M.W., GROBBELAAR, N. & THERON G.K. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 2. The therophyte population. *Journal of South African Botany*, 45: 433 - 452.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1992. The ephemerals of Namaqualand: effect of germination date on development of three species. *Journal of Arid Environments*, 22: 51 - 66.
- VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeerspesies. M.Sc. dissertation. University of Pretoria, Pretoria.
- WENT, F.W. 1949. Ecology of desert plants. 2. Effect of rain and temperature on germination and growth. *Ecology*, 30: 1 - 13.
- WENT, F.W. & WESTERGAARD, M. 1949. Ecology of desert plants. 3. Developments of plants in the Death Valley National Monument, California. *Ecology*, 30: 26 - 38.

CHAPTER 6

THE INFLUENCE OF WATER STRESS ON THE PHENOLOGY OF FIVE NAMAQUALAND EPHEMERAL SPECIES

H.M. STEYN, N. VAN ROOYEN, M.W. VAN ROOYEN & G.K. THERON

(Department of Botany, University of Pretoria, 0002)

ABSTRACT

The germination and successful establishment of winter ephemerals in Namaqualand depend on sufficient soil moisture. Although these ephemerals evade drought conditions during summer as seed, most of them are unable to avoid moisture stress completely during their entire life span.

Seeds/achenes of five Namaqualand ephemeral species were sown on four sowing dates (April, May, June and July) to determine the effect of water stress on the phenology of these species sown on different dates.

Water stress shortened the life span and flowering period of all five ephemeral species. Plants subjected to water stress were also smaller and produced less flowers/inflorescences at peak flowering and less reproductive organs during their flowering period than control plants. Water stress had no significant effect on the number of leaves on the main stem at the time of flower/inflorescence initiation.

KEY WORDS: *Dimorphotheca sinuata*, ephemerals, *Foveolina albida*, *Heliophila seselifolia*, phenology, *Senecio arenarius*, sowing date, *Ursinia cakilefolia*, water stress

INTRODUCTION

Arid and semi-arid regions characteristically support an abundant flora of annual plants which complete their life-cycles in short time periods following substantial rainfall (Beatley 1974; Mulroy & Rundel 1977; Van Rooyen, Theron & Grobbelaar 1979), and survive unfavourable dry periods as seeds. They germinate, grow and reproduce in the weeks following the notoriously variable winter rains, while subsurface soil moisture is available (Went 1948, 1949; Went & Westergaard 1949; Beatley 1967, 1974; Van Rooyen *et al.* 1979). Thus, they have a phenology that is closely related to rainfall and temperature and in particular to soil moisture (Ackerman & Bamberg 1974).

The germination-regulation mechanisms of winter annuals restrict the germination of seeds to periods of comparatively abundant moisture coinciding with favourable temperature regimes (Beatley 1974). In the Mohave Desert, mass germination of winter annuals occurs following autumn precipitation events of at least 25 mm (Tevis 1958; Beatley 1967, 1974).

Water availability following germination in desert regions, is highly unpredictable, leading to a high probability of stress, and possibly death, during the growth season of annual plants (Evenari, Shanan & Tadmor 1982; Le Houerou 1984; Ezcurra & Rodrigues 1986). In arid environments, the unpredictable nature of the rainfall, both in timing and amount, imposes several restrictions on the ability of an individual to reproduce successfully (Mott & Chouard 1979). The timing of the life-cycle, the biomass production and the reproductive effort of winter annuals are largely affected by drought (Newman 1965; Pemadasa & Lovell 1974; Watkinson 1982; Rozijn & Van der Werf 1986). Beatley (1967, 1974) concluded that survival of winter desert annuals is controlled by the availability of soil moisture and Fox (1990a) stated that moisture limitation in particular, appears to play a major role in regulating individual phenologies, through its effect on growth.

The climate of Namaqualand, in the north-western corner of South Africa, is characterised by a hot, dry summer and a sparse and erratic winter rainfall (Schulze

1965; Werger 1986). The survival of seedlings and the subsequent growth and development of Namaqualand's ephemerals, depend on climatic conditions that prevail throughout the growing season. Only rarely do climatic conditions combine to result in the well known springtime mass floral display. Flowering occurs mainly in spring, after the temperature has risen, but before drought conditions set in (Van Rooyen *et al.* 1979).

Although ephemerals are classified as drought evaders (Larcher 1983), most of the ephemeral species of Namaqualand have a life span of several months and during that period are periodically subjected to moisture stress (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1991).

The aim of this study was therefore to investigate the effect of water stress and sowing date on the phenology of selected ephemeral species of Namaqualand. This paper forms part of a study (Steyn 1993) on the influence of environmental conditions and sowing date on the phenology of selected Namaqualand ephemerals, with the prediction of peak flowering as the ultimate goal.

METHODS

Seeds/achenes of *Dimorphotheca sinuata* DC. (disc flower achenes), *Foveolina albida* (DC.) Kallersjo, *Heliophila seselifolia* Burch. ex DC. var. *seselifolia*, *Senecio arenarius* Thunb. and *Ursinia cakilefolia* DC. were collected in 1990 in the Goegap Nature Reserve (between 29°34' - 29°43'S and 17°55' - 18°08'E), near Springbok. The seeds were sown in 1 000 cm³ pots, filled with quartz sand on four different sowing dates from autumn to mid winter: fifth of April (April plants), second of May (May plants), fourth of June (June plants) and the second of July (July plants). Two weeks after emergence, the seedlings were thinned to one individual per pot. All plants were grown out of doors at the University of Pretoria. Control plants were watered daily with tap water to field capacity and received Arnon & Hoagland's complete nutrient solution (Hewitt 1952) once a week, while plants subjected to water stress, were watered only once a week and received nutrient solution every second week. The effect of sowing date on the phenol-

ogy of unstressed plants is dealt with in Steyn, Van Rooyen, Van Rooyen & Theron (In prep.)(see Chapter 5).

Twenty eight days after sowing the weekly recording of phenological data started. The height or length of each plant was measured weekly. From the initiation of flowers/inflorescences, all plants were examined phenologically, twice a week. The following phenological stages were distinguished and the number of days from the sowing date on which each stage was reached, was noted for each plant: flower/inflorescence initiation, first flower/inflorescence at anthesis and peak flowering time. The term peak flowering indicates the stage at which the mean number of open inflorescences reached a maximum. In contrast, a flowering peak refers to any distinct culminating point in the flowering curve - not necessarily the highest peak. The total number of open inflorescences for each sowing date of *D. sinuata*, *F. albida* and *U. cakilefolia* was counted twice a week. The flowers/inflorescences of *H. seselifolia* and *S. arenarius* were too numerous to be counted without a destructive harvest. Ten replicates were used per treatment and the mean of the replicates was used in all the Tables and Figures except where stated otherwise.

An one-way analysis of variance (ANOVA)(Statgraphics 5.0. 1989, STSC, Inc., U.S.A.) was used to test for statistical significant differences at $\alpha = 0.05$. The LSD (Least Significant Difference) test was used for comparisons between water treatments and sowing dates, within species. An one-way analysis of variance was also used to test for significant differences in plant height at an age of 40, 80 and 120 days between treatments.

RESULTS AND DISCUSSION

Life span

In all five species water stressed plants which established early in the season had a longer life span than stressed plants which established later in the season (Table 1). The

Table 1. The life span, days till the onset of anthesis, days until peak flowering, the number of open inflorescences per plant during peak flowering and the total number of reproductive organs per plant, produced during the life span of five ephemeral species sown on different sowing dates and grown under different water regimes

Sowing date	Life span (weeks)		Days till anthesis		Days till peak flowering		Number of open inflorescences at peak		Total number reproductive organs	
	Control	Water stress	Control	Water stress	Control	Water stress	Control	Water stress	Control	Water stress
<i>Dimorphotheca sinuata</i>										
April	24	21	96	101	136	122	15.5	2.9	65.1	10.4
May	40	21	88	82	118	116	14	3.1	73.9	10
June	21	16	76	69	100	86	11	2.5	81.1	4.6
July	18	12	65	62	104	69	11.1	1	46.6	2
<i>Foveolina albida</i>										
April	24	21	109	122	136	136	33.3	7.3	59.2	13.7
May	21	21	104	95	125	111	25	8.8	34.8	18
June	21	16	90	83	121	86	14.6	1.7	90	6.3
July	18	12	79	-	90	-	18.7	-	55.7	-
<i>Heliophila seselifolia</i>										
April	21	-	59	-	109	-	Not counted		Not counted	
May	20	18	71	77	111	104				
June	19	14	69	62	100	83				
July	17	18	62	62	90	76				
<i>Senecio arenarius</i>										
April	21	21	96	101	122	122	Not counted		Not counted	
May	21	19	95	88	116	116				
June	20	16	79	79	100	97				
July	16	11	72	65	90	65				
<i>Ursinia cakilefolia</i>										
April	24	21	87	89	136	136	21.9	2.5	39.9	7.3
May	40	21	82	88	118	111	12.6	3.9	69.3	0.1
June	21	16	72	72	128	86	7.5	1.7	50.9	4.3
July	18	18	69	65	104	72	6.0	0.7	34	3.5

differences in life span between plants of different sowing dates can be attributed to differences in climatic conditions (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992). Van Rooyen *et al.* (1992) also found that ephemerals could not grow indefinitely even under favourable conditions. Persistent high temperatures experienced at the end of the growing season apparently caused plants, sown towards the end of the season, to die sooner.

Compared to non-stressed plants, water stress in most cases led to a shortening of the life span of the tested species, with the most distinct effect on the life span of June and July plants (Table 1). This reduction in the life span by water stress confirms the statement of Aronson, Kigel, Shmida & Klein (1992) that plant senescence was strongly enhanced by water stress and the length of the life cycle was greatly shortened.

Plant height

As in the case of unstressed plants (Steyn *et al.* In prep.)(see Chapter 5) the maximum height of water stressed plants, decreased significantly with successive sowing dates (Table 2). In all species tested, except *S. arenarius*, April and May water stressed plants were significantly taller than June and July plants. These results support those of Van Rooyen (1988) and Steyn *et al.* (In prep.) (see Chapter 5) who found that plants sown early in the season (April), and watered daily, were significantly taller than the plants sown from May to July.

No *Heliophila seselifolia* plants sown in April, survived the water stress treatment. In the four other species tested, April water stressed plants showed the longest lag phase before the onset of rapid elongation, with the exception of *U. cakilefolia* plants, where the lag phase of July plants was the longest. The length of this lag phase decreased at later sowing dates and June and July plants reached their maximum height sooner than April and May plants (Figure 1a - e).

In contrast to unstressed plants where July plants had the shortest lag phase (Steyn *et al.* In prep.)(see Chapter 5), June water stressed plants were first to elongate relatively

Table 2. The mean height (mm) of the examined species, sown on different dates and grown under different watering regimes.

Species	Sowing date	Height at day						Maximum height	
		40		80		120		Control	Water stress
		Control	Water stress	Control	Water stress	Control	Water stress		
<i>Dimorphotheca sinuata</i>	April	15.8	12.1	56.1	36.5 *	250.0	189.6 *	299.80	218.70 *
	May	15.0	22.1	70.1	57.4	261.6	159.4 *	261.60	183.80 *
	June	16.5	23.4 *	112.8	112.6	206.0	-	232.00	112.60 *
	July	26.1	25.8	236.0	71.6 *	206.0	-	239.00	71.70 *
<i>Foveolina albida</i>	April	4.0	4.0	37.0	16.0 *	222.0	134.7 *	264.00	167.00 *
	May	3.6	5.8 *	31.7	52.4 *	217.6	184.6 *	236.00	192.00 *
	June	8.7	11.8	73.0	84.2	186.0	-	201.00	84.20 *
	July	5.4	6.2	188.0	26.6	227.8	-	219.00	20.60 *
<i>Heliophila seselifolia</i>	April	8.3	-	104.0	-	251.9	-	251.90	-
	May	5.8	9.6 *	129.8	116.1	209.0	161.0 *	229.00	189.00 *
	June	8.7	19.8 *	164.7	155.9	207.1	-	221.10	155.90 *
	July	15.1	12.2 *	217.8	107.0	205.6	-	217.80	115.00 *
<i>Senecio arenarius</i>	April	11.3	10.1	167.9	62.4 *	450.0	256.0 *	489.90	285.00 *
	May	9.1	8.9	131.9	153.5	361.2	285.0 *	371.50	335.60
	June	18.3	23.4 *	296.5	114.3 *	345.0	-	383.00	126.10 *
	July	13.8	18.3	291.0	74.2 *	342.0	-	342.00	78.10 *
<i>Ursinia cakilefolia</i>	April	17.3	15.7	83.9	66.3 *	345.5	206.6 *	481.40	274.00 *
	May	17.3	20.2	94.3	81.4	395.4	248.4 *	428.60	248.40 *
	June	24.9	27.4	161.8	144.6	312.0	-	326.00	162.50 *
	July	25.5	15.5	302.0	42.0 *	364.0	-	390.00	53.00 *

* Denotes a significant difference ($P \leq 0.05$) between the control and water stress treatments

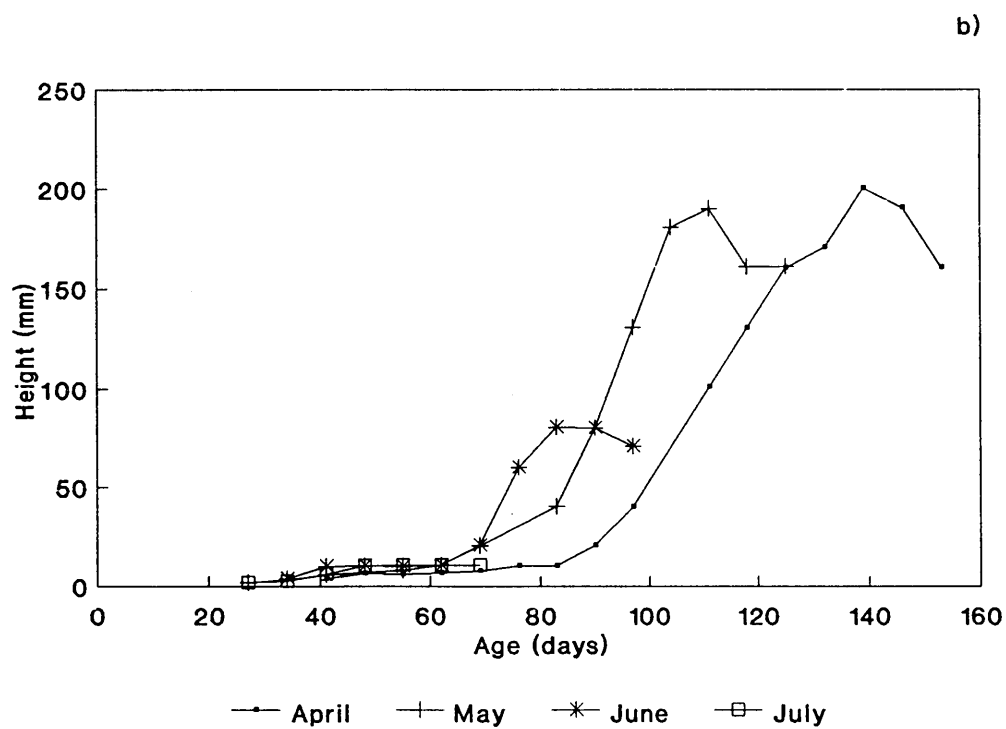
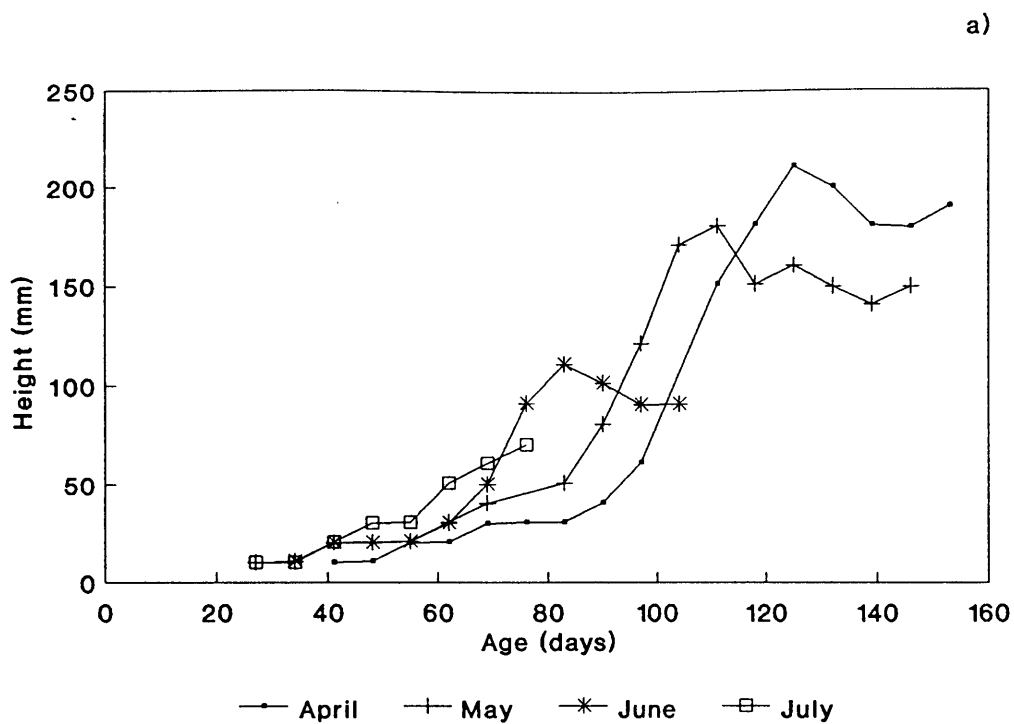


Figure 1. The mean height (mm) of a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and e) *Ursinia cakilefolia* plants, sown on different sowing dates and grown under water stress.

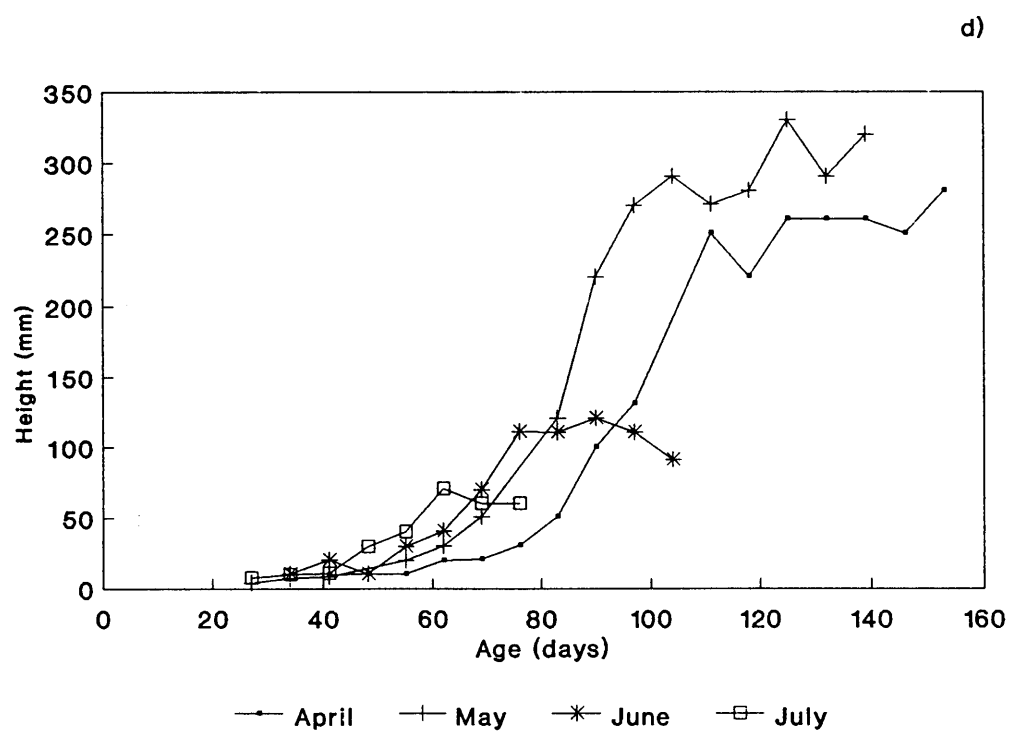
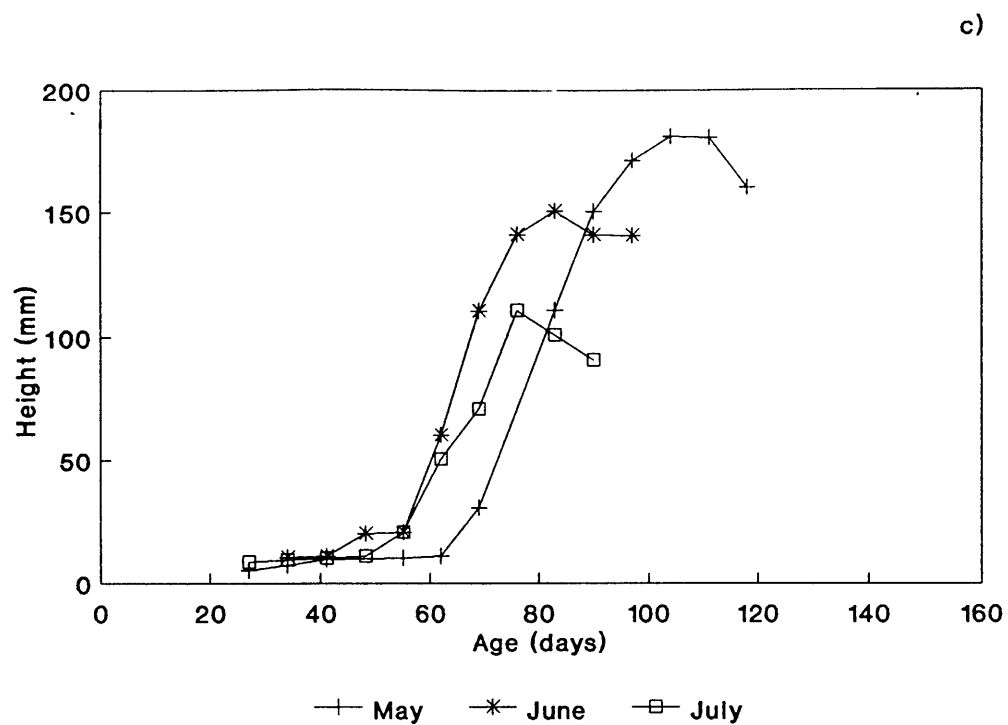


Figure 1. Continued.

e)

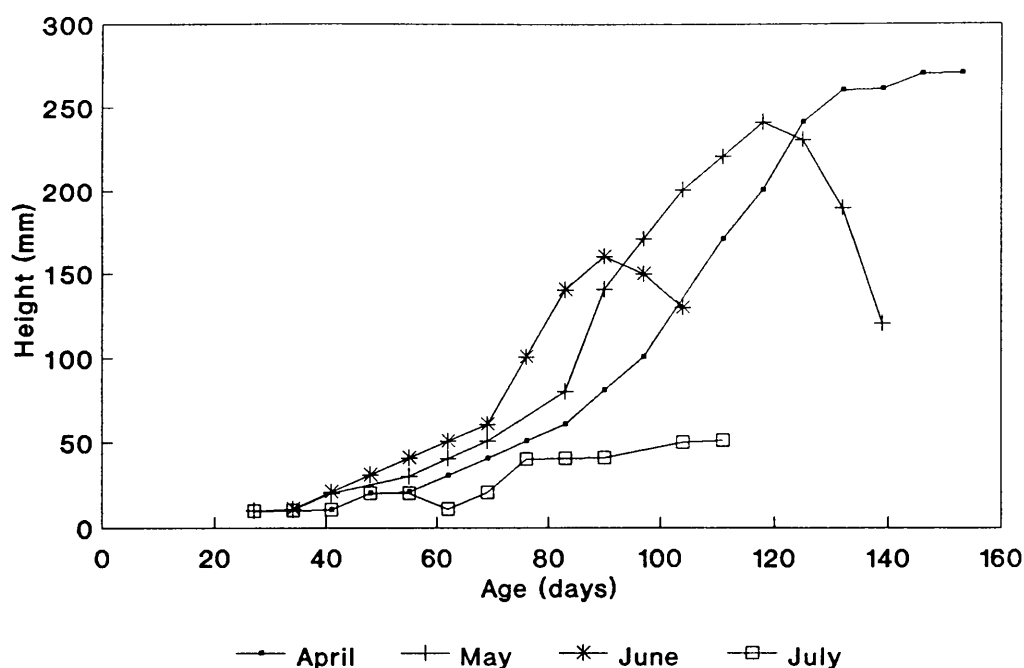


Figure 1. Continued.

rapidly. Forty days after sowing, June plants were usually the tallest (Table 2), although this difference was only significant in the case of *S. arenarius* and *U. cakilefolia*. At 80 days after sowing, May and/or June plants subjected to water stress, tended to be significantly taller than April and July water stressed plants. As June and July plants had already completed their life cycles before 120 days, the heights of the plants could no longer be measured.

The difference in height between plants of different sowing dates of both control and water stressed plants, can probably be attributed to differences in climatic conditions. Mean weekly air temperatures as well as mean weekly maximum and minimum air temperatures from April to October are presented in Figure 2. During the first two months, the mean weekly temperature dropped steadily and the daylength decreased as well. From the middle of June to the end of July, the mean weekly temperature remained more or less constant, with the exception of the first week in July, when the temperatures rose sharply, whereafter it decreased again. From the middle of August temperatures started to rise rapidly.

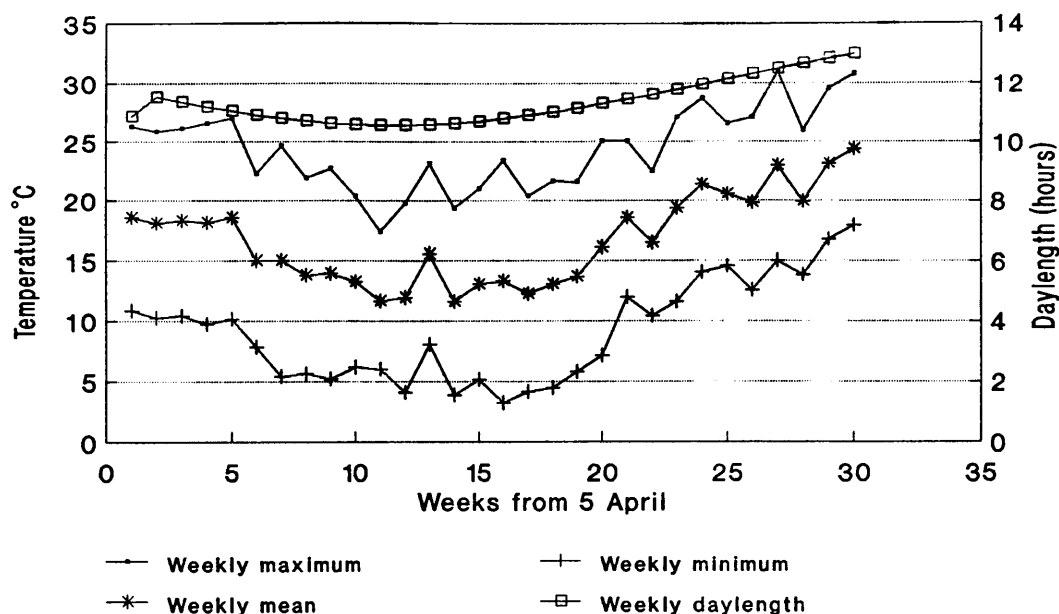


Figure 2. The mean weekly maximum, mean weekly minimum, mean weekly temperature and the mean daylength at Pretoria from April to October 1991.

In all five species examined, water stress led to a significant decrease in the maximum height attained by the plants (Table 2). These results are supported by those of Mulroy & Rundel (1977) who found that species reaching 500 - 1000 mm in height under optimal conditions, may only grow to 50 mm in dry years under less favourable conditions.

The maximum plant height of water stressed April plants, were reduced by 27.05% of the control in the case of *D. sinuata* plants, and up to 43.08% in the case of *U. cakilefolia* plants. The reductions in maximum plant height of May, June and July plants of *D. sinuata* were 29.74%, 51.47% and 70% respectively. In all species the detrimental effect of water stress on plant height was most pronounced in the case of the later sowings (June and especially July).

At an age of 40 days the height of control and water stressed plants of *D. sinuata*, did not differ significantly except in the case of June plants, where the water stressed plants were significantly taller than control plants (Table 2). This unexpected result might be explained by Fox (1990b) who contended that growing in water saturated soil may be

stressful for some desert annuals. At an age of 80 days, however, control plants were taller than water stressed plants, although this difference was not significant in the case of May and June plants. Water stressed plants at an age of 120 days were significantly smaller than control plants.

As in the case of *D. sinuata*, there was no significant difference in height between control and water stressed plants of *U. cakilefolia* at an age of 40 days (Table 2) although water stressed May and June plants tended to be taller than control plants. At an age of 80 days, this difference was reversed and control plants were the tallest, although this difference was only significant in the case of April and July plants. After 120 days control plants were significantly taller than the water stressed plants.

The effect of water stress on the height of plants of *F. albida*, *H. seselifolia* and *S. arenarius* basically followed the same pattern as for *D. sinuata* and *U. cakilefolia*. Significant differences in plant height between control and water stressed plants are indicated in Table 2.

Number of leaves on the main stem at flower/inflorescence initiation

During the initial period of slow growth in all species, leaves were produced on the main stem only. The apical meristem of the main stem produced the first floral primordium. The number of leaves produced on the main stem was thus determined by factors controlling flower initiation (Van Rooyen *et al.* 1992).

The number of leaves on the main stem of all species examined, control plants and those subjected to water stress, decreased from April plants to July plants (Figure 3a - e). This decrease in the number of leaves produced on the main stem from plants sown early in the season to those sown in the middle of the season, can probably be explained by the fact that low temperatures promote flower initiation in winter annual species (Mott & McComb 1975; Van Rooyen *et al.* 1992). Plants of the late sowing dates were "physiologically" (developmentally) younger at the stage of flower/inflorescence initiation (Krekule & Hajkova 1972) as they had experienced low temperatures early in their life

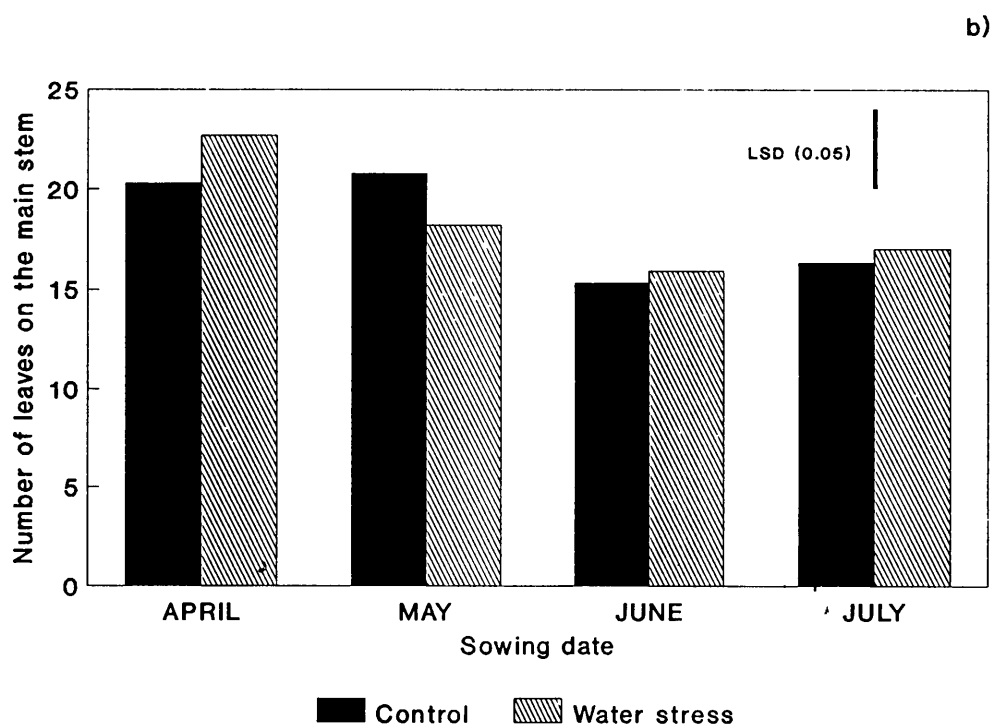
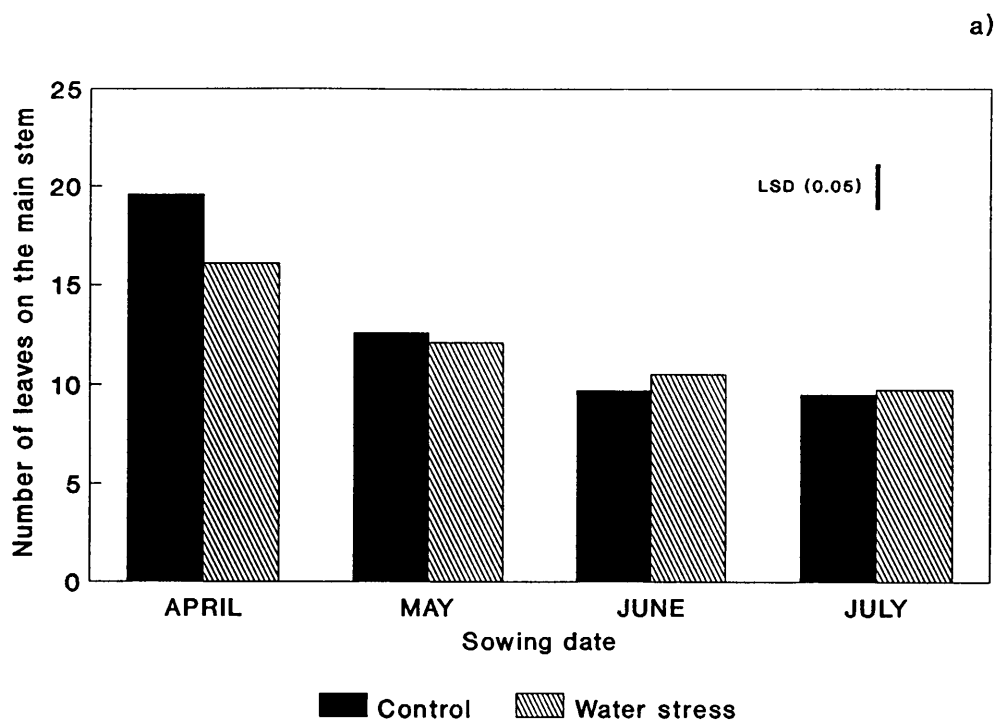


Figure 3. The mean number of leaves on the main stem at flower/inflorescence initiation of
a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and
e) *Ursinia cakilefolia* plants from different sowing dates and grown under different watering
regimes.

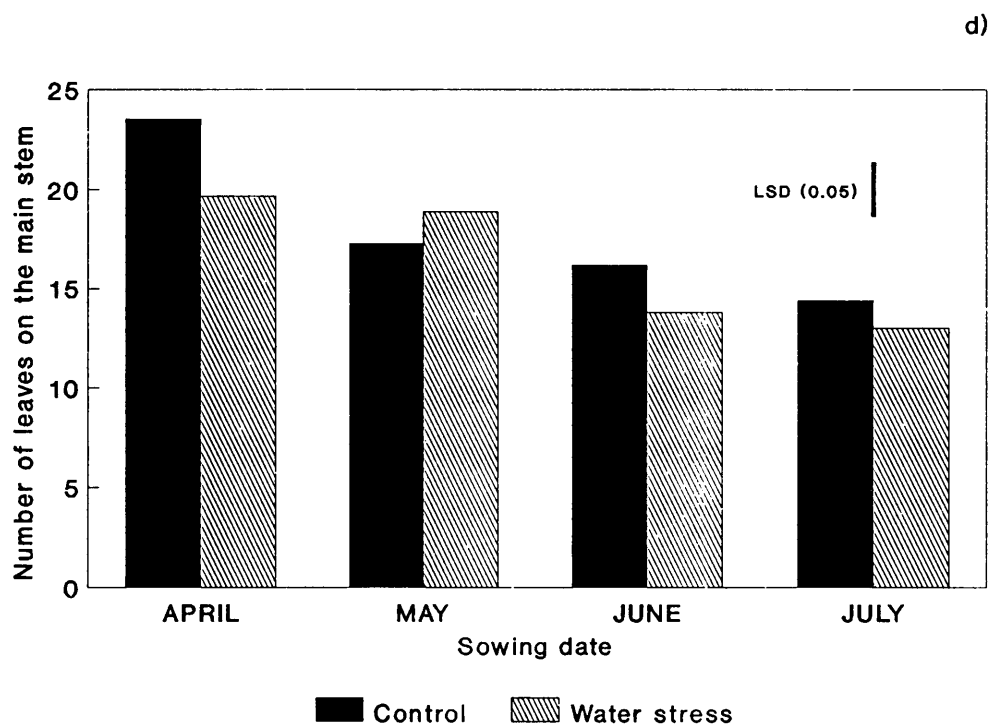
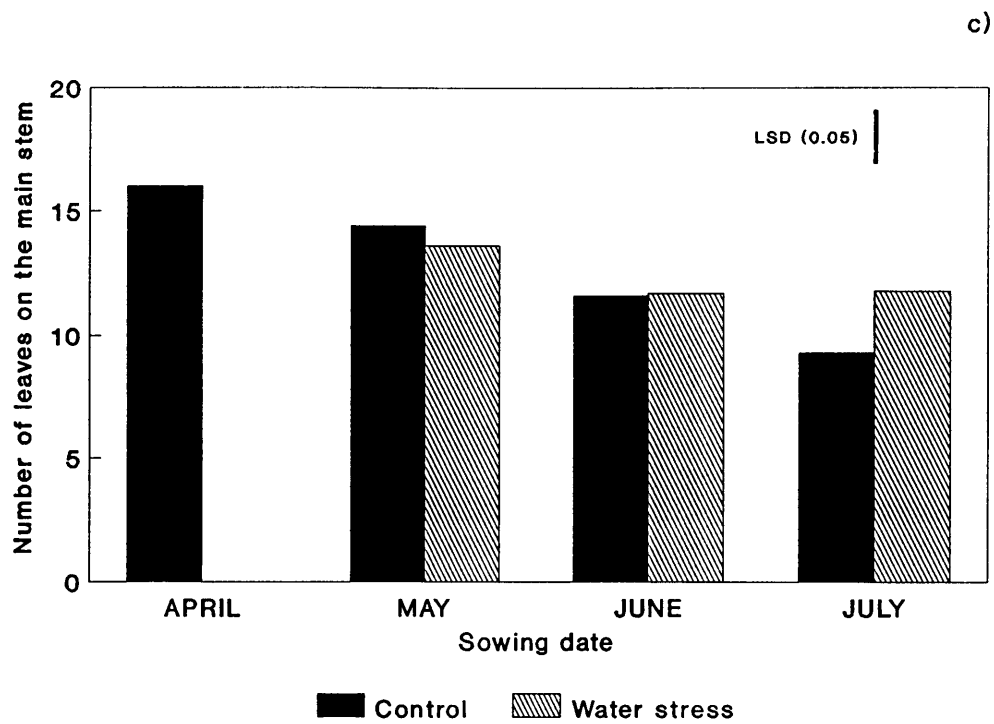


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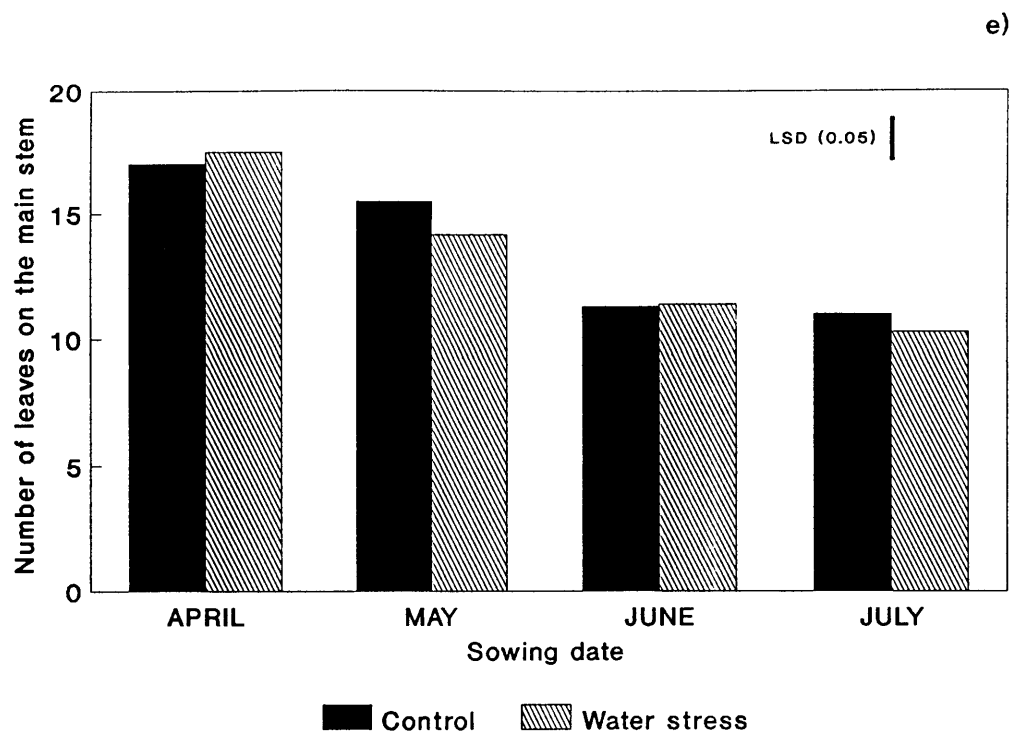


Figure 3. Continued.

cycle (Elphinstone & Rees 1990; Van Rooyen *et al.* 1992).

In general, there was no significant difference in the number of leaves on the main stem between control and water stressed plants (Figure 3a - e), except in the case of July *H. seselifolia* and April *D. sinuata* and *S. arenarius* plants. This could be explained by the fact that the plants were still very small at the stage of flower/inflorescence initiation and they were not affected by water stress. Although, Van Rooyen *et al.* (1991) also found that the number of leaves on the main stem was unaffected by water stress, Mott & McComb (1975) observed a decrease in the number of leaves on the main stem, with increased water stress.

Production of flowers/inflorescences

In all five species studied, the time to the onset of anthesis and peak flowering of water stressed plants decreased, the later the seeds had been sown (Table 1, Figure 4b, d & f). Similar results were obtained by Gutterman (1988), Van Rooyen *et al.* (1992) and

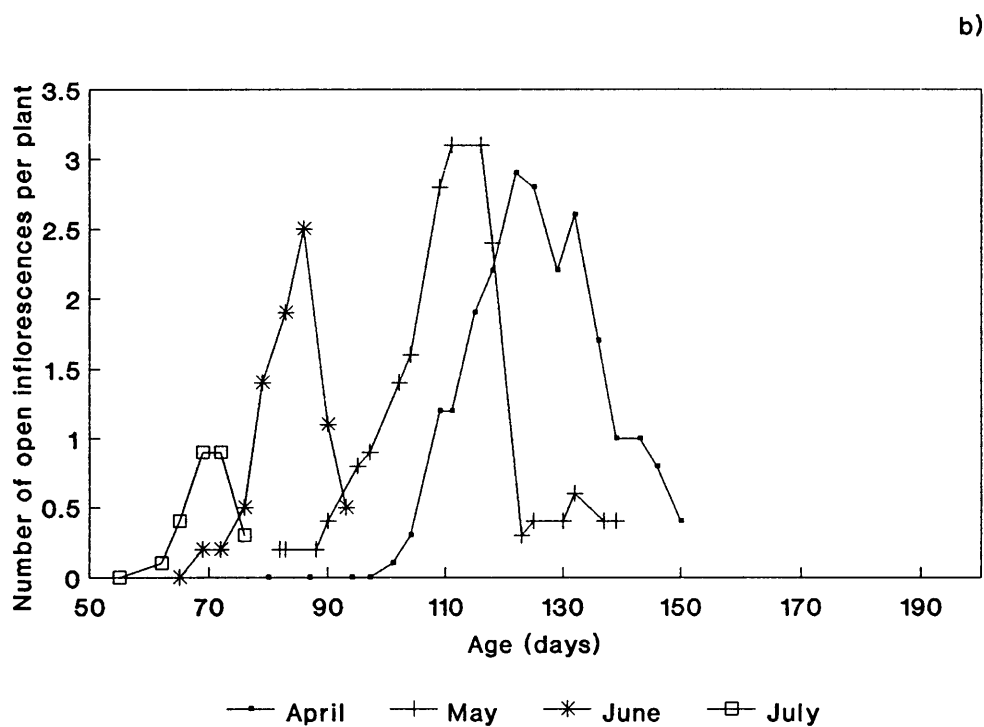
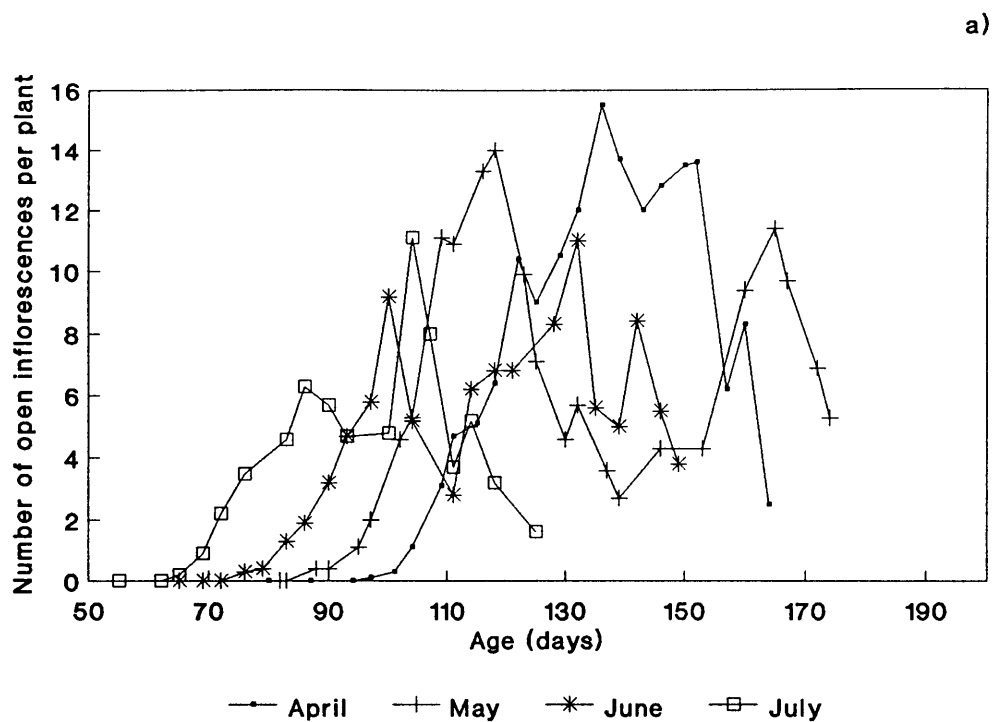


Figure 4. The mean number of open inflorescences per plant of a) control plants of *Dimorphotheca sinuata*, b) water stressed plants of *D. sinuata*, c) control plants of *Foveolina albida*, d) water stressed plants of *F. albida*, e) control plants of *Ursinia cakilefolia* and f) water stressed plants of *U. cakilefolia*.

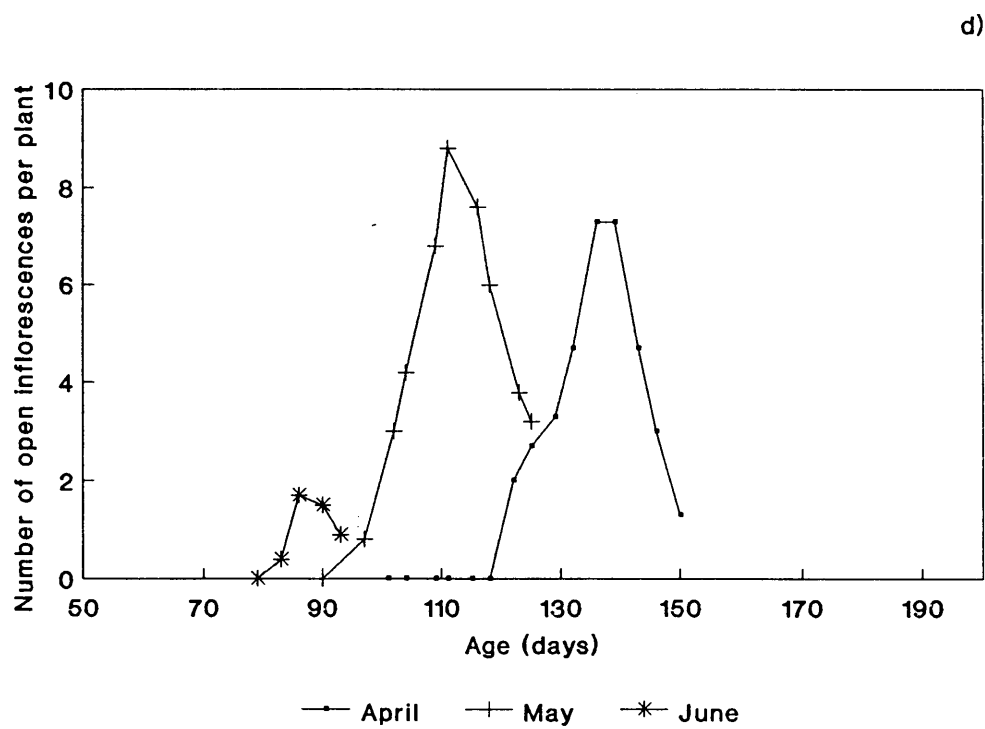
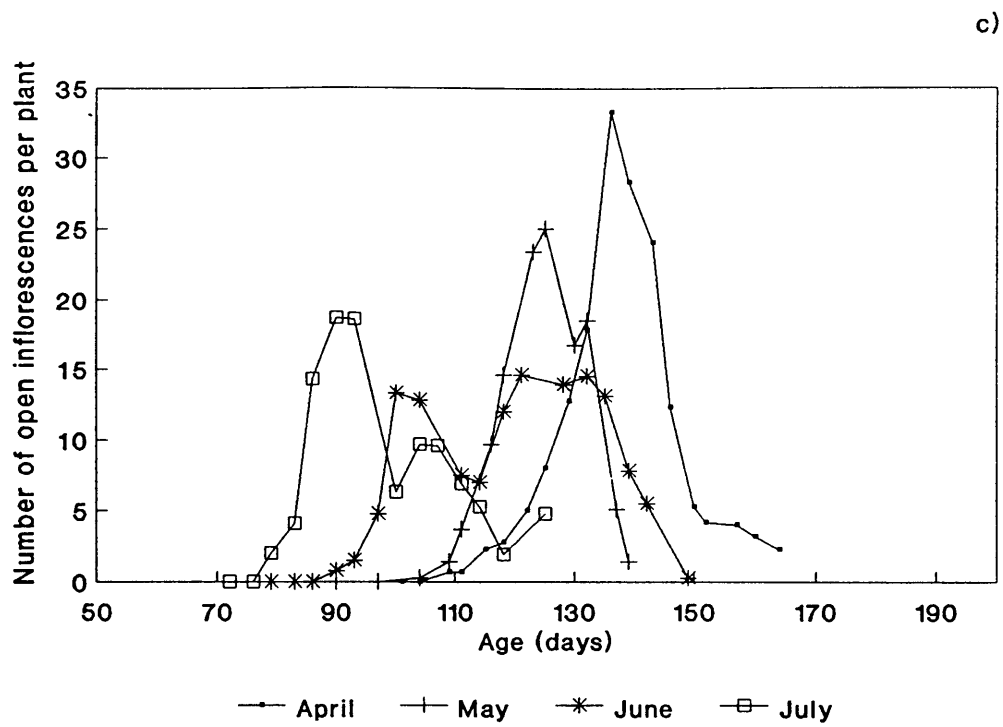
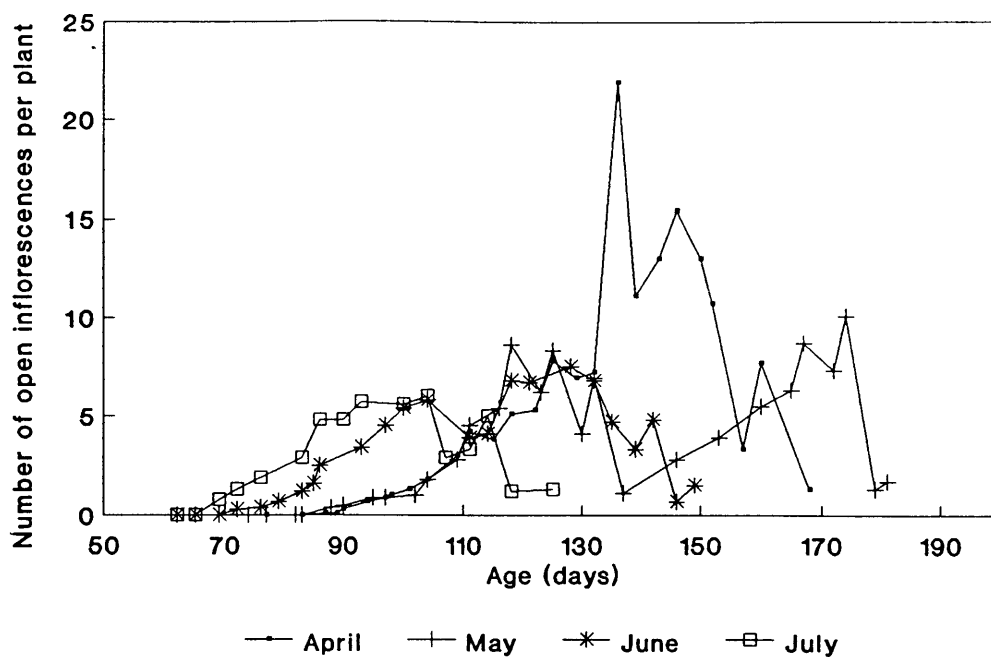


Figure 4. Continued.

e)



f)

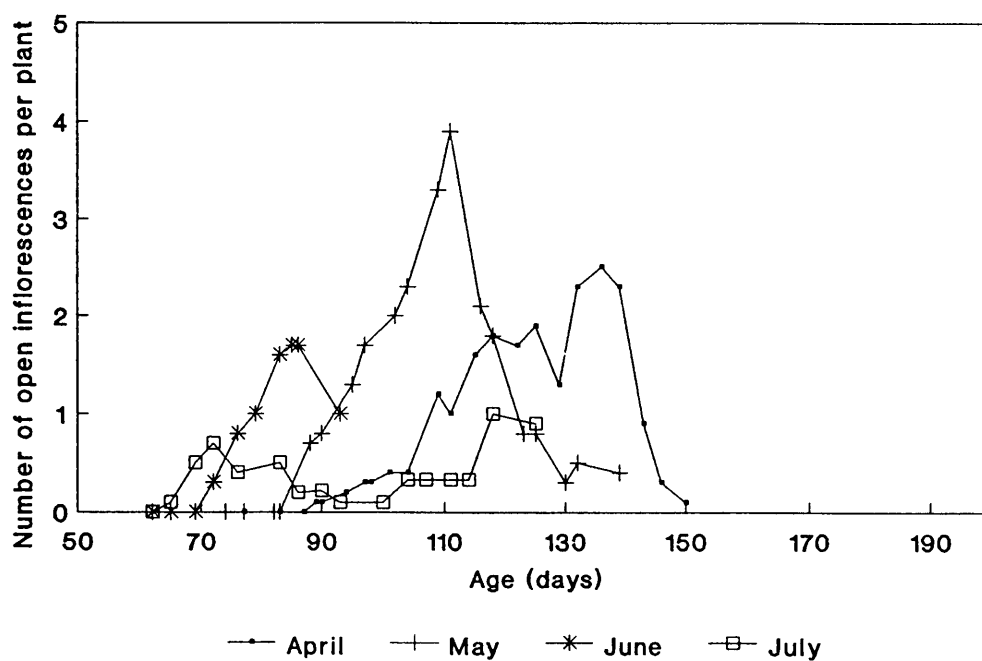


Figure 4. Continued.

Steyn *et al.* (In prep.)(see Chapter 5) on unstressed plants (Figure 4a, c & e). The late peak of April plants may have been the result of the delay in flower/inflorescence initiation until low temperatures set in during winter.

The effect of water stress on the time span from sowing to the onset of anthesis varied between species and sowing date (Table 1). In the case of April plants, water stress delayed the time to anthesis in all species, although this delay was only significant for *S. arenarius* and *U. cakilefolia*. In May plants of two species viz. *H. seselifolia* and *U. cakilefolia*, flowering was once more delayed by water stress, while in the case of the remaining three species, flowering was accelerated by water stress (significantly so for *F. albida*). Flowering in June as well as July plants was either accelerated by water stress or unaffected by it. Literature records on the effect of water stress on the time span from sowing to anthesis, indicate the same lack of a uniform response. The delay of anthesis in water stressed April and some May plants corresponds to the findings of Aspinall & Husain (1970), Boot, Raynal & Grime (1986) and Fox (1990b) who found that water stress delayed flowering in specific annual species. Clarkson & Russell (1976) also found that water stress delayed flowering by an average of 14 days in five out of six annual *Medicago* species.

On the other hand, the fact that water stressed June and July plants reached anthesis sooner than control plants, supports the widely held idea that the onset of flowering is stimulated by drought (Fox 1990a). Plants of *F. albida* sown in July did not flower at all (Table 1). According to Ackerman & Bamberg (1974) the amount of moisture in the soil at the start of the spring growth period determines initial flowering response of shrubs and the lack of moisture at this time results in some species producing few or no flowers.

Aronson *et al.* (1992) stated that water stress had no effect on the annual *Erucaria hispanica*, but slightly accelerated the transition to flowering in the annuals *Bromus fasciculatus* (by 1 - 2 days) and *Brachypodium distachyon* (4 - 6 days). Angus & Mancur (1977) found that a relative mild degree of water stress could hasten the seasonal occurrence of anthesis, while exposure to severe water stress can delay the time of

anthesis later in the growing season. In the study of two winter ephemeral species of Australia, Mott & McComb (1975) reported that the time to initiation of visible floral primordia was delayed in severely stressed plants, although no significant difference was found in the time to anthesis between unstressed plants and those grown under moisture stress. In a detailed field study, Klikoff (1966) found a slight delay in the time to flowering under high moisture stress. It was not clear, however, if high water stress delayed flowering by affecting flower initiation directly or indirectly by slowing down the vegetative development.

Water stress also tended to reduce the time span from sowing to peak flowering (Table 1). The stimulation of peak flowering time was the most obvious in the case of July plants.

Drought-stimulated flowering in desert annuals can maximize their size at flowering, but still assure that they set seed before the season's end (Solbrig, Barbour, Cross, Goldstein, Lowe, Morello & Yang 1977; Rathcke & Lacey 1985). Aronson *et al.* (1992) suggested that although flowering of many winter annuals is under photoperiodic control, adequate daylength requirements for flowering induction decrease or even disappear along gradients of increasing aridity and rainfall unpredictability. This would allow flowering earlier after germination.

Although control April plants produced the most open inflorescences at peak flowering (Steyn *et al.* In prep.)(see Chapter 5), May plants of *D. sinuata*, *F. albida* and *U. cakilefolia*, subjected to water stress, produced the most open inflorescences at peak flowering (Table 1, Figure 4b, d & f). Water stressed April plants produced relatively less open inflorescences, followed by June and July plants. In general, the flowering period of water stressed plants was shorter than that of control plants (Figure 4a - f)

Water stressed plants of *D. sinuata*, *F. albida* and *U. cakilefolia*, of all four sowing dates produced one distinct flowering peak (Figure 4b, d & f), with the exception of July plants of *Ursinia cakilefolia* that produced two peaks. These flowering curves (Figure 4b, d & f) differ markedly from those of unstressed plants (Figure 4a, c & e), where more

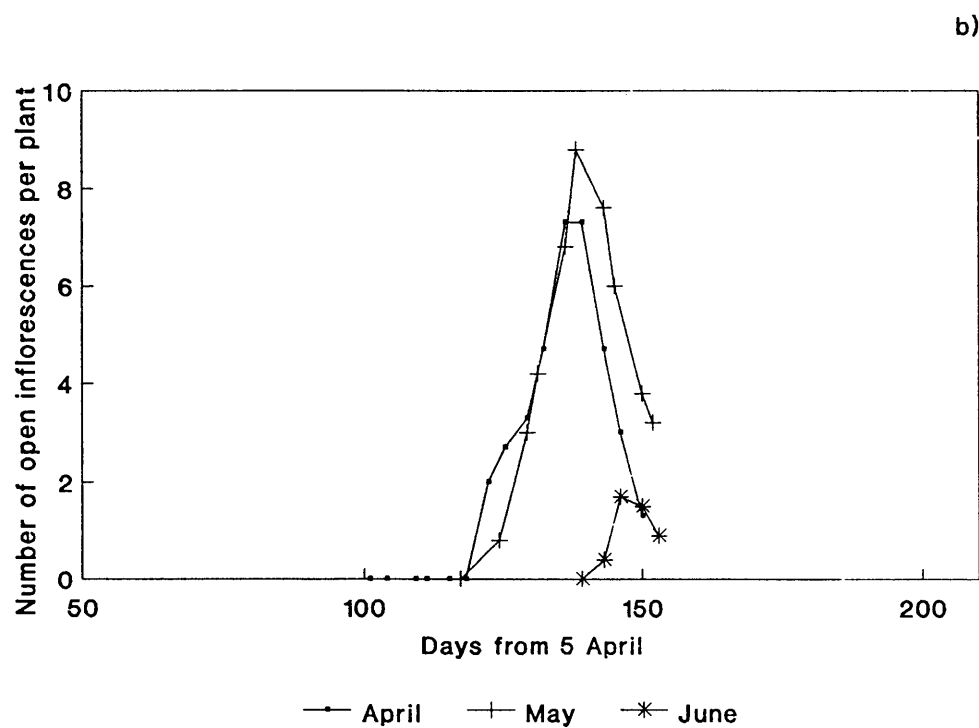
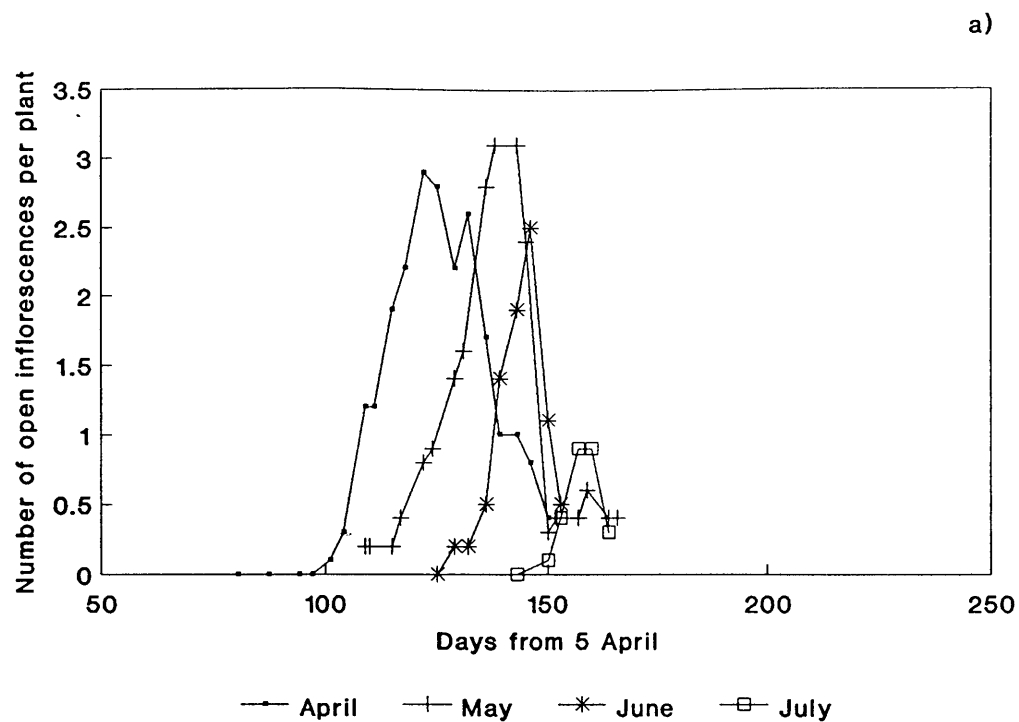


Figure 5. The mean number of open inflorescences per plant of water stressed plants of a) *Dimorphotheca sinuata*, b) *Foveolina albida* and c) *Ursinia cakilefolia*.

c)

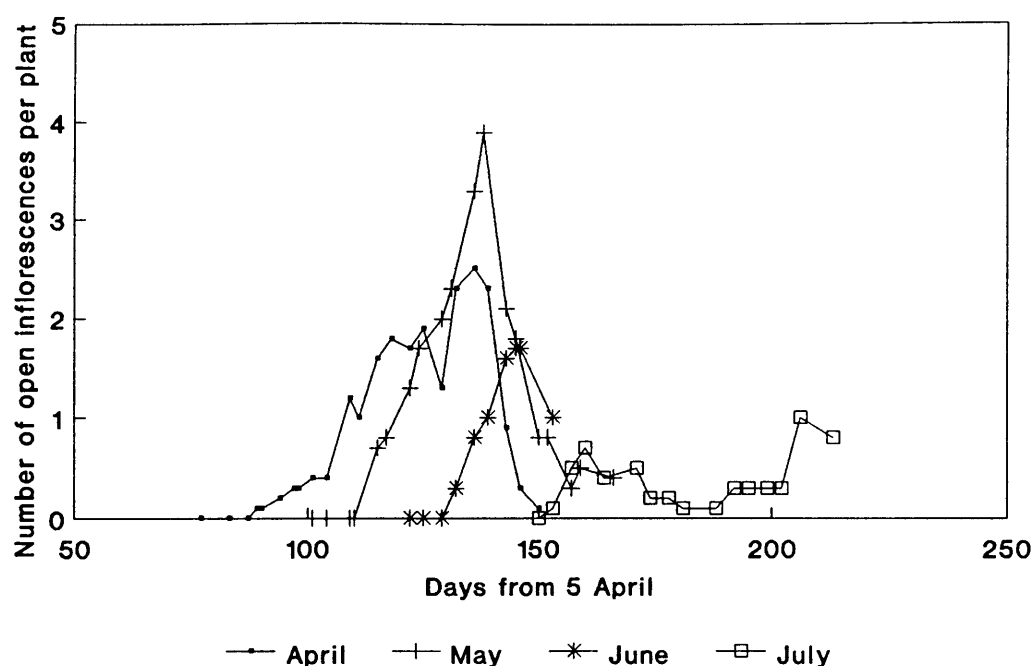


Figure 5. Continued.

than one peak was often observed.

If the time course of open inflorescence production at different sowing dates are plotted chronologically (Figure 5 a - c), it becomes clear that the sequence of anthesis and peak flowering follow the sowing date sequence in the case of *D. sinuata* (Figure 5a). However, peak flowering of April and May plants of *F. albida* and *U. cakilifolia* coincided (Figure 5 b & c).

The total number of reproductive organs per plant (which included buds, inflorescences at anthesis, withered inflorescences, developing fruit heads and empty fruit heads) present at the end of the life span for three of the five species, is presented in Table 1. In all three species, water stressed plants of the early sowing dates (April and May) generally had the highest number of reproductive organs. In contrast unstressed May and June plants in general produced the most reproductive organs during their life span (Steyn *et al.* In prep.)(see Chapter 5). There was also a significant decrease in the total number of reproductive organs between control and water stressed plants of all sowing

dates in three species (Table 1).

Water stress had the most severe effect on various plant characteristics in July plants, followed by June plants. The combined effects of water stress and high temperatures, experienced by plants of these sowing dates towards the end of the growing season, seemed to have the greatest negative influence.

CONCLUDING REMARKS

Later sowing and/or water stress, led to a shortening in the life span of all five species examined.

The maximum height of water stressed plants, decreased at later sowing dates. April plants were significantly taller than plants of later sowing dates, due to a longer and more favourable growing period. At an age of 80 days, a significant reduction in plant height was established as a result of water stress.

The number of leaves on the main stem at flower/inflorescence initiation, was unaffected by water stress although it decreased with later sowing dates. This could be ascribed to the fact that plants were still very small at this stage and the water stress treatment had no effect as it was not yet severe enough.

Later sowing resulted in the shortening of the time span between sowing and anthesis/peak flowering in both control and water stressed plants. May water stressed plants produced the most open inflorescences at peak flowering, and April and May plants produced the most reproductive organs during their life span. Water stress reduced the time span from sowing to the onset of anthesis and peak flowering at the later sowing dates, possibly to ensure seed set before the end of the season.

Plants of *D. sinuata*, *F. albida* and *U. cakilefolia*, subjected to water stress, produced less open inflorescences than control plants during peak flowering and their flowering period

was shorter than that of control plants.

Water stress also resulted in a significant decrease in the total number of reproductive organs at all sowing dates in the species examined.

From these results it can be concluded that ephemeral plants subjected to water stress will probably have a shorter life span, be smaller with relatively fewer flowers/inflorescences and a shorter flowering period than plants which were grown with sufficient water.

ACKNOWLEDGEMENTS

The authors would like to thank the Foundation for Research Development for financial support and the University of Pretoria for the use of the facilities. Riaan de Villiers is also gratefully acknowledged for his assistance during this experiment and with the preparation of this paper.

REFERENCES

- ACKERMAN, T.L. & BAMBERG, S.A. 1974. Phenological studies in the Mojave desert at Rock Valley (Nevada test site). In: LIETH, H. (ed.) Phenology and seasonality modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 215 - 226.
- ANGUS, J.F. & MANCUR, W.M. 1977. Water stress and phenology of wheat. *Australian Journal of Agricultural Research*, 28: 177 - 181.
- ARONSON, J., KIGEL, J., SHMIDA, A. & KLEIN, J. 1992. Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia (Berl.)*, 89: 17 - 26.
- ASPINALL, D. & HUSAIN, I. 1970. The inhibition of flowering by water stress. *Australian Journal of Biological Science*, 23: 925 - 936.

- BEATLEY, J.C. 1967. Survival of winter annuals in the northern Mojave Desert. *Ecology*, 48: 745 - 750.
- BEATLEY, J.C. 1974. Phenological events and their environmental triggers in the Mojave desert ecosystem. *Ecology*, 55: 856 - 863.
- BOOT, R., RAYNAL, D.J. & GRIME, J.P. 1986. A comparative study of the influence of drought stress on flowering in *Urtica dioica* and *Urtica urens*. *Journal of Ecology*, 74: 485 - 495.
- CLARKSON, N.M. & RUSSELL, J.S. 1976. Effect of water stress on the plastic development of annual *Medicago* species. *Australian Journal of Agricultural Research*, 27: 227 - 234.
- ELPHINSTONE, E.D. & REES, A.R. 1990. Temperature and development in *Iris x hollandica* during pre-planting storage. II. Floral initiation. *Journal of Horticultural Science*, 62: 185 - 192.
- EVENARI, M., SHANAN, L. & TADMOR, N. 1982. The Negev: Challenge of a Desert, 2nd edn. Harvard University, Cambridge.
- EZCURRA, E. & RODRIGUES, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *Journal of Arid Environments*, 10: 13 - 28.
- FOX, G.A. 1990a. Components of flowering time variation in a desert annual. *Evolution*, 44: 1404 - 1423.
- FOX, G.A. 1990b. Drought and the evolution of flowering time in desert annuals. *American Journal of Botany*, 77: 1508 - 1518.
- GUTTERMAN, Y. 1988. Day-neutral flowering in some desert *Blepharis* spp.. *Journal of Arid Environments*, 14: 157 - 167.
- HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- KLIKOFF, L.G. 1966. Competitive responses to moisture stress of a winter annual of the Sonoran Desert. *American Midland Naturalist*, 75: 383 - 391.
- KREKULE, J. & HAJKOVA, L. 1972. The developmental pattern in a group of therophytes. II. Vernalization and photoperiodic induction. *Flora*, 161: 121 - 128.
- LARCHER, W. 1983. *Physiological Plant Ecology*. Springer-Verlag, New York.
- LE HOUEROU, H.N. 1984. Rain use efficiency: a unifying concept in arid-land

- ecology. *Journal of Arid Environments*, 7: 213 - 247.
- MOTT, J.J. & CHOUARD, P. 1979. Flowering, seed formation and dispersal. In: PERRY, P.A. & GOODALL, D.W. (eds.) *Arid-land Ecosystems: Structure, Functioning and Management*. Cambridge University Press, Cambridge. pp. 627 - 645.
- MOTT, J.J. & McCOMB, A.J. 1975. The role of photoperiod and temperature in controlling the phenology of three annual species from an arid region of Western Australia. *Journal of Ecology*, 63: 633 - 641.
- MULROY, T.W. & RUNDEL, P.W. 1977. Annual plants: adaptations to desert environments. *BioScience*, 27: 109 - 114.
- NEWMAN, E.I. 1965. Factors affecting seed production of *Teesdalia nudicaulis*. II. Soil moisture in spring. *Journal of Ecology*, 53: 211 - 232.
- PEMADASA, M.A. & LOVELL, P.H. 1974. Factors controlling the flowering time of some dune annuals. *Journal of Ecology*, 62: 869 - 880.
- RATHCKE, B. & LACEY, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16: 179 - 214.
- ROZIEN, N.A.M.G. & VAN DER WERF, D.C. 1986. Effect of drought during different stages in the life-cycle on the growth and biomass allocation of two *Aira* species. *Journal of Ecology*, 74: 507 - 523.
- SCHULZE, B.R. 1965. Climate of South Africa. Part 8. General Survey. WB 28. Government Printer, Pretoria.
- SOLBRIG, O.T., BARBOUR, M.A., CROSS, J., GOLDSTEIN, G., LOWE, C.H., MORELLO, J. & YANG, T.W. 1977. The strategies and community patterns of desert plants. In: ORIAN, G.H. & SOLBRIG, O.T. (eds.) *Convergent evolution in warm deserts*. Hutchinson & Ross, Stroudsburg. pp. 68 - 106.
- STEYN, H.M. 1993. Namaqualand ephemerals: phenology and thermal units. M.Sc. dissertation. University of Pretoria, Pretoria.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep.). The influence of sowing date on the phenology of five Namaqualand ephemeral species.
- TEVIS, L. Jr. 1958. A population of desert ephemerals germinated by less than one inch of rain. *Ecology*, 39: 688 - 694.

- VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis. University of Pretoria, Pretoria.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1991. The ephemerals of Namaqualand: effects of photoperiod, temperature and moisture stress on development and flowering of three species. *Journal of Arid Environments*, 20: 15 - 29.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1992. The ephemerals of Namaqualand: effect of germination date on development of three species. *Journal of Arid Environments*, 22: 51 - 66.
- VAN ROOYEN, M.W., THERON, G.K. & GROBBELAAR, N. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 1. General observations. *Journal of South African Botany*, 45: 279 - 293.
- WATKINSON, A.R. 1982. Factors affecting the density response of *Vulpia fasciculata*. *Journal of Ecology*, 70: 149 - 161.
- WENT, F.W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology*, 39: 695 - 704.
- WENT, F.W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology*, 30: 1 - 13.
- WENT, F.W. & WESTERGAARD, M. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. *Ecology*, 30: 26 - 28.
- WERGER, M.J.A. 1986. The Karoo and southern Kalahari. In: EVENARI, M., NOY-MEIR, I. & GOODALL, D.W. (eds.) *Hot Deserts and Arid Shrublands*. Elsevier Science Publishers, Amsterdam. pp. 283 - 358.

CHAPTER 7
THE EFFECT OF ACHENE AGE ON THE PHENOLOGY OF A
NAMAQUALAND EPHEMERAL SPECIES:
***DIMORPHOTHECA SINUATA* DC.**

H.M. STEYN, N. VAN ROOYEN, M.W. VAN ROOYEN & G.K. THERON

(Department of Botany, University of Pretoria, 0002)

ABSTRACT

The disc flower achenes of two different ages were sown on four different dates in 1991, and in April 1992 achenes of three different ages were sown to determine the effect of achene age on the phenology of *Dimorphotheca sinuata* DC., a Namaqualand ephemeral species.

Plants that developed from relatively fresh achenes, tended to be shorter, had more leaves on the main stem at inflorescence initiation and reached anthesis later than plants from older achenes.

KEY WORDS: *Dimorphotheca sinuata*, ephemeral, Namaqualand, phenology, achene age

INTRODUCTION

Seed formation is the only way in which annual plants can ensure continuity in future generations. Most weed seeds have the ability to germinate at the right time and in the right place after remaining dormant for years in the soil seed bank. The special ability of seeds to survive in a dormant state for long periods and to germinate when growth conditions are favourable, confers a very important survival advantage for plants that inhabit unpredictable environments, such as deserts (Guttermann 1985).

Although ephemerals reproduce only once and die, delayed germination enables their progeny to emerge in different cohorts. This gives rise to effective iteroparity and suggests that birth in plants may not be the formation of seed, but rather the germination of seed (Harper 1977).

Many plant species have the capacity to produce seeds that remain dormant in the soil for several years to several decades (Crocker 1938; Darlington & Steinbauer 1961; Odum 1971; Fenner 1985), while some species have evolved the capacity to remain viable for centuries (Cook 1980).

Extensive seed longevity of some annual plant species has been known for some time, however, the importance of a viable and long-lived seed bank for annuals has been appreciated only recently (Sarukhan 1974; Kalisz 1991). The germination of seeds which have remained in the soil for varying lengths of time implies that the generation time of annuals is often greater than one year (Roughgarden 1979).

The aim of this study was to determine whether achene age influenced the phenology of *Dimorphotheca sinuata* DC., a Namaqualand winter ephemeral species.

METHODS

Disc flower achenes of *Dimorphotheca sinuata* were collected in the spring of 1989, 1990

and 1991 in the Goegap Nature Reserve, (between latitude 29°34' and 29°43' and longitude 17°55' and 18°08') approximately 12 km south-east of Springbok. This area lies in the Namaqualand Broken Veld (Acocks 1988), an arid zone in the north-western Cape Province of the Republic of South Africa.

In the beginning of the months April, May, June and July 1991, achenes collected in 1989 and 1990 were sown in 1 000 cm³ pots, filled with quartz sand. In the beginning of April 1992, the experiment was repeated with achenes collected in 1989, 1990 and 1991. All plants were grown out of doors at the University of Pretoria and watered daily to field capacity with tap water. Once a week they received Arnon & Hoagland's complete nutrient solution (Hewitt 1952). Ten replicates were used per treatment and two weeks after sowing the seedlings were thinned to one per pot.

The height of each plant was measured weekly from an age of 28 days after sowing. All plants were examined phenologically twice a week from the initiation of inflorescences. The number of days from sowing until a particular stage was reached, was noted for each plant. The following phenological stages were distinguished: inflorescence initiation, first inflorescence at anthesis and peak flowering time. The term peak flowering refers to the highest mean number of open inflorescences during the flowering phase.

An one-way analysis of variance (ANOVA)(Statgraphics 5.0. 1989, STSC, Inc., U.S.A.), was used to test for statistical differences at $\alpha = 0.05$. The LSD test was used for comparisons between treatments. Differences in plant height data were analyzed statistically at 40, 80 and 120 days after sowing.

RESULTS AND DISCUSSION

Plant height

In the 1991 trial, all plants derived from the fresh achenes (1990 collection), with the exception of those sown in May (May plants), tended to be shorter than plants derived

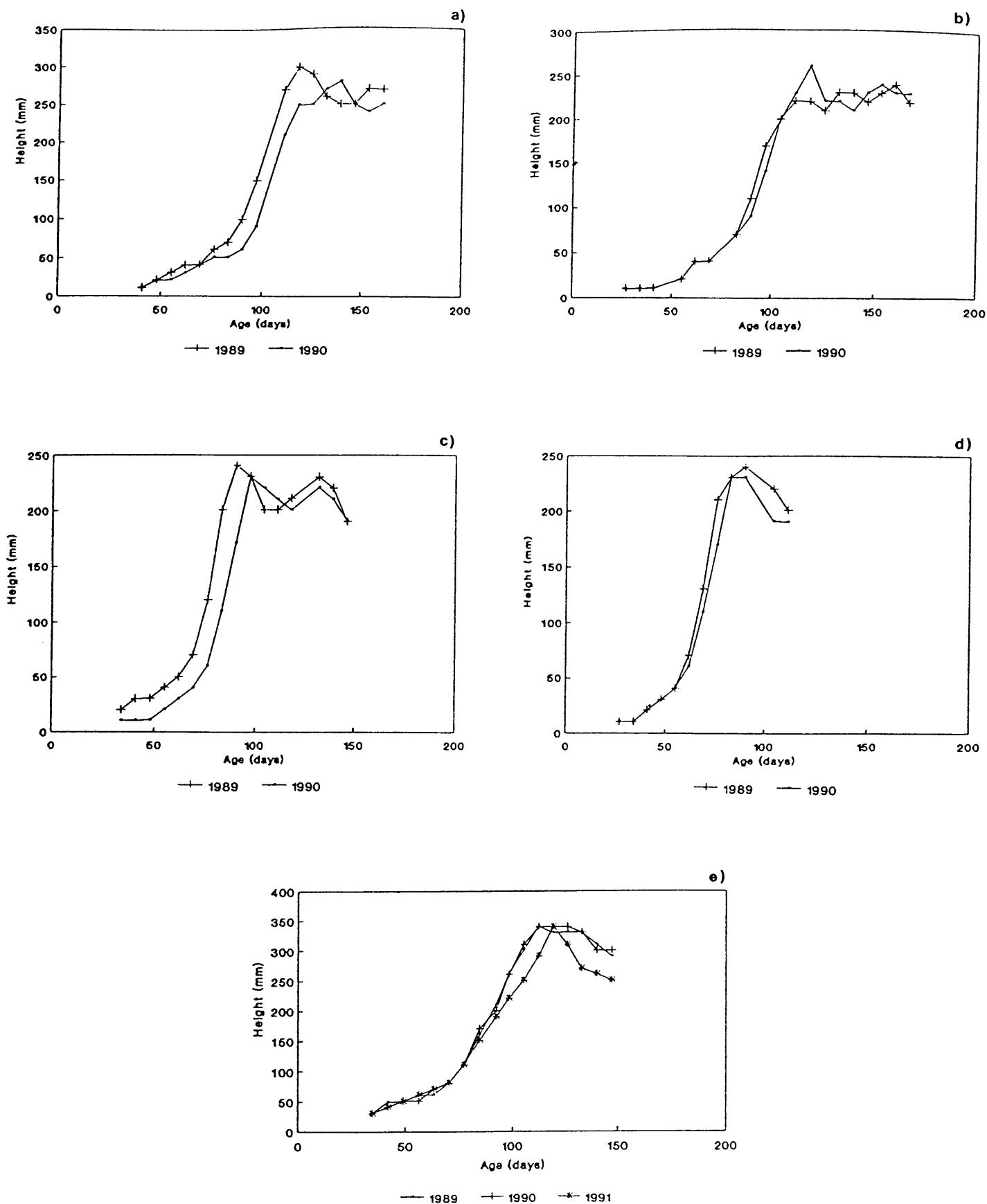


Figure 1. The mean height (mm) of *Dimorphotheca sinuata* plants derived from achenes collected in 1989, 1990 and 1991 and sown in a) April 1991, b) May 1991, c) June 1991, d) July 1991 and e) April 1992.

from older achenes (Figure 1a - d). However, the height difference was only significant in June plants at 40 and 80 days and April plants at 120 days. In contrast to the results on *D. sinuata*, Abdalla & Roberts (1969) found the early stages of plant development to be slower when aged seeds of broad bean, peas and barley were sown. Hurd (1969) also recorded differences between plants from fresh and old seeds and stated that these differences were less evident at later stages of development. Riddell & Gries (1958) stated that in the case of spring wheat, plants grown from seeds of different ages, differed in both their rate of development under normal growth conditions and in their response to short periods of vernalization.

The results of the 1992 experiment indicated no significant differences in mean plant height at an age of 40, 80 or 120 days, nor in the mean maximum height (Figure 1e). Plants which were derived from the fresh achenes (1991 collection) were, however, shorter between 85 and 120 days, as well as between 120 and 150 days after sowing than those from the 1989 and 1990 collections. Studies on maize (*Zea mays*) indicated that plants tended to be shorter, the older the seeds they were derived from (Dungan & Koehler 1944). Reductions in development and yield of plants as a consequence of the use of moderately aged seeds were also noted in wheat (Crocioni 1934, in Priestley 1986; Rajbhandary 1971) and barley (Neoral 1923, in Priestley 1986).

Number of leaves on the main stem at inflorescence initiation

In the 1991 experiment there was no significant difference in the mean number of leaves on the main stem at inflorescence initiation between plants originating from achenes collected in 1989 and 1990 (Table 1). However, plants from 1989 achenes, tended to have less leaves on the main stem at inflorescence initiation than plants from 1990 achenes.

In 1992, the 1990 and 1991 achenes produced plants which had significantly more leaves on the main stem at inflorescence initiation than the plants from the oldest achenes (1989 collection) (Table 2). Therefore, plants that were derived from achenes older than two years, were developmentally younger at the stage of inflorescence initiation than

Table 1. The mean number of leaves on the main stem at flower bud initiation, mean number of open inflorescences per plant at peak flowering, total number of reproductive organs per plant during the life span and the number of days from sowing to the onset of anthesis and peak flowering in *Dimorphotheca sinuata* plants, from disk flower achenes harvested in 1989 and 1990

Sowing date	Number of leaves on the main stem		Number of open inflorescences		Total number of reproductive organs		Days till anthesis		Days till peak flowering	
	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
April	18.6	19.6	9.1	15.5	35.3	65.1 *	97	97	122	136
May	11.8	12.6	13.7	14.0	77.9	73.9	82	88 *	118	118
June	10.6	9.7	12.0	11.0	95.0	81.1	72	76 *	132	132
July	9.2	9.5	12.5	11.1	70.5	46.6 *	69	65	104	104

* Denotes a significant difference ($P \leq 0.05$) between 1989 and 1990 plants

Table 2. The mean number of leaves on the main stem at flower bud initiation, mean number of open inflorescences per plant at peak flowering, total number of reproductive organs per plant during the life span and the number of days from sowing to the onset of anthesis and peak flowering in plants of *Dimorphotheca sinuata* that were derived from disk flower achenes collected in 1989, 1990 and 1991

Achene collection	Number of leaves	Number of open inflorescences	Total number of reproductive organs	Days till anthesis	Days till peak flowering
1989	20.4x	18.6 x	104.9 x	77 x	129 x
1990	25.1 x	20.4 x	121.1 x	77 x	136 x
1991	26.9 x	17.5 x	109.0 x	92 x	136 x

plants from fresh achenes. Napp-Zinn (1964, in Priestley 1986) also found that the number of leaves that appear on the main stem before flowering in *Arabidopsis thaliana* (annual), decreases with the age of the seed sown.

Production of inflorescences

Figure 2a - e, illustrates that plants from achenes older than a year, reached anthesis earlier than plants from achenes sown within a year after collection. Early in the flowering period, plants from older achenes produced more open inflorescences, than plants from fresh achenes (Figure 2a - e). This difference in initial rate of inflorescence production was the clearest in June plants (Figure 2c).

In the case of the spring wheat variety Warden (Riddell & Gries 1958), plants from the oldest seed (older than four years) flowered about 20 days earlier and contained fewer nodes than any other plant. In other spring wheat varieties (White Federation 38 & Chinese), the fresher seed produced plants that developed more rapidly and differentiated fewer nodes.

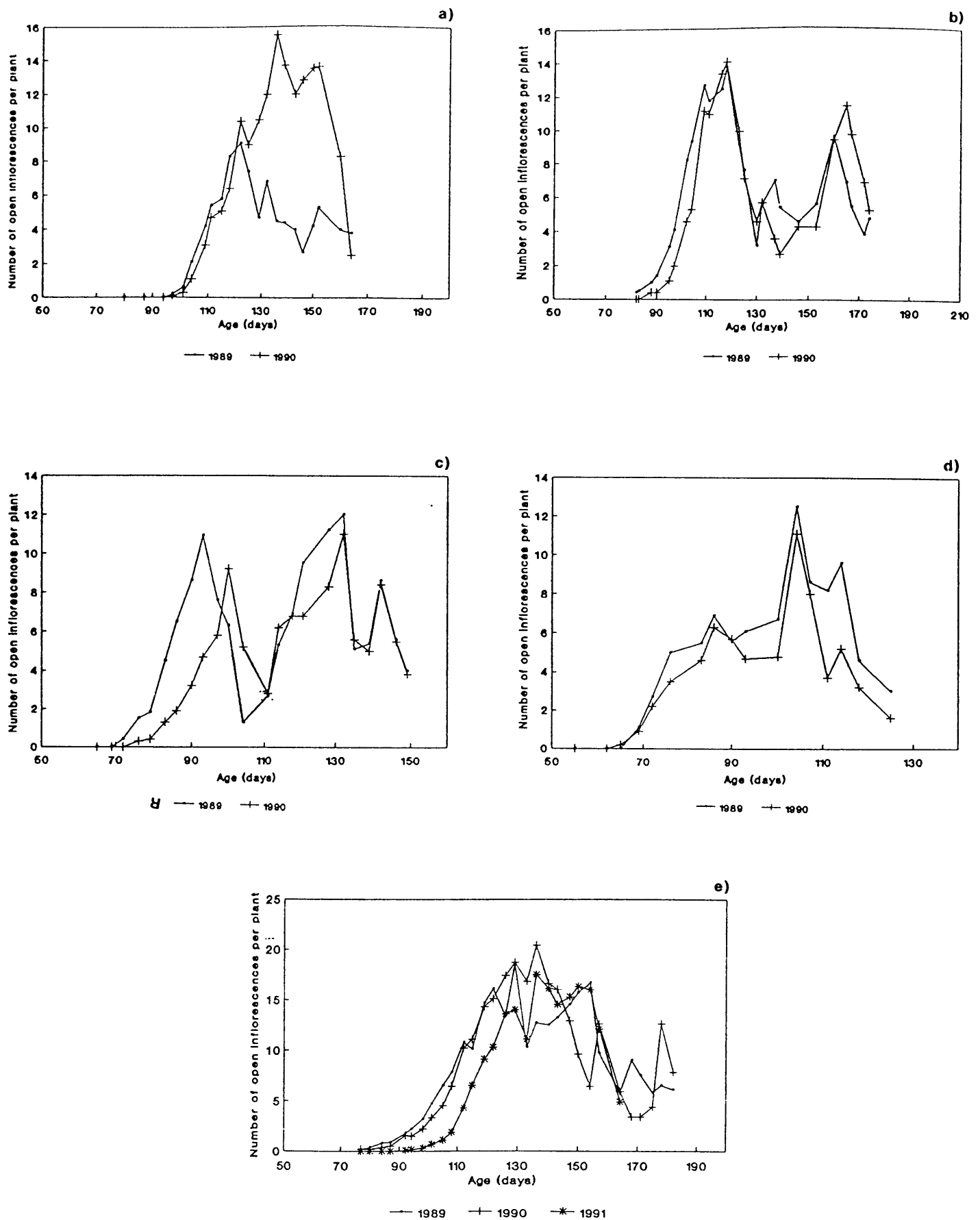


Figure 2. The mean number of open inflorescences per plant of *Dimorphotheca sinuata* plants, derived from achenes of different collection times and sown in a) April 1991, b) May 1991, c) June 1991, d) July 1991 and e) April 1992.

In all trials in 1991 and 1992, 3 - 4 flowering peaks occurred (Figure 2a - e). In April plants of 1991, there was a distinct difference in the production of inflorescences on plants derived from the 1989 and 1990 achene samples, especially from an age of 122 days (Figure 2a). At this stage the number of open inflorescences on plants of the 1989 achenes dropped sharply, while the open inflorescences on plants of the 1990 achene sample, increased till peak flowering was reached at an age of 136 days after sowing. This pattern was not repeated at any of the other sowing dates. In the case of May sowing, plants of both achene age samples produced more or less the same flowering curve (Figure 2b), except that the initial rate of inflorescence production was higher in plants from the older achenes.

June sowing led to differences in the flowering curves as plants from 1989 achenes reached a flowering peak 10 days earlier than plants from 1990 achenes. However, plants from both achene collections reached peak flowering simultaneously at 130 days. As in the case of May sowing, the flowering curves of July plants were almost similar, but plants from 1989 achenes produced more open inflorescences during their entire flowering period than plants from 1990 achenes.

The flowering curves of April plants of the 1992 trial, differ from that of 1991. From Figure 2e it is clear that there was no real difference in the number of open inflorescences during peak flowering between the treatments, although the peaks of 1989 and 1990 plants were higher than those of 1991 plants (Table 2). The life span of plants derived from the youngest achenes (1991) was shorter than that of the other plants.

The results of both years' trials, indicate that plants derived from relatively older achenes, produced more reproductive organs during their life span than plants from fresh achenes. However, this difference was not significant except in the case of July plants sown in 1991.

CONCLUDING REMARKS

The results of a preliminary experiment showed no difference in germination percentage, germination rate and seedling emergence between achenes of different ages. Achenes older than one year are therefore a viable part of the seed bank, and are able to produce plants with the same vigour.

Older achenes produced plants that had a higher rate of development initially, than plants produced by younger achenes. This response was demonstrated in a faster rate of height increase, inflorescence initiation at a developmentally younger stage, precocious flowering and an initial higher rate of inflorescence production. Differences between plants from young and old achenes were less evident at later stages of development as illustrated by the lack of significant differences in mean maximum plant height as well as the number of open inflorescences at peak flowering.

The differences which were found in the growth and phenology between plants of 1989 and 1990 achenes, were not consistent in the 1991 and 1992 experiments, indicating that the reactions of the plants were not a characteristic of the particular year of collection and therefore not due to conditions at the time of achene production. These differences in phenology are therefore attributed to differences in achene age.

The adaptive value of this phenomenon probably lies in the mechanism it provides to extend a species' range of reactions under a particular set of environmental conditions. In an unpredictable environment such heterogeneity in a population could confer an advantage to the species.

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REFERENCES

- ABDALLA, F.H. & ROBERTS, E.H. 1969. The effects of seed storage conditions on the growth and yield of barley, broad beans, and peas. *Annals of Botany (Lond.)*, 33: 160 - 84.
- ACOCKS, J.P.H. 1988. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa*, 57: 1 - 122.
- COOK, R. 1980. The biology of seeds in the soil. In: SOLBRIG, O.T. (ed.) *Demography and Evolution in Plant Populations*. Blackwell, Oxford. pp. 107 - 29.
- CROCKER, W. 1938. Life-span of seeds. *Botanical Review*, 4: 235 - 274.
- DARLINGTON, H.T. & STEINBAUER, G.P. 1961. The eighty-year period for Dr. Beals' seed viability experiment. *American Journal of Botany*, 48: 321 - 325.
- DUNGAN, G.H. & KOEHLER, B. 1944. Age of seed corn in relation to seed infection and yielding capacity. *Agronomy Journal*, 36: 436 - 43.
- FENNER, M. 1985. *Seed ecology*. Chapman & Hall, New York.
- GUTTERMAN, Y. 1985. Flowering, seed development and the influences during seed maturation on seed germination of annual weeds. In: DUKE, S.D. (ed.) *Seed Physiology I*. Boca Raton, Florida. pp. 1 - 25.
- HARPER, J.L. 1977. *The population biology of plants*. Academic Press, London.
- HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition*. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- HURD, R.G. 1969. Effect of tomato seed age on germination and seedling growth. *Annual Report of the Glasshouse and Crops Research Institute (Littlehampton)*,: 151 - 54.
- KALISZ, S. 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology*, 72: 575 - 585.
- ODUM, E.P. 1971. *Fundamentals of Ecology*. Saunders, Philadelphia.
- PRIESTLEY, D.A. 1986. *Seed aging: Implications for seed storage and persistence in the soil*. Cornell University Press, New York.
- RAJBHANDARY, K.L. 1971. Yield potentialities of aged wheat seed. *Nepalese Journal of Agriculture*, 6: 165 - 69.

- RIDDELL, J.A. & GRIES, G.A. 1958. Development of spring wheat: III. Temperature of maturation and age of seeds as factors influencing their response to vernalization. **Agronomy Journal**, 50: 743 - 746.
- ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York.
- SARUKHAN, J. 1974. Studies in plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. II. Reproductive strategies and seed population dynamics. **Journal of Ecology**, 62: 151 - 177.

CHAPTER 8
THE PREDICTION OF PHENOLOGICAL STAGES IN FIVE
NAMAQUALAND EPHEMERAL SPECIES USING THERMAL
UNIT INDICES

H.M. STEYN, N. VAN ROOYEN, M.W. VAN ROOYEN, N. SAUER* & G.K. THERON

(Department of Botany, University of Pretoria, Pretoria, 0002)

*(Dean, Faculty of Science, University of Pretoria, Pretoria, 0002)

ABSTRACT

Flowering time in Namaqualand generally ranges from August through September, depending on the timing of the first substantial winter rains. The precise timing of flowering of species is determined by the individual and integrated effects of a complex of environmental factors.

Phenological data of a number of Namaqualand ephemerals were recorded and used to determine the number of thermal units required by each species to reach a certain phenological stage.

The ephemerals accumulated cold units from sowing until flower/inflorescence initiation, while heat units (growing degree days) were accumulated from the stage of flower/inflorescence initiation onwards.

The use of thermal units resulted in some accurate predictions of phenological stages, especially for plants sown in April and May and can be used to predict the flowering time of ephemeral species in Namaqualand.

KEY WORDS: cold units, *Dimorphotheca sinuata*, ephemerals, *Foveolina albida*, heat units, *Heliophila seselifolia*, phenology, *Senecio arenarius*, thermal units, *Ursinia cakilefolia*

INTRODUCTION

Plant development processes are clearly regulated by environmental factors such as temperature and photoperiod, but these mechanisms are poorly understood (Pilbeam, Hebblethwaite, Ricketts & Hassan 1990). However, ecologists often use heat accumulation above a given base or threshold temperature to measure or predict the effect of temperature on biological processes (Baskerville & Emin 1969).

The degree day/plant growth interaction, whereby certain developmental phases of plant life cycles are correlated with daily accumulations of air temperatures above some base value below which physiological activity is assumed to be inhibited, is one of the oldest and most studied of ecological aspects (Idso, Jackson & Reginato 1978).

Methods of temperature summation (Heat Unit Approach) measure the quantity of thermal or solar thermal units that a plant receives, the hypothesis being that plants of a specific species need a certain constant amount of heat or cold over a period of time to reach a certain phenological stage (Lettau 1965).

In corn (*Zea mays*) (Newman, Blair, Dale, Smith, Stirm & Schaal 1968; Cross & Zuber 1972; Major, Johnson, Tanner & Anderson 1975; Eicker 1979); field beans (Pilbeam *et al.* 1990); soybean (Major, Johnson, Tanner & Anderson 1975; Hadley, Roberts, Summerfield & Minchin 1984; Seddigh, Jolliff & Orf 1989); wheat (*Triticum durum*) (Idso *et al.* 1978); orchids (Lettau 1965); purple lilac (Caprio 1974); sunflowers (Robinson 1971; Doyle 1975; Goyne, Woodruff & Churchett 1977); fruit trees (Matthee 1982) and herbaceous species such as *Galanthus nivalis* (Abrami 1969), temperature summation has proved to be an adequate method of predicting the timing or date of a developmental stage such as flowering or harvest readiness.

Although the Heat Unit Approach has been applied successfully to solve a wide range of problems, from selection of farming areas and crop varieties to scheduling control programs for insects, diseases and weeds, refinements are continually being sought for this highly empirical technique (Idso *et al.* 1978).

Namaqualand, in the north-western Cape, owes its fame mainly to the flowering display of ephemerals, which transforms the normally barren landscape into a land of colour in the spring following a good winter rainy season (Le Roux & Schelpe 1988; Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992). Flowering time in Namaqualand generally ranges from August through September, depending on the timing of the first substantial rains. The use of the Heat Unit Approach to predict a specific phenological stage of Namaqualand ephemerals, has not been undertaken prior to the present investigation.

The aim of this study thus was to determine whether accumulated heat and/or cold units can be used to predict, fairly accurately, the main flowering period of Namaqualand ephemeral species. The prediction of peak flowering time each year will be of great value to aid and promote tourism in the area.

METHODS

Growing of ephemerals

Seeds/achenes of five Namaqualand winter ephemeral species viz. *Dimorphotheca sinuata* DC. (disc flower achenes), *Foveolina albida* (DC.) Kallersjo, *Heliophila seselifolia* Burch. ex DC. var. *seselifolia*, *Senecio arenarius* Thunb. and *Ursinia cakilefolia* DC., were sown in 1 000 cm³ pots filled with quartz sand, on four different dates: fifth of April (April plants), second of May (May plants), fourth of June (June plants) and the second of July (July plants). The plants (one plant per pot) were grown out of doors at the University of Pretoria and watered daily to field capacity with tap water. Once a week they received Arnon & Hoagland's complete nutrient solution (Hewitt 1952). Ten replicates were used per treatment.

Phenological data were recorded weekly from 28 days after sowing. From the initiation of flowers/inflorescences, all plants were examined phenologically, twice a week. The number of days from sowing until a specific phenological stage was reached, was noted for each plant. The phenological stages distinguished were flower/inflorescence

initiation, anthesis and peak flowering. The term peak flowering denotes the highest mean number of open flowers/inflorescences during the flowering phase. The date of flower/inflorescence initiation and anthesis for a species were taken as the date on which 60% of the plants reached the specific stage.

The air temperature (°C) and the relative air humidity (%) were registered continuously by means of a thermohygrograph in a Stevenson screen at the same height as the plants at the experimental site. Daily maximum and minimum temperatures, the daylengths and irradiation of Pretoria (25°24'S, 28°10'E) and Springbok (29°41'S, 17°55'E) were supplied by the Weather Bureau in Pretoria.

The netto leaf photosynthetic rate of three plants per species were determined with a Li-Cor "LI-6200 Portable Photosynthesis System" (Li-Cor, Inc., P.O. Box 4425, Lincoln, NE 68504, USA.) at different controlled temperatures. As a low netto photosynthetic rate was still recorded at 3°C in all five species, 0°C was considered to be the base temperature below which no growth was assumed to take place.

In order to select the best thermal unit index (see Chapter 3) to determine the critical thermal units required by a species, the criteria of Goyne *et al.* (1977) and Eicker (1979) were applied, i.e.:

- a) a low coefficient of variability (C_v) - if development was strictly controlled by temperature, the ideal thermal unit would sum to a constant value, independent of sowing date and temperature fluctuations, and deviations around this constant would be minimal, resulting in a low coefficient of variation (Major, Johnson & Luedders 1975);
- b) a low correlation (r^2 value) should exist between sowing date and the number of thermal units required to reach a phenological stage. Sowing date was taken as the independent variable (X), while the number of required thermal units until this specific stage was reached, was taken as the dependent variable (Y); and

c) the normalized slope coefficient (NSC) value between sowing date and the amount of thermal units should be zero.

The formula used to determine the NSC is:

$NSC = \text{regression (slope) coefficient} \times 100/\text{number of thermal units (Eicker 1979)}.$

Determining the number of heat units

Several formulae were selected (Table 1 & Appendix A) and applied to determine the number of heat units needed to reach a specific phenological stage. The average number of heat units needed by plants of all four sowing dates from sowing until a specific stage had been reached, was taken as the critical number of accumulated heat units needed by that species.

Table 1. Formulae used (see Appendix A) to determine the accumulated number of heat units

Indices	Symbol	Formula	Reference
I1	GDD	Growing degree days	Adanson (in Eicker 1979)
I2	PT	Photothermal units	Nuttonson (1955)
I3	DHU	Day- hour units	Lindsey & Newman (1956)
I4	2HT	2 hourly temperature	Adapted from Lowry (1970)
I5	PTU	Photothermal units	Adapted from Eicker (1979)
I6	STU	Solar thermal units	Caprio (1974)

Determining the number of cold units

To determine the specific base/threshold temperature below which cold units should be accumulated, the following temperatures were selected on the basis of the temperature amplitude experienced in Pretoria in the winter of 1991 as well as results of previous studies on Namaqualand ephemerals (Van Rooyen 1988): 10°C, 13°C, 15°C, 17°C, 18°C, 19°C, 20°C, 21°C, 22°C, 23°C, 24°C and 25°C. The number of cold units was calculated by means of thermographs from sowing (S) until flower/inflorescence initiation (FI) and

anthesis (A), using 12 different temperature cut-offs. The area below each of the 12 temperatures and above the ink trace was determined for the specific period by the summation of the two-hourly temperatures below the specific temperature.

By using the criteria of Goyne *et al.* (1977) and Eicker (1979) the specific cut-off temperature for each species was determined. Thus, the best cut-off temperature should result in the lowest coefficient of variation (Cv), r^2 and NSC values.

Using each species' cut-off temperature, the critical number of cold units needed to reach flower/inflorescence initiation, was taken as the average number of cold units received by plants of all four sowing dates from sowing until flower/inflorescence initiation.

Combined use of cold and heat units

In the case of anthesis and peak flowering, the use of cold and heat units separately as well as a combination of cold and heat units from sowing were investigated to obtain the best index of thermal units required to reach these particular stages.

Model for the prediction of a specific phenological stage

Newman *et al.* (1968) stated that it is necessary to know how many degree days can be expected during the season and from any date to any other date during the season. This expected number of thermal units can be computed by using data from a few consecutive years. By plotting the seasonal average growing degree day accumulation curve (heat units) on a graph, it can be seen how many growing degree days can be expected between any date and the end of the season. By plotting the actual seasonal progress in growing degree days on the same graph, the attainment of a specific phenological stage can be predicted at any time.

By plotting the cumulative weekly cold or heat units expected in an average year in the Springbok region the number of weeks between two phenological stages could be

predicted, for four different germination dates (Figures 1 & 2).

A simplification of these methods, used for the prediction of a phenological phase, is summarized in Appendix B.

RESULTS AND DISCUSSION

Flower/inflorescence initiation

The r^2 and normalized slope coefficient (NSC) values of the heat unit indices (I1 - I6, Table 2) of all five species, indicate a relatively high correlation between sowing date and the amount of heat units accumulated until flower/inflorescence initiation, which is contrary to the Heat Unit Concept. Thus, these indices are unable to predict the timing or date of flower/inflorescence initiation satisfactory.

As the coefficient of variation (Cv), r^2 and NSC values of the hours below 17°C (I7) were lower (closer to zero) than those of the other heat unit indices, the use of cold units was investigated further. This train of thought is supported by the results of Baskin & Baskin (1972) who found that there was an extreme delay of flowering in the dune annual, *Leavenworthia exigua* var. *exigua* without a cold treatment. According to Pemadasa & Lovell (1974) the findings of Baskin & Baskin (1972) indicate that low temperature might be one of the inductive requirements for flowering of winter annuals. In the case of the soya bean (*Glycine max*), Hadley *et al.* (1984) found that the effects of low spring temperatures on flowering predominated during early growth whereas responsiveness to daylength became more important later on.

The coefficient of variation was not used as a criterium to determine the best predictive cold unit index because with progressively higher cut-off temperatures (I8 - I18, Table 2), the coefficient of variation decreased because the standard deviation increased less than the average cold sum.

Table 2. Average amount of thermal units accumulated from sowing until flower bud initiation for four sowing dates, standard deviation (STD), coefficient of variation (Cv), r^2 and normalized slope coefficient values for 18 different thermal unit indices (I 1 - I 6 heat units; I 7 - I 18 cold units) for five species

Index	Formula	Average	STD	Cv	Regression	r^2	NSC
<i>Dimorphotheca sinuata</i>							
I 1	GDD	864.6	193.8	22.4	$y = -5.34x + 1103.67$	0.8391	-0.62
I 2	PT	9361.7	2176.5	23.3	$y = -58.94x + 11999.21$	0.8097	-0.63
I 3	DHU	23158.6	5842.8	25.2	$y = -162.62x + 30435.85$	0.8553	-0.70
I 4	2HT	808.6	196.3	24.3	$y = -5.39x + 1049.69$	0.8320	-0.67
I 5	PTU	8756.2	2198.1	25.1	$y = -59.35x + 11412.23$	0.8050	-0.68
I 6	STU	328174.9	87290.7	26.6	$y = -2120.93x + 423086.7$	0.6519	-0.65
I 7	HOURS < 17°	996.0	80.5	8.1	$y = -2.14x + 1091.94$	0.7839	-0.22
I 8	2HT < 13°C	1599.3	284.5	17.8	$y = 6.94x + 1288.95$	0.6562	0.43
I 9	" 15°C	2426.6	291.7	12.0	$y = 6.30x + 2144.57$	0.5154	0.26
I 10	" 17°C	3402.2	280.0	8.2	$y = 4.54x + 3199.17$	0.2898	0.13
I 11	" 18°C	3941.8	271.7	6.9	$y = 3.23x + 3797.27$	0.1560	0.08
I 12	" 19°C	4506.6	267.1	5.9	$y = 1.76x + 4427.76$	0.0480	0.03
I 13	" 20°C	5095.5	272.9	5.4	$y = 0.27x + 5083.64$	0.0016	0.00
I 14	" 21°C	5712.2	287.7	5.0	$y = -1.33x + 5771.73$	0.0236	-0.02
I 15	" 22°C	6353.8	310.7	4.9	$y = -3.01x + 6488.35$	0.1034	-0.05
I 16	" 23°C	7023.8	341.2	4.9	$y = -4.74x + 7235.93$	0.2132	-0.07
I 17	" 24°C	7708.2	378.2	4.9	$y = -6.61x + 8003.96$	0.3372	-0.09
I 18	" 25°C	8403.3	421.3	5.0	$y = -8.59x + 8787.73$	0.4591	-0.10
<i>Foveolina albida</i>							
I 1	GDD	955.9	191.1	20.0	$y = -5.63x + 1208.00$	0.9602	-0.59
I 2	PT	10349.2	2108.7	20.4	$y = -61.47x + 13100.02$	0.9383	-0.60
I 3	DHU	25656.6	5781.5	22.5	$y = -169.37x + 33235.95$	0.9476	-0.66
I 4	2HT	895.1	191.7	21.4	$y = -5.62x + 1146.68$	0.9501	-0.63
I 5	PTU	9692.1	2114.9	21.8	$y = -61.30x + 12435.22$	0.9276	-0.63
I 6	STU	361752.9	78720.5	21.8	$y = -2133.74x + 457238.1$	0.8113	-0.59
I 7	HOURS < 17°	1117.3	138.9	12.4	$y = -3.38x + 1268.37$	0.6532	-0.30
I 8	2HT < 13°C	1829.1	340.8	18.6	$y = 4.79x + 1614.90$	0.2177	0.26
I 9	" 15°C	2765.4	399.2	14.4	$y = 3.38x + 2614.02$	0.0793	0.12
I 10	" 17°C	3870.1	454.9	11.8	$y = 0.96x + 3827.03$	0.0049	0.02
I 11	" 18°C	4481.3	486.9	10.9	$y = -0.62x + 4509.22$	0.0018	-0.01
I 12	" 19°C	5121.9	523.1	10.2	$y = -2.36x + 5227.40$	0.0224	-0.04
I 13	" 20°C	5791.3	566.7	9.8	$y = -4.09x + 5974.09$	0.0574	-0.07
I 14	" 21°C	6492.0	615.7	9.5	$y = -5.89x + 6755.64$	0.1011	-0.09
I 15	" 22°C	7220.2	667.4	9.2	$y = -7.76x + 7567.62$	0.1494	-0.11
I 16	" 23°C	7980.8	721.5	9.0	$y = -9.66x + 8413.19$	0.1981	-0.12
I 17	" 24°C	8756.8	774.5	8.8	$y = -11.65x + 9278.23$	0.2499	-0.13
I 18	" 25°C	9545.2	826.3	8.7	$y = -13.71x + 10158.47$	0.3038	-0.14

Table 2 (continued)

Index	Formula	Average	STD	Cv	Regression	r ²	NSC
<i>Heliophila seselifolia</i>							
I 1	GDD	841.3	187.7	22.3	y=-5.40x+1082.89	0.9131	-0.64
I 2	PT	9106.6	2111.0	23.2	y=-59.91x+11787.36	0.8893	-0.66
I 3	DHU	22554.3	5706.7	25.3	y=-164.48x+29914.70	0.9173	-0.73
I 4	2HT	786.5	189.9	24.1	y=-5.43x+1029.53	0.9035	-0.69
I 5	PTU	8513.6	2130.3	25.0	y=-60.18x+11206.52	0.8811	-0.71
I 6	STU	318749.1	84885.7	26.6	y=-2211.16x+417698.7	0.7492	-0.69
I 7	HOURS <17°	965.5	78.7	8.2	y=-1.65x+556.77	0.4875	-0.17
I 8	2HT < 13°C	1545.6	340.2	22.0	y=7.99x+1187.98	0.6090	0.52
I 9	" 15°C	2347.3	373.0	15.9	y=7.71x+2002.37	0.4716	0.33
I 10	" 17°C	3292.9	389.9	11.8	y=6.34x+3009.44	0.2915	0.19
I 11	" 18°C	3816.2	394.8	10.3	y=5.25x+3581.31	0.1951	0.14
I 12	" 19°C	4363.9	400.1	9.2	y=4.0x+4185.16	0.1101	0.09
I 13	" 20°C	4934.9	412.0	8.3	y=2.72x+4813.41	0.0480	0.06
I 14	" 21°C	5532.8	428.4	7.7	y=1.32x+5473.58	0.0105	0.02
I 15	" 22°C	6155.4	447.7	7.3	y=-0.16x+6162.48	0.0000	0.00
I 16	" 23°C	6806.3	469.8	6.9	y=-1.70x+6882.43	0.0145	-0.03
I 17	" 24°C	7471.0	493.8	6.6	y=-3.40x+7623.24	0.0524	-0.05
I 18	" 25°C	8146.2	519.9	6.4	y=-5.23x+8380.07	0.1116	-0.06
<i>Senecio arenarius</i>							
I 1	GDD	949.4	188.6	19.9	y=-5.54x+1197.09	0.9508	-0.58
I 2	PT	10279.7	2087.3	20.3	y=-60.42x+12983.37	0.9251	-0.59
I 3	DHU	25476.7	5723.0	22.5	y=-166.64x+32933.95	0.9362	-0.65
I 4	2HT	889.1	189.7	21.3	y=-5.53x+1136.61	0.9392	-0.62
I 5	PTU	9628.0	2097.2	21.8	y=-60.33x+12327.54	0.9136	-0.63
I 6	STU	359536.8	78705.6	21.9	y=-2100.13x+453517.7	0.7862	-0.58
I 7	HOURS <17°	1107.8	129.4	11.7	y=-3.23x+1252.43	0.6894	-0.29
I 8	2HT < 13°C	1424.6	794.7	55.8	y=6.01x+1570.72	0.3656	0.42
I 9	" 15°C	2743.3	383.3	14.0	y=3.72x+2576.88	0.1040	0.14
I 10	" 17°C	3839.4	427.4	11.1	y=1.43x+3775.62	0.0123	0.04
I 11	" 18°C	4445.4	451.9	10.2	y=-0.08x+4448.99	0.0000	0.00
I 12	" 19°C	5080.8	480.4	9.5	y=-1.73x+5158.35	0.0144	-0.03
I 13	" 20°C	5744.7	516.0	9.0	y=-3.38x+5895.81	0.0473	-0.06
I 14	" 21°C	6439.4	556.5	8.6	y=-5.09x+6667.29	0.0925	-0.08
I 15	" 22°C	7161.5	600.1	8.4	y=-6.88x+7469.19	0.1449	-0.10
I 16	" 23°C	7916.2	646.1	8.2	y=-8.68x+8304.70	0.1994	-0.11
I 17	" 24°C	8686.2	691.4	8.0	y=-10.58x+9159.66	0.2586	-0.12
I 18	" 25°C	9468.5	735.6	7.8	y=-12.54x+10029.83	0.3211	-0.13

Table 2 (continued)							
Index	Formula	Average	STD	Cv	Regression	r ²	NSC
<i>Ursinia cakilefolia</i>							
I 1	GDD	842.8	130.7	15.5	y=-3.81x+1013.09	0.9368	-0.45
I 2	PT	9135.8	1490.6	16.3	y=-42.63x+11043.39	0.9030	-0.47
I 3	DHU	22564.4	4195.1	18.6	y=-122.31x+28037.76	0.9386	-0.54
I 4	2HT	788.5	136.5	17.3	y=-3.95x+965.13	0.9230	-0.50
I 5	PTU	8548.9	1550.7	18.1	y=-44.05x+10520.10	0.8909	-0.52
I 6	STU	322290.7	64774.3	20.1	y=-1617.01x+394652.0	0.6881	-0.50
I 7	HOURS <17°	957.3	94.3	9.9	y=0.25x+946.18	0.0076	0.03
I 8	2HT < 13°C	1553.2	465.0	29.9	y=10.94x+1063.41	0.6117	0.71
I 9	" 15°C	2349.6	560.6	23.8	y=12.33x+1797.60	0.5345	0.52
I 10	" 17°C	3288.8	642.9	19.5	y=12.92x+2710.60	0.4460	0.39
I 11	" 18°C	3808.7	678.2	17.8	y=12.89x+3231.75	0.3990	0.34
I 12	" 19°C	4353.4	710.1	16.3	y=12.73x+3783.68	0.3550	0.29
I 13	" 20°C	4922.0	745.8	15.2	y=12.60x+4358.13	0.3153	0.26
I 14	" 21°C	5516.9	782.4	14.2	y=12.44x+4960.37	0.2790	0.23
I 15	" 22°C	6137.3	816.4	13.3	y=12.19x+5591.62	0.2463	0.20
I 16	" 23°C	6785.3	850.5	12.5	y=11.96x+6250.23	0.2182	0.18
I 17	" 24°C	7448.5	878.7	11.8	y=11.57x+6930.80	0.1914	0.16
I 18	" 25°C	8122.7	901.2	11.1	y=10.81x+7504.06	0.1667	0.13

Dimorphotheca sinuata

Compared to other temperature cut-offs the r² and NSC values for cold units accumulated below 20°C (I13, Table 2), were closest to zero. Therefore 20°C was taken as the specific cut-off temperature for *D. sinuata*. The average number of cold units below 20°C required by plants of the four sowing dates was taken as the critical number of cold units that *D. sinuata* plants require to reach the stage of inflorescence initiation (Table 3). In the case of *D. sinuata* under average conditions in Springbok, Namaqualand, the length of the period to accumulate the required amount of cold units should vary from 7 to 11 weeks depending on the sowing date (Table 3 & Figure 1a).

In Figure 1a the average seasonal cold unit accumulation curve is plotted from sowing for the different sowing dates. The horizontal line indicates the average number of cold units needed between sowing (S) and flower/inflorescence initiation (FI) (Table 3). The weeks needed to reach flower/inflorescence initiation can therefore be determined where line (FI) intercepts the cold unit accumulation curve.

Table 3. The number of cold units needed by five ephemeral species, the actual number of days recorded in Pretoria (1991) and the predicted number of weeks at Springbok from sowing until flower/inflorescence initiation (FI)

Species	Germination	Cold units	Actual days	Weeks
<i>Dimorphotheca sinuata</i> First week in:				
	April	4944.66	73	11 ^{0.7}
	May	5092.00	60	9 ⁷
	June	5535.50	55	7 ^{4.7}
	July	4810.00	51	7 ⁰
	Average cold units	5095.54		
<i>Foveolina albida</i>				
	April	4011.16	77	13
	May	4993.00	74	10
	June	4942.50	62	8
	July	3978.50	58	8
	Average cold units	4481.29		
<i>Heliophila seselifolia</i>				
	April	5820.16	69	11
	May	6361.50	60	9
	June	6785.00	55	7
	July	5655.00	48	7
	Average cold units	6155.42		
<i>Senecio arenarius</i>				
	April	4011.16	77	13
	May	4849.50	72	10
	June	4942.50	62	8
	July	3978.50	58	8
	Average cold units	4445.40		
<i>Ursinia cakilefolia</i>				
	April	868.00	62	9
	May	1009.00	60	9
	June	1086.00	59	6
	July	866.00	51	6
	Average cold units	957.25		

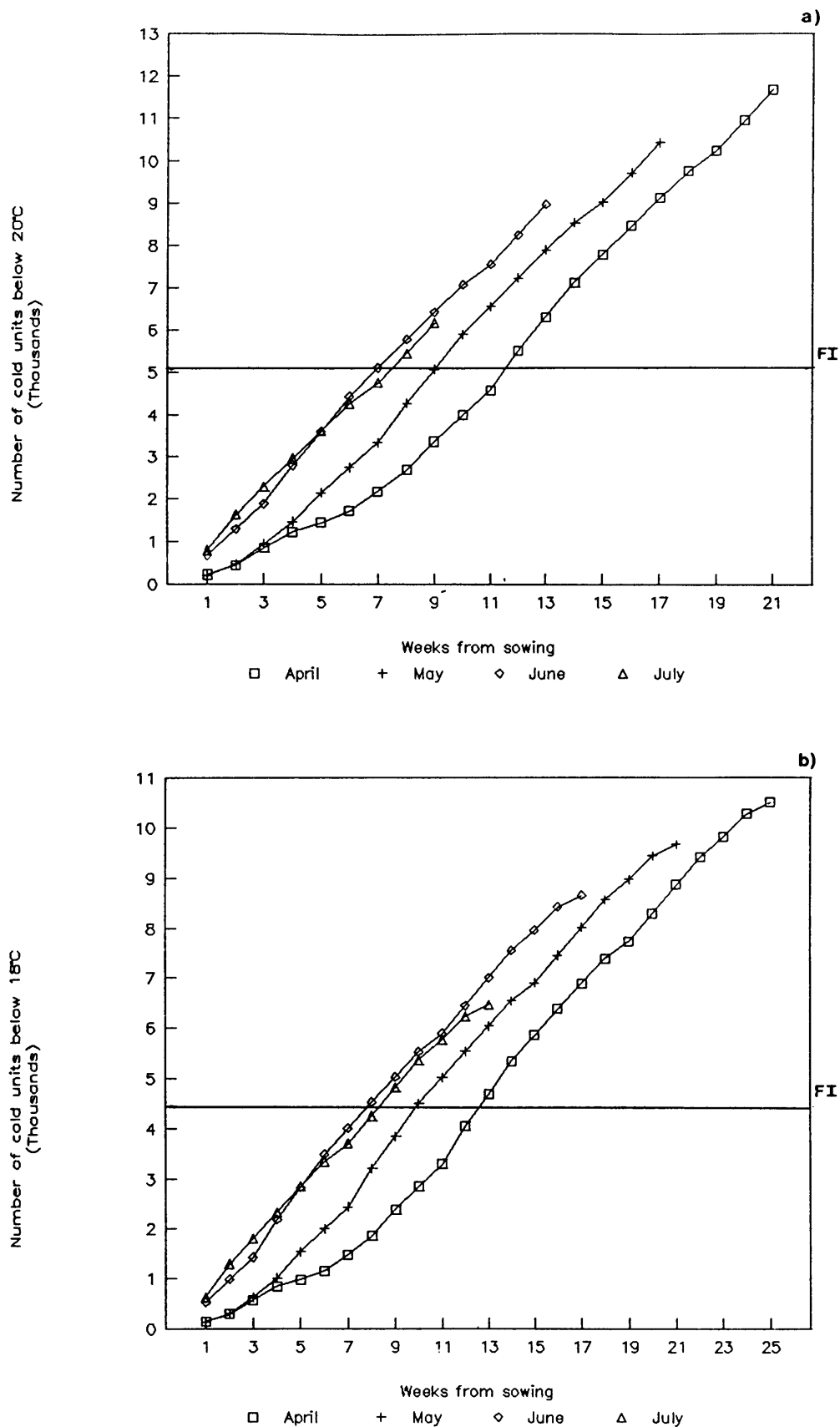


Figure 1. The cumulative number of cold units experienced in an average year in Springbok from sowing for four sowing dates and the average number of cold units required from sowing until flower/inflorescence initiation (FI) in a) *Dimorphotheca sinuata*, b) *Foveolina albida* and *Senecio arenarius*, c) *Heliophila seselifolia* and d) *Ursinia cakilefolia*.

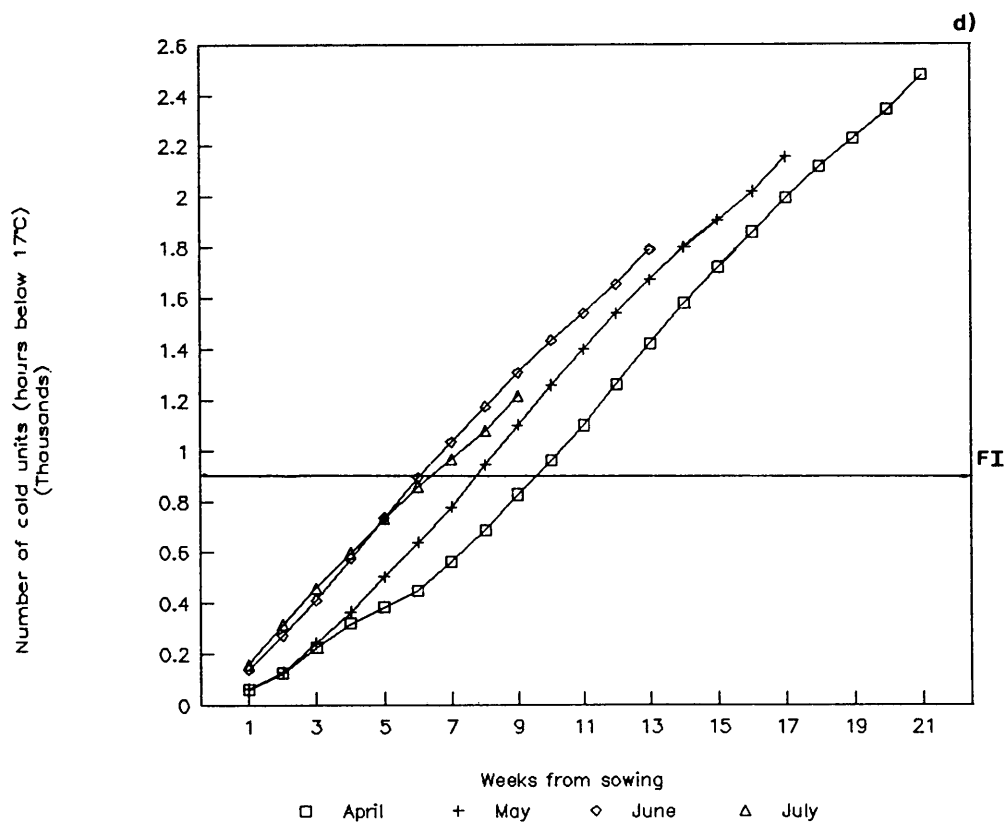
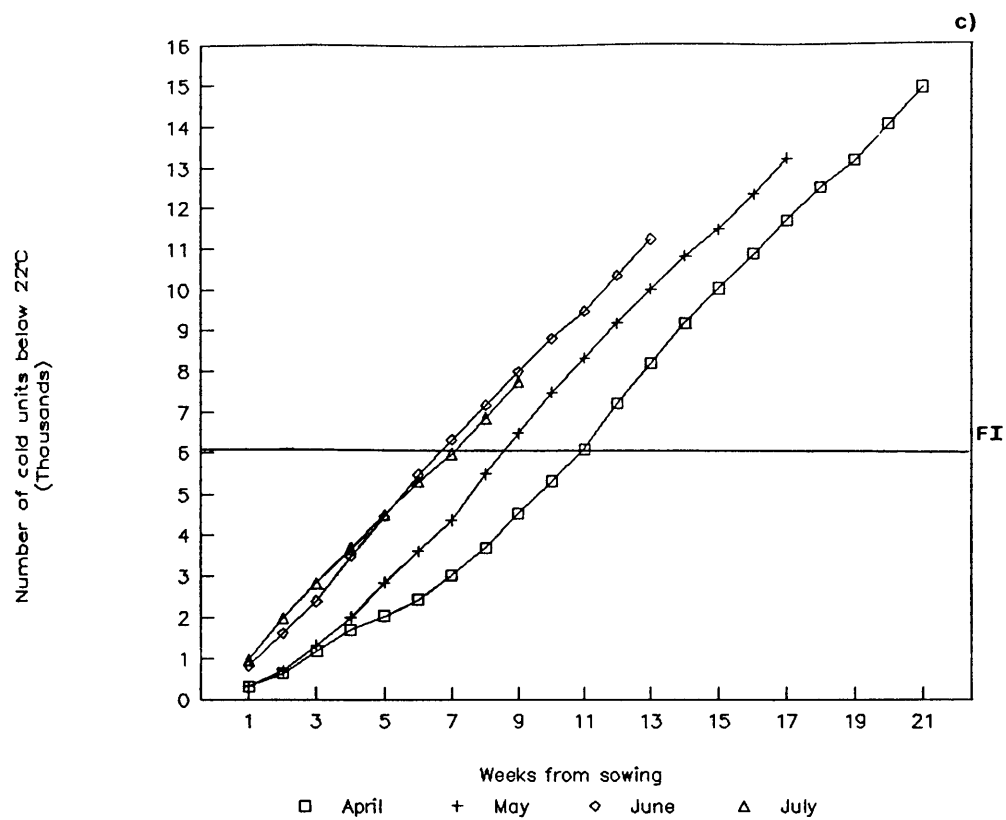


Figure 1. Continued.

Foveolina albida

Plants of *F. albida* seemed to require lower temperatures to initiate inflorescences than *D. sinuata* and the temperature cut-off of *F. albida* was 18°C (I11, Table 2). In an average year in Springbok, Namaqualand it would take from 8 to 13 weeks for *F. albida* plants to initiate inflorescences (Table 3 & Figure 1b).

Heliophila seselifolia

The r^2 and NSC values of the area below 22°C (I15, Table 2) were closest to zero, which means that *H. seselifolia* plants did not require low temperatures to initiate flower buds. The time period from sowing till flower initiation in an average year, could vary from 7 to 11 weeks (Table 3 & Figure 1c).

Senecio arenarius

Senecio arenarius also required low temperatures for the initiation of inflorescences and the cut-off temperature of this species was 18°C (I11, Table 2). In an average year in the Springbok region, inflorescences of *S. arenarius* plants should appear from 8 to 13 weeks after sowing (Table 3 & Figure 1b).

Ursinia cakilefolia

Ursinia cakilefolia plants don't seem to have a cut-off temperature and the best index to predict inflorescence initiation was the number of hours below 17°C (I7)(Table 2). The predicted time from sowing until inflorescence initiation range from 6 to 9 weeks (Table 3 & Figure 1d).

The marked decline in weeks from sowing until flower/inflorescence initiation with a later sowing date, could be explained by the fact that plants from later sowing dates are subjected to low temperatures early in their life cycle. Although there was a substantial decrease in the time from sowing to flower/inflorescence initiation with later sowing, the average number of required cold units of the four sowing dates of a species were relatively constant (Table 3), which means that plants from later sowing dates, accumulate cold units faster than plants of earlier sowing dates and would therefore accumulate the required number of cold units over a shorter period.

Anthesis and peak flowering

As in the case of flower/inflorescence initiation, heat unit indices (I1 - I6) showed a definite high correlation between sowing date and the accumulated amount of heat units from sowing to anthesis (Table 4a). The r^2 and NSC values of cold unit indices (I8 - I18, Table 4a) were closer to zero than those for the heat unit indices, but these values were still not low enough to ensure accurate predictions. By combining the cold units until flower/inflorescence initiation and the heat units from flower/inflorescence initiation until anthesis (I19 - I24, Table 4a), the r^2 and NSC values closest to zero were found and the best heat unit index to combine with the cold unit index could be determined.

On the basis of the r^2 and NSC values of all 24 indexes and all five species, cold plus growing degree days (GDD)(I19, Table 4a) and cold plus mean two hourly temperature (2HT)(I22, Table 4a) gave the best results (Table 4a) and I19 was used in further calculations. Although the r^2 and NSC values of I19 from sowing until anthesis and peak flowering were not consistently the closest to zero (Table 4a & b), overall, it seemed the most accurate index to predict not only anthesis but also peak flowering, for all five species. The index combining cold units and mean two hourly temperatures (I22), also gave good results (Table 4a & b) but is not recommended because two hourly temperatures for a specific locality are not always available.

These results quantify the findings of Pemadasa & Lovell (1974) who found that plants exposed to low temperatures during the early stages of flowering, failed to produce mature inflorescences as long as they remained in the cold. However, inflorescence development was quite successful when these plants were subjected to higher temperatures later, indicating that exposure of plants to low temperatures did not irreversibly inhibit the flowering process. The combined effect of low and high temperatures in the initiation and anthesis of inflorescences were also documented by Aitken (1955), Lindsey & Newman (1956) and Clark (1969).

Although results of this study demonstrated that the combined use of cold units and growing degree days (heat units) gave the best estimate of the total number of thermal

Table 4a. Average amount of thermal units, standard deviation (STD), coefficient of variance (Cv), r^2 and normalized slope coefficient (NSC) for 24 thermal unit indices from sowing until anthesis for five species

Index	Formula	Average	STD	Cv	Regression	r^2	NSC
<i>Dimorphotheca sinuata</i>							
I 1	GDD	1258.09	215.13	17.10	$y = -6.32x + 1541.06$	0.9540	-0.50
I 2	PT	13689.79	2265.73	16.55	$y = -65.61x + 16625.97$	0.9260	-0.48
I 3	DHU	33923.25	6019.01	17.74	$y = -172.62x + 41647.83$	0.9082	-0.51
I 4	2HT	1178.58	209.23	17.75	$y = -6.08x + 1450.62$	0.9320	-0.52
I 5	PTU	12829.03	2208.81	17.22	$y = -63.03x + 15649.60$	0.8991	-0.49
I 6	STU	480819	81527.27	16.96	$y = -2235.87x + 580874.4$	0.8305	-0.47
I 7	HOURS < 17°C	1442.50	234.63	16.27	$y = -6.63x + 1739.33$	0.8824	-0.46
I 8	2HT < 13°C	2381.10	405.30	17.00	$y = -4.90x + 2600.21$	0.1612	-0.21
I 9	" 15°C	3585.70	567.60	15.80	$y = -9.59x + 4014.76$	0.3151	-0.27
I 10	" 17°C	5004.70	758.90	15.20	$y = -15.47x + 5696.72$	0.4585	-0.31
I 11	" 18°C	5788.29	867.13	15.00	$y = -18.84x + 6631.32$	0.5212	-0.33
I 12	" 19°C	6610.79	980.26	14.80	$y = -22.39x + 7612.81$	0.5761	-0.34
I 13	" 20°C	7472.42	1098.77	14.70	$y = -26.06x + 8638.41$	0.6209	-0.35
I 14	" 21°C	8375.42	1223.90	14.60	$y = -29.89x + 9712.94$	0.6585	-0.36
I 15	" 22°C	9314.40	1354.39	14.50	$y = -33.87x + 10830.21$	0.6906	-0.36
I 16	" 23°C	10295.41	1490.13	14.50	$y = -37.97x + 11994.51$	0.7169	-0.37
I 17	" 24°C	11297.29	1627.77	14.40	$y = -42.15x + 13183.72$	0.7405	-0.37
I 18	" 25°C	12316.04	1764.92	14.30	$y = -46.35x + 14390.18$	0.7615	-0.38
I 19	c+GDD	5497.32	295.10	5.40	$y = -1.04x + 5543.90$	0.0137	-0.02
I 20	c+PT	9431.87	614.15	6.51	$y = -6.74x + 9733.27$	0.1328	-0.07
I 21	c+DHU	15868.46	739.40	4.66	$y = -10.06x + 16318.49$	0.2043	-0.06
I 22	c+2HT	5473.79	288.97	5.28	$y = -0.75x + 5507.44$	0.0075	-0.01
I 23	c+PTU	9176.58	520.21	5.67	$y = -3.74x + 9343.89$	0.0570	-0.04
I 24	c+STU	157748	19483.22	12.35	$y = -114.99x + 162894.1$	0.0385	-0.07
<i>Foveolina albida</i>							
I 1	GDD	1468.61	197.50	13.45	$y = -5.83x + 1729.58$	0.9627	-0.40
I 2	PT	16094.48	1979.51	12.30	$y = -57.53x + 18668.75$	0.9325	-0.36
I 3	DHU	40002.25	4904.61	12.26	$y = -138.73x + 46210.59$	0.8835	-0.35
I 4	2HT	1378.11	187.09	13.58	$y = -5.45x + 1622.06$	0.9374	-0.40
I 5	PTU	15110.77	1879.35	12.44	$y = -53.53x + 17506.31$	0.8959	-0.35
I 6	STU	568486	71666.63	12.61	$y = -1972.94x + 656775.7$	0.8368	-0.35
I 7	HOURS < 17°C	1605.75	311.20	19.38	$y = -8.76x + 1997.62$	0.8743	-0.55
I 8	2HT < 13°C	2630.43	510.70	19.40	$y = -11.58x + 3148.80$	0.5681	-0.44
I 9	" 15°C	3967.20	763.10	19.20	$y = -18.48x + 4794.12$	0.6474	-0.47
I 10	" 17°C	5556.70	1040.70	18.70	$y = -26.405x + 6738.05$	0.7105	-0.48
I 11	" 18°C	6438.17	1190.39	18.50	$y = -30.75x + 7814.06$	0.7366	-0.48
I 12	" 19°C	7365.04	1343.00	18.20	$y = -35.21x + 8940.58$	0.7589	-0.48
I 13	" 20°C	8336.67	1497.03	18.00	$y = -39.69x + 10112.68$	0.7776	-0.48
I 14	" 21°C	9355.29	1656.07	17.70	$y = -44.30x + 11337.68$	0.7901	-0.47
I 15	" 22°C	10416.60	1820.67	17.50	$y = -49.11x + 12614.28$	0.8034	-0.47
I 16	" 23°C	11526.91	1990.77	17.30	$y = -54.10x + 13947.69$	0.8153	-0.47
I 17	" 24°C	12663.66	2163.23	17.10	$y = -59.19x + 15312.46$	0.8267	-0.47
I 18	" 25°C	13822.53	2333.67	16.90	$y = -64.24x + 16697.32$	0.8368	-0.46
I 19	c+GDD	4994.03	494.41	9.90	$y = -0.82x + 5030.80$	0.0031	-0.02
I 20	c+PT	10226.61	736.69	7.20	$y = 3.32x + 10077.94$	0.0225	0.03
I 21	c+DHU	18826.99	1698.16	9.02	$y = 30.01x + 17483.85$	0.3449	0.16
I 22	c+2HT	4964.32	490.49	9.88	$y = -0.45x + 4984.59$	0.1014	-0.01
I 23	c+PTU	9899.94	745.48	7.53	$y = 7.14x + 9580.30$	0.0009	0.07
I 24	c+STU	211215	17921.40	8.49	$y = 160.18x + 204046.6$	0.0882	0.08

Table 4a. (continued)

Index	Formula	Average	STD	Cv	Regression	r ²	NSC
<i>Heliophila seselifolia</i>							
I 1	GDD	1134.75	168.35	14.84	y=-4.89x+1352.15	0.9195	-0.43
I 2	PT	12331.36	1801.11	14.61	y=-50.84x+14606.34	0.8797	-0.41
I 3	DHU	30605.72	4944.08	16.15	y=-138.65x+36810.27	0.8684	-0.45
I 4	2HT	1061.42	168.48	15.87	y=-4.80x+1276.11	0.8954	-0.45
I 5	PTU	11537.01	1808.77	15.68	y=-50.23x+13784.75	0.8515	-0.44
I 6	STU	431625	68490.43	15.87	y=-1765.31x+510622.5	0.7336	-0.41
I 7	HOURS <17°	1302.25	157.86	12.12	y=-3.56x+1461.48	0.5610	-0.27
I 8	2HT < 13°C	2105.80	401.60	19.10	y=2.21x+2007.02	0.0334	0.11
I 9	" 15°C	3187.30	509.20	16.00	y=0.21x+3177.76	0.0002	0.01
I 10	" 17°C	4464.30	620.30	13.90	y=-2.74x+4587.12	0.0216	-0.06
I 11	" 18°C	5169.17	679.86	13.20	y=-4.58x+5373.90	0.0500	-0.09
I 12	" 19°C	5908.04	741.78	12.60	y=-6.53x+6200.06	0.0854	-0.11
I 13	" 20°C	6680.67	808.71	12.10	y=-8.50x+7061.01	0.1220	-0.13
I 14	" 21°C	7490.17	880.45	11.80	y=-10.55x+7962.23	0.1585	-0.14
I 15	" 22°C	8332.30	955.33	11.50	y=-12.71x+8900.96	0.1954	-0.15
I 16	" 23°C	9211.42	1032.93	11.20	y=-14.89x+9877.76	0.2295	-0.16
I 17	" 24°C	10110.54	1111.15	11.00	y=-17.19x+10879.98	0.2644	-0.17
I 18	" 25°C	11025.29	1188.50	10.80	y=-19.53x+11899.14	0.2981	-0.18
I 19	c+GDD	6448.85	468.31	7.26	y=0.38x+6431.75	0.0007	0.01
I 20	c+PT	9380.22	730.69	7.79	y=8.91x+8981.45	0.1642	0.09
I 21	c+DHU	14206.79	1013.41	7.10	y=25.67x+13058.03	0.7085	0.18
I 22	c+2HT	6430.36	462.30	7.19	y=0.48x+6409.06	0.0012	0.01
I 23	c+PTU	9178.80	683.83	7.45	y=9.79x+8740.72	0.2263	0.11
I 24	c+STU	119031	21797.15	18.31	y=445.69x+99086.27	0.4616	0.37
<i>Senecio arenarius</i>							
I 1	GDD	1301.21	181.67	13.96	y=-5.00x+1524.77	0.8350	-0.34
I 2	PT	14196.05	1907.61	13.44	y=-49.75x+16422.11	0.7509	-0.35
I 3	DHU	35331.63	5049.96	14.29	y=-126.89x+40976.07	0.6889	-0.36
I 4	2HT	1219.13	179.14	14.69	y=-4.79x+1433.59	0.7903	-0.39
I 5	PTU	13305.54	1891.82	14.22	y=-47.67x+15438.66	0.7010	-0.36
I 6	STU	499021	70907.76	14.21	y=-1677.23x+574076.6	0.6178	-0.34
I 7	HOURS <17°	1456.00	230.68	15.84	y=-6.51x+1747.16	0.8784	-0.45
I 8	2HT < 13°C	2395.60	421.80	17.60	y=-5.10x+2623.93	0.1617	-0.21
I 9	" 15°C	3609.80	586.00	16.20	y=-9.76x+4046.61	0.3064	-0.27
I 10	" 17°C	5047.90	764.80	15.20	y=-15.26x+5731.01	0.4399	-0.30
I 11	" 18°C	5844.29	862.17	14.80	y=-18.35x+6665.38	0.5000	-0.31
I 12	" 19°C	6681.29	962.70	14.40	y=-21.57x+7646.49	0.5543	-0.32
I 13	" 20°C	7559.29	1065.35	14.10	y=-24.83x+8670.23	0.5996	-0.33
I 14	" 21°C	8479.79	1172.64	13.80	y=-28.21x+9742.00	0.6388	-0.33
I 15	" 22°C	9436.79	1284.64	3.80	y=-31.72x+10856.11	0.6731	-0.34
I 16	" 23°C	10437.66	1399.67	13.40	y=-35.28x+12016.39	0.7015	-0.34
I 17	" 24°C	11460.29	1515.13	13.20	y=-38.90x+13200.88	0.7277	-0.34
I 18	" 25°C	12501.79	1628.43	13.00	y=-42.48x+14402.58	0.7513	-0.34
I 19	c+GDD	4797.25	420.57	8.77	y=0.46x+4776.67	0.0013	0.01
I 20	c+PT	8361.79	364.73	4.36	y=10.59x+7887.74	0.9314	0.13
I 21	c+DHU	14300.38	1628.57	11.39	y=40.43x+12491.11	0.6805	0.28
I 22	c+2HT	4775.46	417.42	8.74	y=0.66x+4745.98	0.0028	0.01
I 23	c+PTU	8122.97	422.50	5.20	y=12.58x+7560.11	0.9786	0.16
I 24	c+STU	143929	15902.32	11.05	y=422.82x+125007.8	0.7806	0.29

Table 4a. (continued)

Index	Formula	Average	STD	Cv	Regression	r ²	NSC
<i>Ursinia cakilefolia</i>							
I 1	GDD	1227.03	169.72	13.82	y=-5.09x+1454.92	0.9942	-0.42
I 2	PT	13357.93	1762.80	13.20	y=-52.46x+15705.70	0.9781	-0.39
I 3	DHU	33130.48	4789.68	14.46	y=-141.21x+39449.42	0.9597	-0.43
I 4	2HT	1150.40	166.72	14.49	y=-4.96x+1372.45	0.9781	-0.43
I 5	PTU	12527.91	1740.49	13.89	y=-51.10x+14814.59	0.9518	-0.41
I 6	STU	469518	63038.63	13.43	y=-1788.08x+549534.3	0.8884	-0.38
I 7	HOURS <17°	1396.75	203.32	14.56	y=-4.82x+1612.46	0.6206	-0.35
I 8	2HT < 13°C	2287.80	470.50	20.60	y=-1.21x+2341.62	0.0072	-0.05
I 9	" 15°C	3452.80	624.90	18.10	y=-4.32x+3646.28	0.0529	-0.13
I 10	" 17°C	4828.40	793.20	16.40	y=-8.48x+5207.96	0.1263	-0.18
I 11	" 18°C	5588.67	885.03	15.80	y=-10.93x+6077.74	0.1684	-0.20
I 12	" 19°C	6386.29	979.55	15.30	y=-13.50x+6990.25	0.2096	-0.21
I 13	" 20°C	7221.17	1078.60	14.90	y=-16.10x+7941.67	0.2460	-0.22
I 14	" 21°C	8096.17	1182.74	14.60	y=-18.82x+8938.56	0.2797	-0.23
I 15	" 22°C	9006.60	1290.98	14.30	y=-21.67x+9976.45	0.3112	-0.24
I 16	" 23°C	9957.04	1404.16	14.10	y=-24.56x+11058.17	0.3379	-0.25
I 17	" 24°C	10928.91	1517.25	13.90	y=-27.56x+12162.18	0.3643	-0.25
I 18	" 25°C	11917.66	1628.49	13.70	y=-30.57x+13285.46	0.3890	-0.26
I 19	c+GDD	1341.53	112.50	8.39	y=-1.04x+1388.01	0.0941	-0.06
I 20	c+PT	5179.37	438.66	8.47	y=-9.59x+5608.48	0.5276	-0.19
I 21	c+DHU	11523.35	690.99	6.00	y=-18.65x+12357.84	0.8042	-0.16
I 22	c+2HT	1319.10	104.07	7.89	y=-0.77x+1353.50	0.0602	-0.06
I 23	c+PTU	4936.26	329.67	6.68	y=-6.80x+5240.68	0.4701	-0.14
I 24	c+STU	148184	16282.51	10.99	y=-170.82x+155828.5	0.1215	-0.12

units required from sowing to anthesis and peak flowering, the use of growing degree days has been criticized by various authors. Caprio (1974) found that the use of growing degree days (GDD) to predict the flowering date of purple lilacs (*Syringa vulgaris*), did not give an accurate prediction as an error of more than 20 days occurred, while solar thermal units (STU) estimated the flowering date of lilacs with an accuracy of a day or two. Furthermore, Baskerville & Emin (1969) found that the data used in computing accumulated heat with the growing degree day-index is limited to a narrow range of maximum and minimum temperatures and does not allow the introduction of an upper threshold. Lindsey & Newman (1956) also found that growing degree days fail to take into account the duration of the various temperature levels.

Indices which include photoperiod as a factor (I2/I20 & I5/I23), showed a correlation between sowing date and the accumulated number of heat units (Table 4a), although Evenari & Gutterman (1985) stated that flowering in annuals is mostly quantitatively

controlled by daylength.

As a result of the low correlation found if cold and heat units were combined (Table 4a), only I19 to I24 were used to calculate the thermal units required until peak flowering time (Table 4b). As in the case of flower/inflorescence initiation, the critical amount of thermal units needed between two phenological stages was taken as the average of the four sowing dates of a specific species (Table 5).

Dimorphotheca sinuata

The number of weeks from inflorescence initiation until anthesis and peak flowering were reached, could be determined using the required amounts of 393.53 and 852.36 heat units respectively (Table 5 & Figure 2a). The curves in Figure 2 represent the accumulated number of growing degree days from the initiation of flowers/inflorescences for the four sowing dates. Plants of *D. sinuata* are predicted to reach anthesis from 4 to 5 weeks and peak flowering from 9 to 10 weeks after inflorescence initiation depending on the sowing date (Table 5). These time spans are remarkably constant if the four week difference between sowing dates is kept in mind.

Foveolina albida

Plants of *F. albida* required an average of 512.74 and 822.49 heat units from inflorescence initiation until anthesis and peak flowering respectively (Table 5), which represent approximately 6 to 7 weeks from inflorescence initiation until anthesis and 8 - 10 weeks from inflorescence initiation until peak flowering, depending on the sowing date (Table 5 & Figure 2b).

Heliophila seselifolia

Plants of *H. seselifolia* required an average of 293.44 and 677.30 heat units from flower initiation until anthesis and peak flowering respectively (Table 5) and should need 3 to 4 and 7 to 8 weeks respectively to reach the stages of anthesis and peak flowering. Steyn, Van Rooyen, Van Rooyen & Theron (In prep.)(Chapter 5) stated that *H. seselifolia* plants flower earlier than most other Namaqualand ephemeral species. The predicted number of weeks from flower initiation until anthesis and peak flowering

Table 4b. Average amount of thermal units, standard deviation (STD) and coefficient of variation (Cv), r^2 and normalized slope coefficient (NSC) values for six thermal unit indices using cold units until flower/inflorescence initiation and heat units from flower/inflorescence initiation until peak flowering for five species

Indices	Formula	Average	STD	Cv	Regression	r^2	NSC
<i>Dimorphotheca sinuata</i>							
I 19	c+GDD	5947.90	181.76	3.06	$y=2.18x+5850.54$	0.1582	0.04
I 20	c+PT	14775.40	1578.70	10.60	$y=34.84x+13216.29$	0.5378	0.24
I 21	c+DHU	29581.34	5349.95	18.09	$y=120.95x+24168.83$	0.5644	0.41
I 22	c+2HT	5903.87	190.87	3.23	$y=2.72x+5782.27$	0.2238	0.05
I 23	c+PTU	14287.31	1712.49	11.99	$y=40.42x+12478.75$	0.6150	0.28
I 24	c+STU	359456	71601.11	19.90	$y=1512.85x+291756.1$	0.4929	0.42
<i>Foveolina albida</i>							
I 19	c+GDD	5303.78	576.54	10.87	$y=-0.32x+5317.90$	0.0003	0.01
I 20	c+PT	13876.36	2079.76	14.99	$y=12.69x+13308.45$	0.0411	0.09
I 21	c+DHU	28619.68	5409.55	18.90	$y=70.39x+25469.67$	0.1870	0.25
I 22	c+2HT	5264.54	574.62	10.91	$y=0.24x+5254.02$	0.0002	0.01
I 23	c+PTU	13440.90	2101.38	15.63	$y=18.50x+12612.86$	0.0856	0.14
I 24	c+STU	342475	69952.53	20.43	$y=418.47x+323748.6$	0.0395	0.12
<i>Heliophila seselifolia</i>							
I 19	c+GDD	6832.72	470.76	6.89	$y=2.86x+6704.88$	0.0407	0.04
I 20	c+PT	13777.81	1547.30	11.23	$y=42.80x+11862.65$	0.8447	0.31
I 21	c+DHU	25537.70	4513.38	17.67	$y=135.48x+19474.83$	0.9950	0.53
I 22	c+2HT	6797.31	467.18	6.87	$y=3.17x+6655.27$	0.0510	0.05
I 23	c+PTU	13388.29	1613.98	12.10	$y=45.99x+11330.28$	0.8965	0.34
I 24	c+STU	277485	57291.88	20.65	$y=1631.56x+204472.5$	0.9855	0.59
<i>Senecio arenarius</i>							
I 19	c+GDD	5076.78	443.62	8.74	$y=1.13x+5026.16$	0.0072	0.02
I 20	c+PT	11583.39	800.03	6.91	$y=22.05x+10596.89$	0.8384	0.19
I 21	c+DHU	22622.47	2898.43	12.81	$y=86.68x+18743.72$	0.9874	0.38
I 22	c+2HT	5044.03	440.81	8.74	$y=1.52x+4976.19$	0.0131	0.03
I 23	c+PTU	11222.08	905.41	8.07	$y=26.02x+10057.89$	0.9116	0.23
I 24	c+STU	260193	24782.31	9.53	$y=729.01x+227569.6$	0.9555	0.28
<i>Ursinia cakilefolia</i>							
I 19	c+GDD	1979.80	216.35	10.93	$y=2.80x+1854.32$	0.1855	0.14
I 20	c+PT	12677.19	2322.18	18.32	$y=45.21x+10654.06$	0.4185	0.36
I 21	c+DHU	30892.60	6947.22	22.49	$y=152.08x+24087.22$	0.5291	0.49
I 22	c+2HT	1931.48	224.66	11.63	$y=3.40x+1779.17$	0.2534	0.18
I 23	c+PTU	12139.84	2447.14	20.16	$y=51.34x+9842.36$	0.4860	0.42
I 24	c+STU	431477	94071.71	21.80	$y=2043.12x+340047.1$	0.5209	0.47

Table 5. The number of heat units needed by five ephemeral species and the predicted number of weeks needed between flower/inflorescence initiation and anthesis (FI - A) as well as between flower/inflorescence initiation and peak flowering (FI - P) in the Springbok region, as well as the predicted date of peak flowering

Species	Sowing	FI - A		FI - P		Date of peak flowering
		Heat units	Weeks	Heat units	Weeks	
<i>Dimorphotheca sinuata</i>	First week in:					
	April	403.00	5	832.75	10	23/8 - 29/8
	May	444.75	5	804.00	10	6/9 - 12/9
	June	406.75	5	718.10	10	20/9 - 26/9
	July	319.60	4	1054.60	9	11/10 - 17/10
Average heat units		393.53		852.36		
<i>Foveolina albida</i>	April	535.25	7	786.00	10	6/9 - 12/9
	May	468.00	7	742.00	10	13/9 - 19/9
	June	570.60	6	1063.85	9	20/9 - 26/9
	July	477.10	6	698.10	8	11/10 - 17/10
Average heat units		512.74		822.49		
<i>Heliophila seselifolia</i>	April	260.50	3	511.50	8	9/8 - 15/8
	May	281.50	4	679.50	8	23/8 - 29/8
	June	337.75	4	718.10	8	6/9 - 12/9
	July	294.00	3	800.10	7	27/9 - 3/10
Average heat units		293.44		677.30		
<i>Senecio arenarius</i>	April	356.25	5	584.00	8	23/8 - 29/8
	May	321.00	5	612.00	8	30/8 - 5/9
	June	320.00	4	631.35	7	6/9 - 12/9
	July	410.10	4	698.10	7	4/10 - 10/10
Average heat units		351.84		631.36		
<i>Ursinia cakilefolia</i>	April	415.50	4	969.50	12	23/8 - 29/8
	May	444.75	5	804.00	12	20/9 - 26/9
	June	357.25	5	1262.10	12	27/9 - 3/10
	July	319.60	4	1054.60	11	18/10 - 24/10
Average heat units		384.28		1022.55		

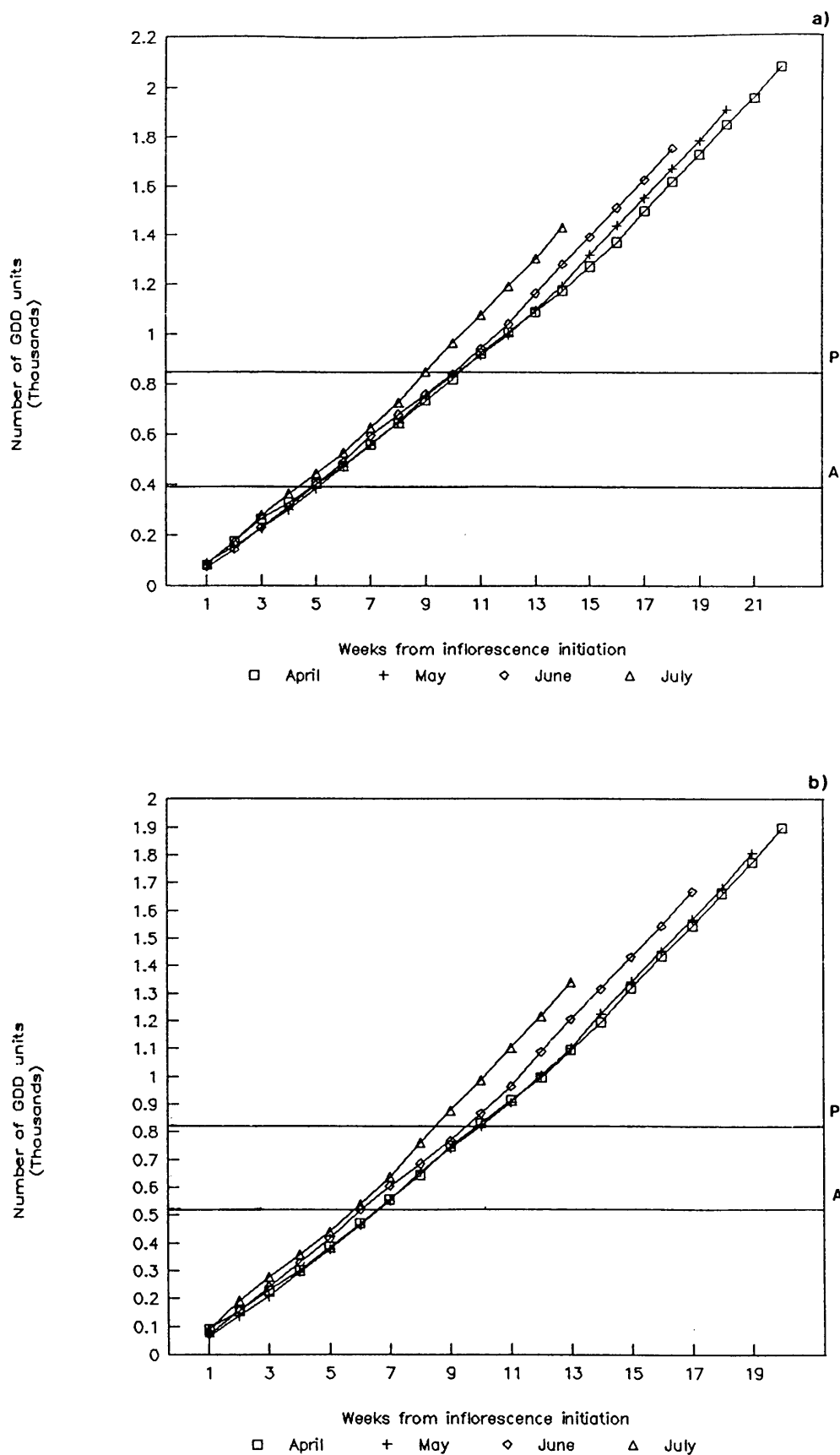


Figure 2. The cumulative number of growing degree days (GDD) experienced in an average year in Springbok, for four sowing dates and the average number of (GDD) required from flower/inflorescence initiation (FI) until anthesis (A) and peak flowering (P) in a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and e) *Ursinia cakilefolia*.

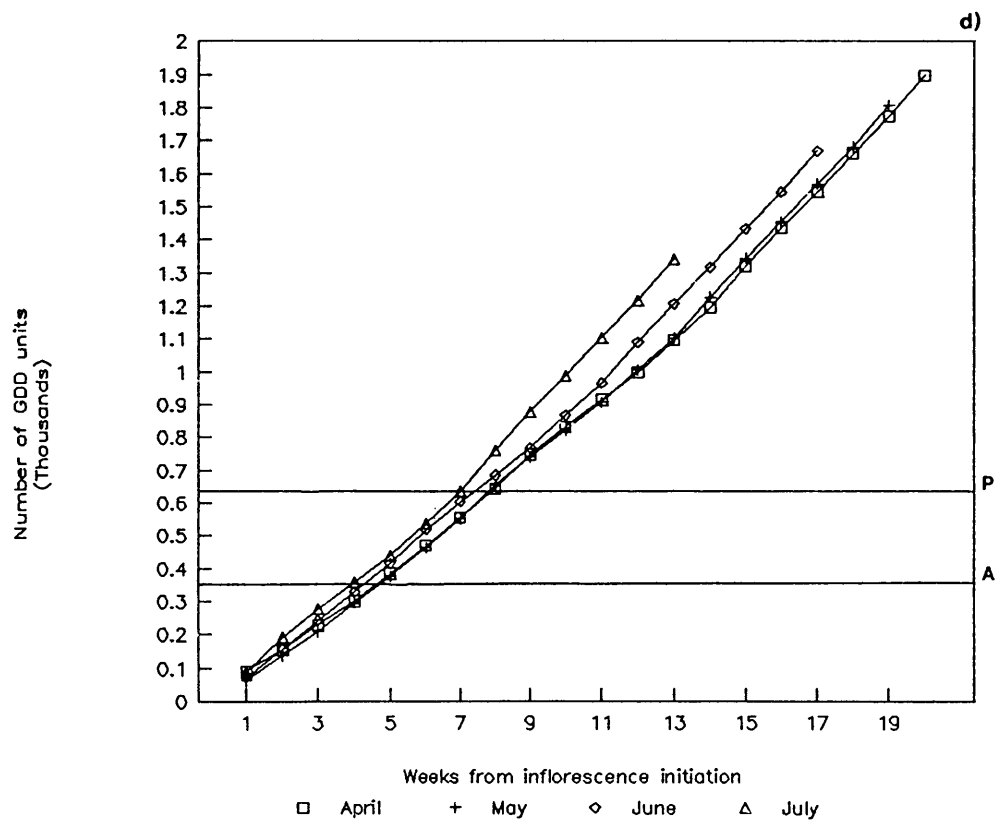
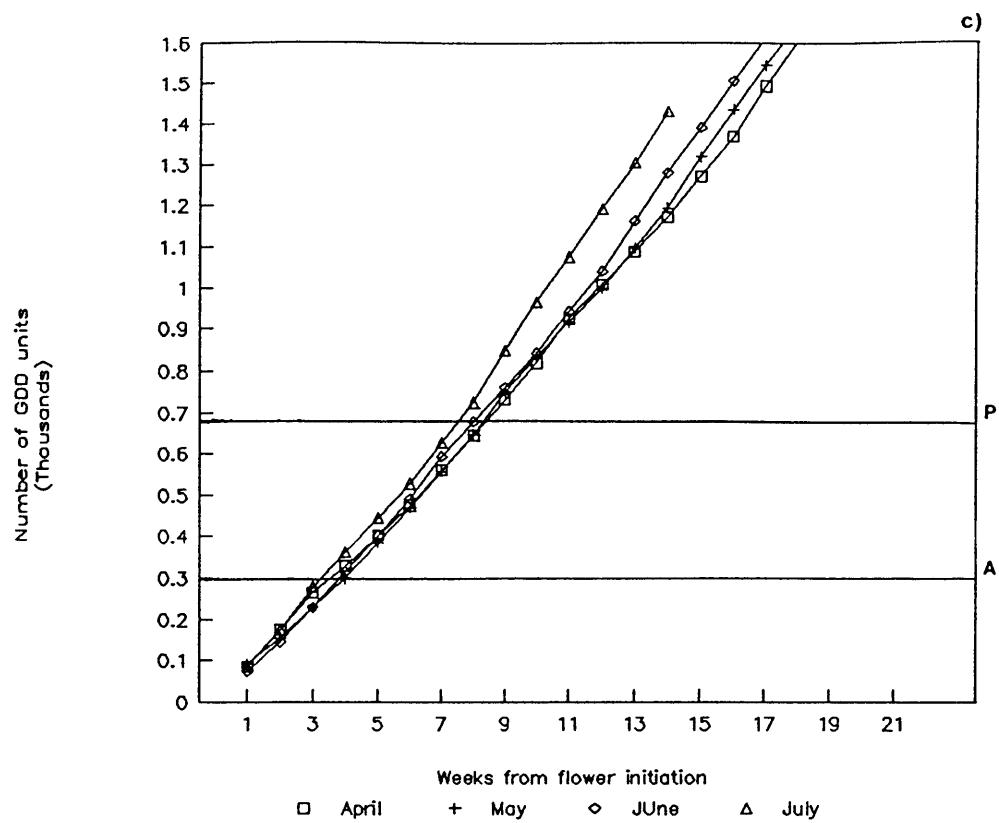


Figure 2. Continued.

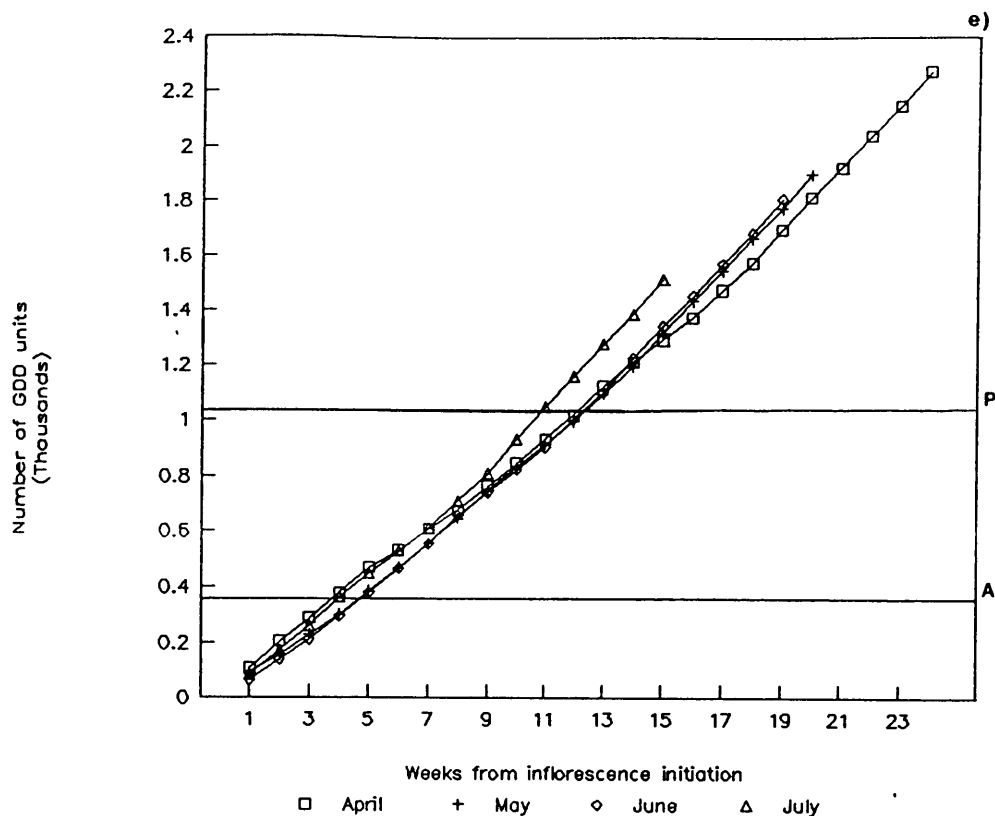


Figure 2. Continued.

(Table 5 & Figure 2c) support this result as plants of this species needed a relatively shorter time span to accumulate the required heat units to reach anthesis and peak flowering than any of the other species.

Senecio arenarius

Senecio arenarius plants require more heat units (351.84 and 631.36) than plants of *H. seselifolia* and therefore need a longer period to accumulate that specific amount (Table 5). By using Figure 2d it could be predicted that depending on the germination date, plants of *S. arenarius* should reach anthesis and peak flowering within 4 to 5 and 7 to 8 weeks from the initiation of inflorescences respectively (Table 5).

Ursinia cakilefolia

From the initiation of inflorescences plants of *U. cakilefolia* should need approximately 3 to 5 weeks to accumulate enough heat units to reach anthesis and 11 - 12 weeks to reach peak flowering in an average year (Figure 2e & Table 5). The time span between

inflorescence initiation and peak flowering is the longest of the five species as *U. cakilefolia* plants required the relatively high number of 1022.55 heat units from inflorescence initiation to peak flowering.

The predicted date of peak flowering in the Springbok area for plants of all five species emerging after the first seasonal rains on four different dates can be seen in Table 5. Later sowing of all five species delayed the calendar date of flowering but not by as many days as the initial difference in sowing date (Table 5). These results support the findings of Pilbeam *et al.* (1990) and Steyn *et al.* (In prep.)(Chapter 5).

Flowering display for tourists

Plants growing under natural conditions in the field do not always reach the theoretical stage of peak flowering due to environmental factors such as water stress and high temperatures (Eliovson 1972; Le Roux & Schelpe 1988). It would therefore be more appropriate to use a criterion of flowering display that could be tested in the field under prevailing climatic conditions. A stage was subjectively chosen to resemble a flowering stage when the number of open flowers/inflorescences per plant were enough to create a flowering display from a tourist point of view. In the case of *D. sinuata* and *U. cakilefolia*, this stage was reached when each plant had at least six open inflorescences while *F. albida* needed 10 open inflorescences per plant to be attractive to tourists. As the number of open flowers/inflorescences of *H. seselifolia* and *S. arenarius* was not counted (Steyn *et al.* In prep.) (Chapter 5), the onset of this flowering stage in these two species was determined visually. The average number of heat units required by plants of all five species to produce a display for tourists, and the predicted number of weeks in an average year at Springbok from flower/inflorescence initiation until this flowering display, are summarised in Table 6. The combined cold/heat unit index (I19) was used in the calculations.

As in the cases of sowing until flower/inflorescence initiation, flower/inflorescence initiation until anthesis and flower/inflorescence initiation until peak flowering, there was a decline in predicted weeks from flower/inflorescence initiation until a flowering display

Table 6. The number of heat units required by five ephemeral species and the predicted number of weeks from flower/inflorescence initiation until a flowering display for for tourists (FD) and from sowing until a flowering display for tourists (S - FD) in an average year in Springbok, as well as the predicted date of a flowering display

Species	Sowing	(FI - FD)		(S - FD)	Date of flowering display
		Heat units	Weeks	Weeks	
<i>Dimorphotheca sinuata</i>	First week in:				
	April	582.00	8	19	9/8 - 15/8
	May	664.25	8	17	23/8 - 29/8
	June	678.85	7	14	30/8 - 5/9
	July	674.10	7	14	27/9 - 3/10
Average heat units		649.80			
<i>Foveolina albida</i>					
	April	682.50	8	21	23/8 - 29/8
	May	603.50	8	18	30/8 - 5/9
	June	631.35	7	15	6/9 - 12/9
	July	621.10	7	15	4/10 - 10/10
Average heat units		634.61			
<i>Heliophila seselifolia</i>					
	April	511.50	7	18	2/8 - 8/8
	May	664.25	7	16	16/8 - 22/8
	June	531.25	7	14	30/8 - 5/9
	July	663.35	6	13	20/9 - 26/9
Average heat units		592.59			
<i>Senecio arenarius</i>					
	April	420.75	6	19	9/8 - 15/8
	May	511.50	6	16	16/8 - 22/8
	June	496.00	6	14	30/8 - 5/9
	July	561.35	5	13	20/9 - 26/9
Average heat units		497.40			
<i>Ursinia cakilefolia</i>					
	April	810.00	9	18	2/8 - 8/8
	May	697.00	9	18	30/8 - 5/9
	June	751.35	8	14	30/8 - 5/9
	July	812.85	8	14	27/9 - 3/10
Average heat units		767.80			

as well as from sowing until a flowering display, with a later sowing date, as plants of the later sowing dates accumulated the required number of thermal units in a shorter period.

Model testing

As a result of the lack of detailed information on the phenology of ephemerals in the Springbok region, the data recorded in Pretoria had to be re-used to test the model (Table 7).

The prediction of flower/inflorescence initiation of plants sown in June, was less reliable than the predictions of flower/inflorescence initiation for the other sowing dates. Actual dates for June plants showed an average deviation of two weeks later than the predicted date (Table 7). For plants sown in April, May and July there was either no difference or 1 week's difference between the actual and predicted number of weeks to reach flower/inflorescence initiation, except in the case of May plants of *Senecio arenarius* where the difference was two weeks. The best prediction was obtained in the case of *D. sinuata*.

As in the case of flower/inflorescence initiation, the prediction of anthesis was less reliable in plants sown in June than plants from other sowing dates. For *D. sinuata*, *F. albida*, *H. seselifolia* and *U. cakilefolia*, the weeks until anthesis were accurately predicted for plants sown in April. Deviations between the predicted and the actual number of weeks from sowing until anthesis for plants of May and July sowing were 1 to 2 weeks.

In the case of the prediction of a flowering display for tourists and peak flowering, the differences between the predicted and actual number of weeks became more frequent and larger (up to 4 weeks) than the prediction of anthesis (Table 7). The prediction of a flowering display, however, was more reliable than the predictions of peak flowering.

The only phenological data available for 1992 was those of April and May plants of *D. sinuata*. The results of the prediction of the timing of various phenological stages are summarised in Table 8. The biggest deviation (2 weeks) between predicted and actual

Table 7. The predicted and actual number of weeks between sowing and flower/inflorescence initiation, anthesis, flowering display and peak flowering of five ephemeral species grown in Pretoria

Species	Sowing date	Sowing - flower/infl. initiation		Sowing - anthesis		Sowing - flowering display		Sowing - peak flowering	
		Predicted weeks	Actual weeks	Predicted weeks	Actual weeks	Predicted weeks	Actual weeks	Predicted weeks	Actual weeks
<i>Dimorphotheca sinuata</i>	First week in:								
	April	11	11	15	15	18	17	20	20
	May	9	9	13	14	16	16	17	17
	June	8	9	12	13	14	15	16	20
	July	8	8	11	11	13	13	14	16
<i>Foveolina albida</i>									
	April	12	11	17	17	18	19	20	20
	May	10	11	15	16	16	17	18	18
	June	8	10	13	15	14	15	15	15
	July	10	9	13	12	14	13	16	14
<i>Heliophila seselifolia</i>									
	April	10	10	13	13	16	16	17	17
	May	8	9	11	12	14	16	15	16
	June	7	9	10	12	13	14	13	15
	July	8	8	10	10	12	13	13	14
<i>Senecio arenarius</i>									
	April	12	11	16	15	17	16	19	17
	May	9	11	13	14	14	16	16	17
	June	8	10	12	13	13	14	14	15
	July	10	9	12	12	13	13	14	14
<i>Ursinia cakilefolia</i>									
	April	10	9	14	14	19	18	21	20
	May	8	9	12	14	16	16	18	17
	June	7	9	11	13	14	16	16	19
	July	8	8	11	11	14	16	16	16

Table 8. The predicted and actual number of weeks between sowing (S) and flower initiation (FI), anthesis (A), flowering display for tourists (FD) and peak flowering (P) of *Dimorphotheca sinuata* plants grown in Pretoria in 1992

Sowing date	Weeks	S - FI	FI - A	S - A	FI - FD	S - FD	FI - P	S - P
April	Predicted	10	5	15	8	18	10	20
	Actual	9	5	14	7	16	10	19
May	Predicted	8	4	12	8	16	9	17
	Actual	9	5	14	7	16	9	18

number of weeks occurred in the timespan from sowing until a flowering display (April plants) and between sowing and anthesis (May plants).

The prediction of the timing of a specific phenological stage from the initiation of inflorescences, seemed more accurate than the same predictions from sowing (Table 8). In both April and May plants, the timing of peak flowering was predicted accurately.

According to Baskerville & Emin (1969) one cannot expect heat accumulation alone to explain all variation in a biological response. Newman *et al.* (1968) found that growing degree days become less accurate as a predictor of maturity if there is a problem such as low soil moisture.

It should be remembered that the results obtained at the University of Pretoria are not directly applicable to conditions in Springbok as Levitt (1956) and Lang (1963) stated that the response of plants in controlled environments may be partly determined by their environmental history, i.e. by the conditioning that they have previously received. Furthermore, the results were obtained from plants grown under optimal conditions, while plants in the field are subjected to water stress, wind, widely fluctuating temperatures and herbivory which can all affect the phenological development of the plants.

CONCLUDING REMARKS

All species examined seem to require and accumulate cold units to reach the phenological stage of flower/inflorescence initiation. The cut-off temperature below which cold units are accumulated differed between species, while *U. cakilefolia* did not have a specific cut-off temperature.

From the results it seems that all five species require heat after the initiation of flowers/inflorescences, for the development of their flowers/inflorescences. The combination of cold and heat (thermal) units from sowing are thus necessary to predict anthesis, a flowering display and peak flowering from sowing.

Of the 24 thermal unit indices used, cold units from sowing until flower/inflorescence initiation combined with growing degree days from flower/inflorescence initiation until anthesis/flowering display/peak flowering (I19, Table 4a & b), gave the most accurate predictive values. Therefore, it is clear that these species accumulate heat units once their flowers/inflorescences have been initiated.

By using thermal units it seems possible to predict certain flowering stages in the Namaqualand flowering period with varying degrees of success. The most accurate predictions can be made for plants establishing early in the growing season (April & May).

It can be concluded that a showy floral display of the species can be predicted in the beginning of the growing season when the first sufficient rain has fallen. By accumulating the actual cold and heat units of the specific growing season, refinements in the prediction can be made throughout the season that could lead to a more accurate prediction, especially once flower/inflorescence initiation has been reached.

The results of this study look promising but more species should be included and the indices should be tested on actual phenological data of plants growing in the field. The predictions can also be refined if data are collected from plants sown fortnightly from

mid-March until mid-July.

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REFERENCES

- ABRAMI, G. 1969. Optimum mean temperature for plant growth calculated by a new method of summation. *Ecology*, 53: 893 - 900.
- AITKEN, Y. 1955. Flower initiation in pasture plants. III. Flower initiation in *Medicago tribuloides* Desr. and other annual *Medics*. *Australian Journal for Agricultural Research*, 6 ; 258 - 64.
- BASKERVILLE, G.L. & EMIN, P. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, 50: 515 - 517.
- BASKIN, J.M. & BASKIN, C.C. 1972. The ecological life cycle of the cedar glade endemic *Leavenworthia exigua* var. *exigua*. *Canadian Journal of Botany*, 50: 1711 - 1723.
- CAPRIO, J.M. 1974. The solar thermal unit concept in problems related to plant development and potential evapotranspiration. In: LIETH, H. (ed.) *Phenology and seasonality modeling*. Ecological Studies 8. Springer-Verlag, New York. pp. 353 - 364.
- CLARK, S.C. 1969. Some effects of temperature and photoperiod on growth and floral development in three winter annuals. *New Phytologist*, 68: 1137 - 44.
- CROSS, H.Z. & ZUBER, M.S. 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. *Agronomy Journal*, 64: 351 - 355.
- DOYLE, A.D. 1975. Influence of temperature and daylength on phenology of sunflowers in the field. *Australian Journal of Experimental Agriculture and*

- Animal Husbandry**, 15: 88 - 92.
- EICKER, R. 1979. Die ondersoek van die invloed van temperatuur en straling op die blomtyd van mielies te Potchefstroom. M.Sc. dissertation. University of the Orange Free State, Bloemfontein.
- ELIOVSON, S. 1972. Namaqualand in flower. Macmillan, Johannesburg.
- EVENARI, M. & GUTTERMAN, Y. 1985. Desert plants. In HALEVY, A.H. (ed.) CRC Handbook of Flowering. Vol. 1. CRC Press, Florida. pp. 41 - 59.
- GOYNE, P.J., WOODRUFF, D.R. & CHURCHETT, J.D. 1977. Prediction of flowering in sunflowers. **Australian Journal of Experimental Agriculture and Animal Husbandry**, 17: 475 - 481.
- HADLEY, P., ROBERTS, E.H., SUMMERFIELD, R.J. & MINCHIN, F.R. 1984. Effects of temperature and photoperiod on flowering in Soya bean (*Glycine max* (L.) Merrill): a quantitative model. **Annals of Botany**, 53: 669 - 681.
- HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- IDSO, S.B., JACKSON, R.D. & REGINATO, R.J. 1978. Extending the "Degree day" concept of plant phenological development to include water stress effects. **Ecology**, 59: 431 - 433.
- LANG, A. 1963. Achievements, challenges and limitations of phytotrons. In: EVANS, L.T. (ed.) Environmental control of plant growth. New York. pp. 405 - 419.
- LE ROUX, A. & SCHELPE, E.A.C.L.E. 1988. Namakwaland. Veldblomgids van Suid-Afrika 1. Revised Edition. Botanical Society of South Africa, Cape Town.
- LETTAU, K. 1965. A new method for predicting the blooming date of spring flowers. **Wisconsin Academy of Sciences Arts and Letters Transactions**, 54: 135 - 142.
- LEVITT, J. 1956. The hardiness of plants. Academic Press, New York.
- LINDSEY, A.A. & NEWMAN, J.E. 1956. Use of official weather data in spring time temperature analysis of an Indian phenological record. **Ecology**, 37: 812 - 823.
- LOWRY, W.P. 1970. Weather and life. An introduction to biometeorology. Academic Press, New York.
- MAJOR, D.J., JOHNSON, D.R. & LUEDDERS, V.D. 1975. Evaluation of eleven thermal unit methods for predicting soybean development. **Crop Science**, 5: 172 - 174.

- MAJOR, D.J., JOHNSON, D.R., TANNER, J.W. & ANDERSON, I.C. 1975. Effects of daylength and temperature on soybean development. *Crop Science*, 15: 174 - 179.
- MATTHEE, G.W. 1982. Koue-eeenhede in die winterreëng gebied van Suid-Afrika. Government Printer, Pretoria.
- NEWMAN, J.E., BLAIR, B.O., DALE, R.F., SMITH, L.H., STIRM, W.L. & SCHAAL, L.A. 1968. Growing degree days. *Crops and Soils Magazine*, 21 : 9 - 12.
- NUTTONSON, M.Y. 1955. Wheat-climate relationships and the use of phenology in ascertaining the thermal and photothermal requirements of wheat. American Institution for Crop Ecology, Washington, D.C..
- PEMADASA, M.A. & LOVELL, P.H. 1974. Factors controlling the flowering time of some dune annuals. *Journal of Ecology*, 62: 869 - 880.
- PILBEAM, C.J., HEBBLETHWAITE, P.D., RICKETTS, H.E. & HASSAN, O.A. 1990. Effects of autumn sowing dates on growth and yield of indeterminate and determinate field beans (*Vicia faba*). *Journal of Agricultural Science*, 114: 339 - 352.
- ROBINSON, R.G. 1971. Sunflower phenology - year, variety, and date of planting effects on day and Growing Degree-day summations. *Crop Science*, 11: 635 - 638.
- SEDDIGH, M., JOLLIFF, G.D. & ORF, J.H. 1989. Night temperature effects on soybean phenology. *Crop Science*, 29: 400 - 406.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep.). The influence of sowing date on the phenology of five Namaqualand ephemeral species.
- VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis. University of Pretoria, Pretoria.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1992. The ephemerals of Namaqualand: effect of germination date on development of three species. *Journal of Arid Environments*, 22: 51 - 66.
- WENT, F.W. 1953. The effect of temperature on plant growth. *Annual review of Plant Physiology*, 4: 347 - 358.

APPENDIX A

Formulae used in determining the number of heat units (Chapter 8):

I1 - Growing degree days (GDD) per day

$$\text{GDD} = [(T_x + T_n)/2 - T_b]$$

T_x - daily maximum temperature

T_n - daily minimum temperature

T_b - base temperature

I2 - Photothermal units (PT) per day

$$\text{PT} = T \times L$$

T - mean daily temperature

L - daylength in hours

I3 - Day-hour units (DH) per day

$$\text{DH} = 12(h-t)^2/(h-w)$$

h - daily maximum temperature

w - daily minimum temperature

t - base temperature

I4 - Two hourly temperatures

Sum of the actual two hourly temperatures from the beginning of the period until a specific phenological stage has been reached.

I5 - Photothermal units (PTU) per day

$$\text{PTU} = 2\text{HT} \times \text{daylength}$$

2HT - mean two hourly temperature

I6 - Solar thermal units (STU) per day

$$\text{STU} = [\text{cal}(0.3 - 4 \text{ micron})\text{cm}^2 \text{ per day}][T_m + T_n)/2] - T_b]$$

T_m - daily maximum temperature

T_n - daily minimum temperature

T_b - base temperature

APPENDIX B

To predict the timing of a certain phenological stage; the base temperature (temperature below which no growth is assumed to take place) of the species, the required number of thermal units (cold and/or heat units) to reach a certain phenological stage and the average seasonal accumulation of thermal units for the locality must be known. For a detailed description on the calculation of thermal units, the reader is referred to Steyn *et al.* (In prep. e).

- 1) The base temperature of the Namaqualand ephemerals that were examined, was taken as 0°C.
- 2) The average number of thermal units required by a species to reach a specific phenological stage is the varietal constant.

It is important to remember that cold units are accumulated from sowing until flower/inflorescence initiation, whereafter heat units (growing degree days) are accumulated for further development. Thus, to predict peak flowering, two graphs per species are needed.

- 2.1 The varietal constant for five tested species from sowing until flower/inflorescence initiation are as follows:

Dimorphotheca sinuata (Namaqualand daisy) - 5095.54 cold units, below 20°C

Foveolina albida (Stinkkruid) - 4481.29 cold units, below 18°C

Heliophila seselifolia (Sporrie) - 6155.42 cold units, below 22°C

Senecio arenarius (Hongerblom) - 4445.40 cold units, below 18°C

Ursinia cakilefolia - 957.25 cold units, below 17°C

The average seasonal cold unit accumulation from 15 March is plotted in Figure 1. There is a different figure for each species, because the cut-off temperature below which the cold units were accumulated differed between species and therefore the accumulation curves of the species differ.

If the sowing date (date of substantial rainfall) is known, the date of flower/inflorescence initiation for a species can be predicted by using the varietal constants and the corresponding Figure (Figure 1a - e).

For example: if the first substantial rain fell on 8 April, this is taken as the sowing date. A vertical line can be drawn from the sowing date to the cold unit accumulation curve from where the varietal constant (cold units) until inflorescence initiation should be added on the Y-axis (Figure 1a). By drawing a horizontal line from this cold unit total, the expected date of inflorescence initiation will be the x-axis coordinate for the point where line FI (flower/inflorescence initiation) intercepts the cold unit accumulation curve.

- 2.2 From the initiation of flowers/inflorescences (dates derived from Figure 1a - e), heat units are accumulated (Figure 2) until the varietal constant (growing degree days) for a specific phenological stage has been reached.

Table 1. The varietal constants from flower/inflorescence initiation until a specific phenological stage for five ephemeral species.

Species	Anthesis	Flowering display	Peak flowering
<i>D. sinuata</i>	393.53	649.80	852.36
<i>F. albida</i>	512.74	634.61	822.49
<i>H. seselifolia</i>	293.44	592.59	677.30
<i>S. arenarius</i>	351.84	497.40	631.36
<i>U. cakilefolia</i>	384.28	767.80	1022.55

Growing degree days is a way of measuring how fast a species is growing by adding up the average daily temperatures above the base temperature during the growing season. Subtracting the base temperature from the daily mean temperature gives the number of growing degree days for the 24-hour period. The average seasonal growing degree days accumulation curve from 31 May in Springbok is presented in Figure 2. As all five species accumulate growing degree days from the initiation of flowers/inflorescences, only one accumulation curve is necessary for predictions. If the predicted or actual date of flower/inflorescence initiation is known, the date of a specific flowering stage can be predicted by using the varietal constant and Figure 2 in a similar way as in the case of the cold unit accumulation curve (Figure 1).

Thus, by using these accumulation curves the timing of specific phenological stages can be predicted at the beginning of the season. By accumulating the actual heat units of the specific growing season, refinements of the prediction can be made once flower/inflorescences have been initiated that could lead to a more accurate prediction.

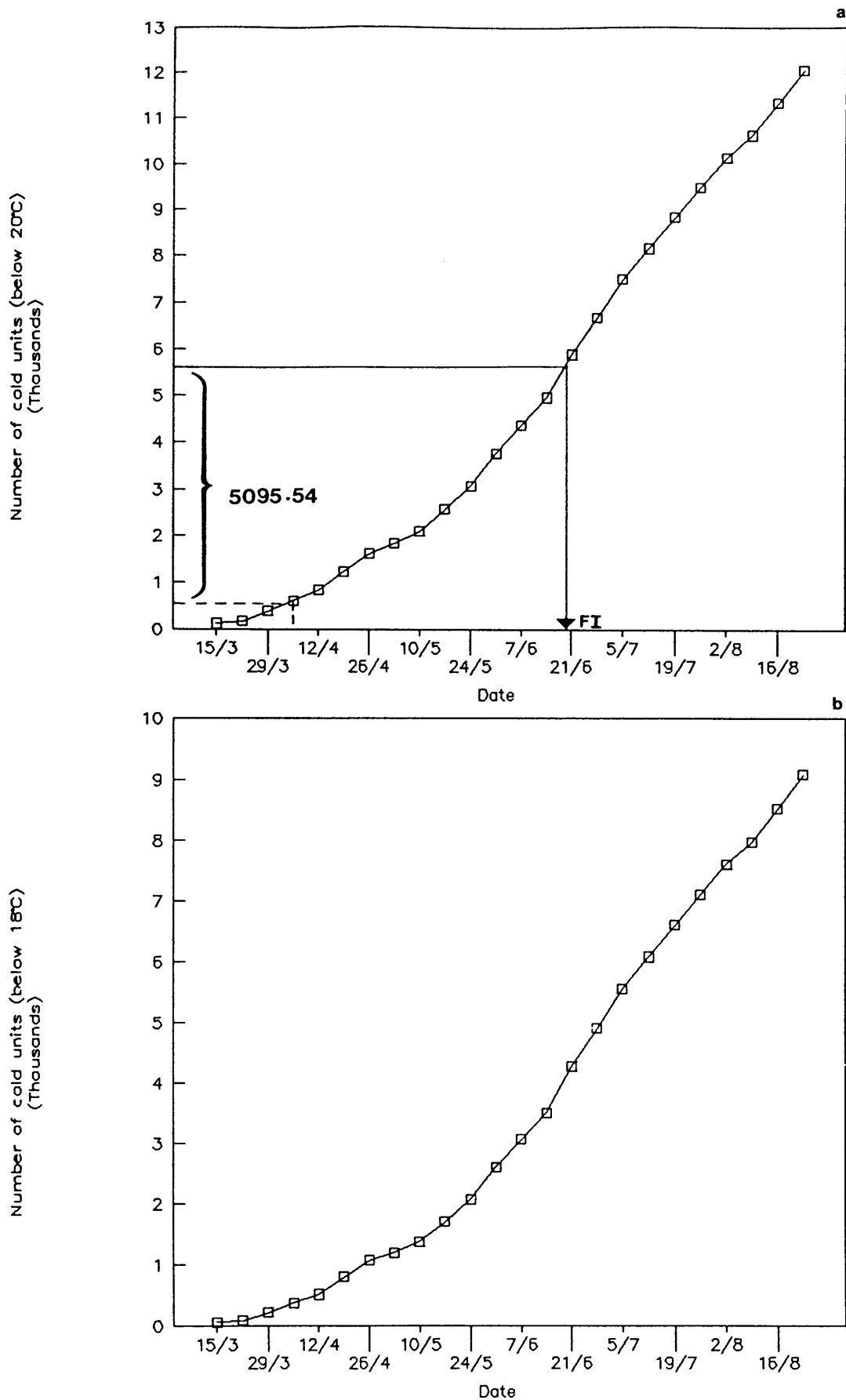


Figure 1. The cold unit accumulation curves for an average year in Springbok from 15 March for
a) *Dimorphotheca sinuata*, b) *Foveolina albida*, c) *Heliophila seselifolia*, d) *Senecio arenarius* and
e) *Ursinia cakilefolia*.

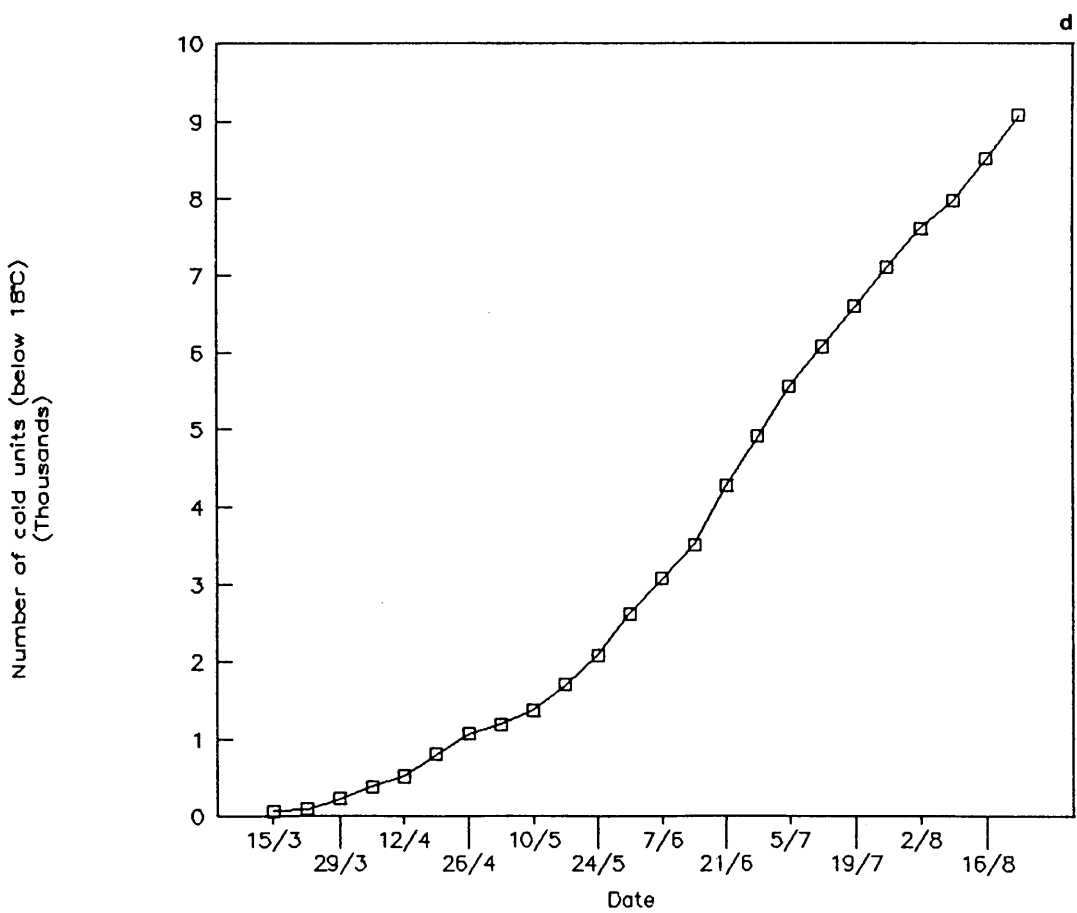
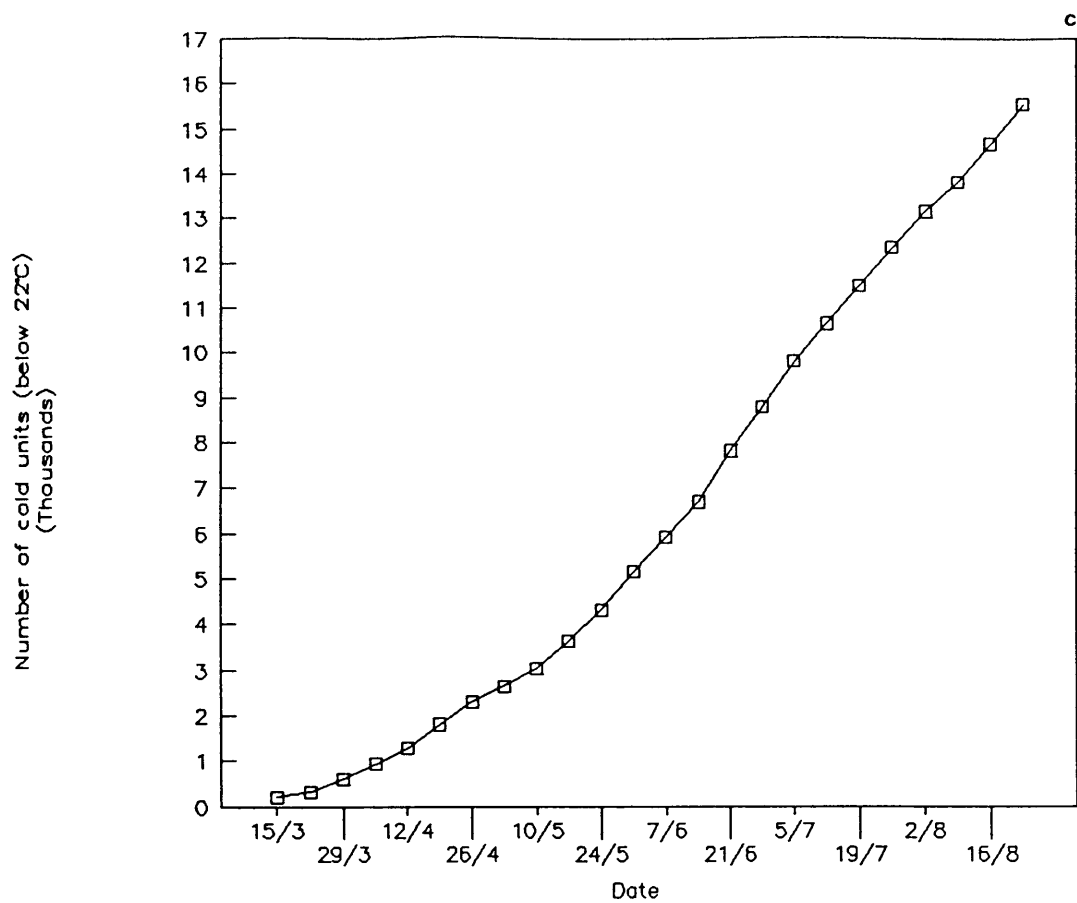


Figure 1. Continued.

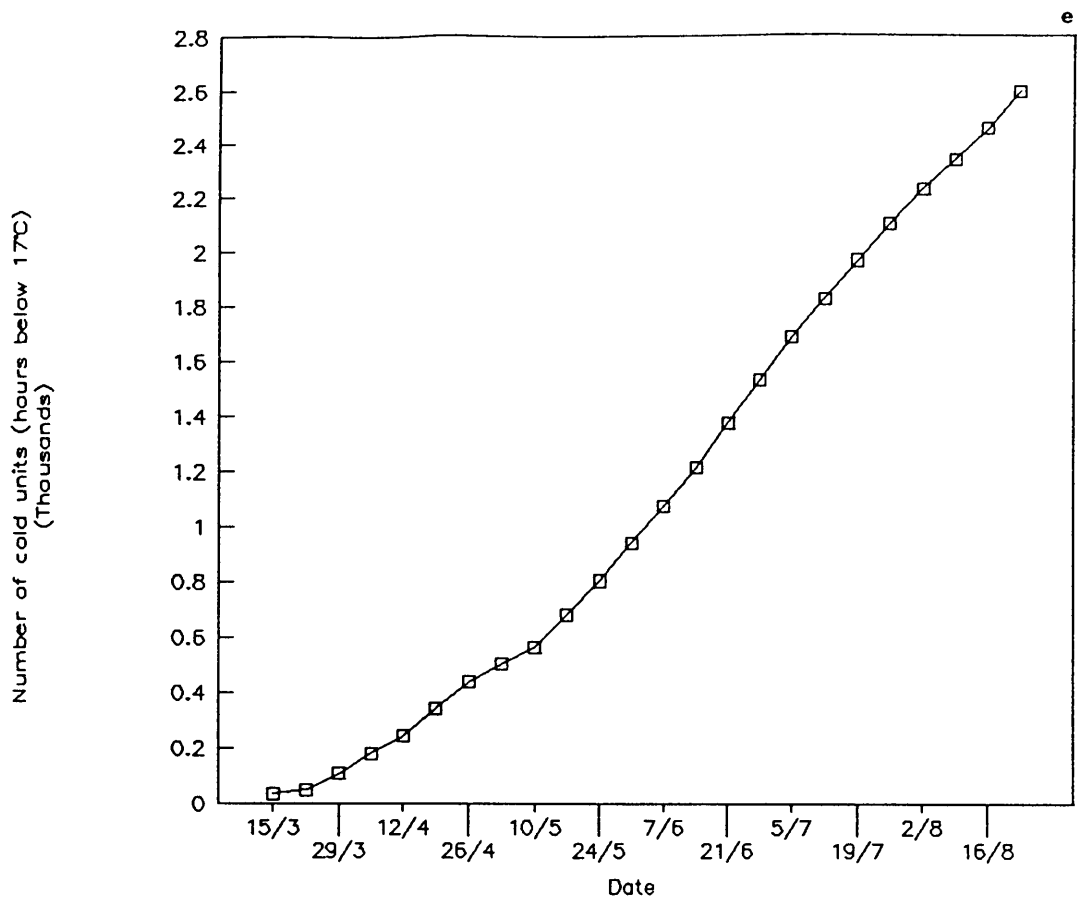


Figure 1. Continued.

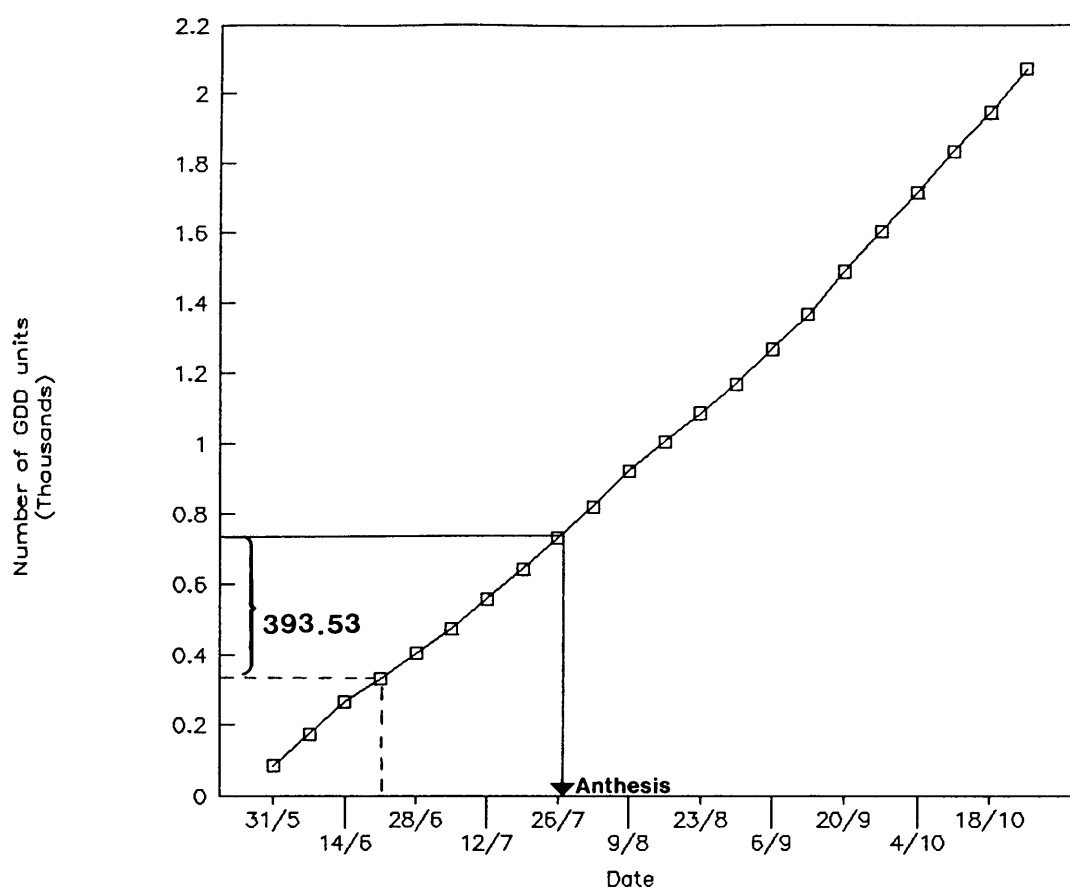


Figure 2. The heat unit (growing degree days) accumulation curve for an average year in Springbok from 31 May.

CHAPTER 9

CONCLUDING REMARKS

The different environmental variables i.e. controlled temperatures, sowing date, water stress and achene age resulted in phenological differences in the ephemeral species examined.

Under controlled temperature conditions height of *Ursinia cakilefolia* plants seemed to be stimulated by higher temperatures. In both species, *Dimorphotheca sinuata* and *U. cakilefolia*, a cold treatment early in the growing season accelerated inflorescence initiation in plants of April sowing. The initiation of inflorescences started at a younger age in plants of June sowing, than in plants of April sowing, which can possibly be regarded as an adaptation to ensure spring flowering. In both species, June plants produced more inflorescences during their peak and had a longer flowering period than April plants. The effect of alternating high and low temperature treatments in specific phenophases could be examined to determine if the effect of one treatment is neutralized if followed by the opposite treatment. This could be important in the prediction of flowering time of the ephemerals.

There were distinct differences in the growth and phenology of plants from different sowing dates in all five species examined. Seeds/achenes sown in April produced the tallest plants with the highest number of open inflorescences per plant at peak flowering, than those of later sowing dates, probably because April plants were subjected to higher temperatures early in their life cycle. The number of leaves on the main stem at flower/inflorescence initiation tended to decrease, the later the sowing date and the time to the onset of anthesis and peak flowering also decreased in all five species. From these results it seems that early rain will result in the establishment of plants which will take a long period to reach anthesis and peak flowering, but at their peak these plants will be taller and produce more open inflorescences/flowers and consequently a more spectacular show than plants which established later in the season. This differed from the results obtained under controlled conditions where June plants had more open

inflorescences than those of April sowing, probably because there was no significant difference in plant height between these April and June plants. In the case of plants grown out of doors, however, April plants were significantly taller than June plants as a result of a more favourable growing period and therefore could produce more inflorescences.

Water stress shortened the life span and flowering period of all five ephemeral species. Plants subjected to water stress were smaller and produced less open inflorescences per plant at peak flowering and in total less reproductive organs per plant during their flowering period than control plants. The number of leaves on the main stem at flower/inflorescences initiation was unaffected by water stress as the plants were still very small. Water stress, however, reduced the time span from sowing to the onset of anthesis and peak flowering at the later sowing dates, possibly to ensure seed set before the end of the season. The phenological development of plants subjected to water stress at specific phenological stages could differ from the above mentioned results and should be examined to predict the effect of water stress on flower/inflorescence production under natural conditions.

Achene age had an effect on the phenology of *D. sinuata* plants, as plants derived from fresh achenes, initially were shorter than those of older achenes, although the maximum plant height was unaffected. Furthermore, plants from fresh achenes produced more leaves on the main stem until inflorescence initiation and reached anthesis later than plants from older achenes. There was, however, no significant difference in the number of open inflorescences per plant between plants from different achene collections. Achenes from previous years (older than one year) thus seemed to be a viable part of the seed bank, and can produce plants with the same vigour, number of open inflorescences at peak flowering and total number of reproductive organs as plants from fresh achenes. Apart from achene age, differences between plants of different achene samples could also be due to the parental environment (Fenner 1985) and storage conditions (Cook 1980).

The use of thermal units resulted in some accurate predictions of the timing of

phenological stages and can be used to predict flowering time in Namaqualand in aid of tourism. All five species seemed to accumulate cold units until the stage of flower/inflorescence initiation. After the initiation of flowers/inflorescences, however, these plants required heat for anthesis and further development. Growing degree days and two-hourly temperatures seemed to be the most accurate heat unit indices to use from the initiation of flowers/inflorescences onwards. The combination of cold and heat units are thus necessary to predict the beginning and length of the flowering period in these Namaqualand ephemerals.

Predictions are not perfect for it is not uncommon for a phenological event at a given elevation to differ by more than a week due solely to differences in slope and aspect (Caprio, Hopp & Williams 1974). This could be supported by preliminary phenological observations done in the Springbok region in 1991. Evans, Lawn & Watkinson (1992) found that precision is lost in the prediction of flowering in subterranean clover, *Trifolium subterraneum*, when sowings are made outside the time normally recommended for the species. According to Anderson (1974) genetical differences within a species have resulted in strikingly different phenological patterns. Differing phenological responses within a species that are controlled by genetic differences demonstrate the role of selection in producing populations adapted to local environmental regimes.

Further research could be important in the refinement of the formulae used to predict phenological stages. The inclusion of soil temperature, different base temperatures for different developmental stages, water stress and more replicates of sowing dates could enhance the accuracy of the predictions. Lieth (1974) also stated that phenological observations on selected indicator plants may help forecast or estimate the occurrence of succeeding phenological events in the same or other species.

SUMMARY

NAMAQUALAND EPHEMERALS: PHENOLOGY AND THERMAL UNITS

by

H.M. STEYN

Supervisor: Dr. N. van Rooyen

Co-supervisors: Dr. M.W. van Rooyen

Prof. G.K. Theron

DEPARTMENT OF BOTANY

MAGISTER SCIENTIAE

Annually thousands of tourists visit Namaqualand to see the wild flower display. Flowering time in Namaqualand generally ranges from August through September, depending on the timing of the first good rains. A prediction of the timing of certain phenological stages could be of importance for tourists.

The phenological development of five Namaqualand ephemeral species (*Dimorphotheca sinuata*, *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* and *Ursinia cakilefolia*) under a range of conditions was investigated.

Under controlled temperature conditions plants of June sowing produced more open inflorescences during their peak and had a longer flowering period than plants of April sowing. High temperatures seemed to enhance the height growth of *Ursinia cakilefolia* plants, while low temperatures seemed to stimulate the initiation of inflorescences.

Plants that established early in the growing season, needed a relatively long period to reach flower/inflorescence initiation, anthesis and peak flowering, due to different lengths

of periods needed to accumulate the required number of thermal units. Seeds/achenes sown in April furthermore produced the tallest plants with the highest number of open flowers/inflorescences per plant at peak flowering, and thus a more spectacular show than plants of later sowing dates.

Water stress reduced the number of inflorescences produced per plant and shortened the life span and flowering period of all five species and would therefore result in a less spectacular flowering display. In the case of June and July sowing, water stress reduced the time span from sowing to the onset of anthesis and peak flowering, possibly to ensure seed set before the end of the season.

Achene age had some effect on the early development and phenology of *D. sinuata* plants, although the differences were less evident at maturity. Therefore, no significant differences existed between the number of leaves on the main stem at inflorescence initiation and the number of open inflorescences at peak flowering between plants of the different achene samples.

All five species seem to accumulate cold units until flower/inflorescence initiation, after which the plants require heat for anthesis and further development. Growing degree days seem to be the most accurate heat unit index to use in combination with cold units. It can be concluded that thermal units can be used to explain phenological differences within and between plant species, as well as predict the timing of certain phenological stages.

OPSOMMING

NAMAKWALANDSE EFEMERE: FENOLOGIE EN TERMIESE EENHEDE

deur

H.M. STEYN

Leier: Dr. N. van Rooyen

Mede-leiers: Dr. M.W. van Rooyen

Prof. G.K. Theron

DEPARTEMENT PLANTKUNDE
MAGISTER SCIENTIAE

Duisende toeriste besoek Namakwaland jaarliks om die blommeskouspel te sien. Blomtyd in Namakwaland strek gewoonlik vanaf Augustus tot die einde van September, afhangende van die datum van die eerste goeie reën. Die voorspelling van die tydsverloop tot sekere fenologiese stadia kan van belang wees vir toeriste.

Die fenologiese ontwikkeling van vyf Namakwalandse efemeerspesies (*Dimorphotheca sinuata*, *Foveolina albida*, *Heliophila seselifolia*, *Senecio arenarius* en *Ursinia cakilefolia*) is onder verskillende toestande ondersoek.

Onder gekontroleerde temperatuurtoestande, het plante van die Junie saai tyd meer oop blomme tydens hul piek geproduseer en 'n langer blomperiode gehad as plante van die April saai tyd. Hoë temperature bevorder klaarblyklik lengtegroei in plante van *Ursinia cakilefolia*, terwyl lae temperature die inisiasie van bloei wyses stimuleer.

Plante wat vroeg in die groeiseisoen gevestig is, benodig 'n relatief lang tydperk tot blom/bloei wyses inisiasie, antese en piek blom tyd, aangesien tydperke van verskillende

lengtes nodig is om die benodigde aantal termiese-eenhede te akkumuleer. Sade/agene wat in April gesaai is, het die langste plante met die grootste aantal oop bloeiwyses per plant tydens piekblomtyd geproduseer en sodoende 'n meer aanskoulike blommeskouspel as plante van later saaitye gelever.

Waterstremming het die aantal bloeiwyses per plant, asook die lewensduur en blomperiode van al vyf spesies verkort en sal sodoende lei tot 'n minder aanskoulike blommeskouspel. In die geval van die Junie en Julie saaitye het waterstremming die tydsduur vanaf saaityd tot die aanvang van antese en piekblomtyd verkort; moontlik om saadproduksie te verseker voor die einde van die seisoen.

Ageen-ouderdom het 'n invloed op die vroeë ontwikkeling en fenologie van *Dimorphotheca sinuata* plante gehad, maar die verskille was minder opvallend tydens volwassenheid. Sodoende het geen betekenisvolle verskille tussen die aantal blare op die hoofas tydens blom/bloeiwyse inisiasie en die aantal oop bloeiwyses tydens piekblomtyd tussen plante van verskillende ageenmonsters voorgekom nie.

Dit blyk dat al vyf spesies koue-eenhede akkumuleer tot die inisiasie van blomme/bloeiwyses, waarna die plante hitte benodig vir antese en verdere ontwikkeling. Groeidageenhede blyk die mees akkurate hitte-eenheidsindeks te wees om in kombinasie met koue-eenhede te gebruik. Daar kan tot die gevolgtrekking gekom word dat termiese-eenhede gebruik kan word om fenologiese verskille tussen en binne plantspesies te verklaar, asook om die tydsverloop tot bepaalde fenologiese stadia te voorspel.

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REFERENCES

- ABDALLA, F.H. & ROBERTS, E.H. 1969. The effects of seed storage conditions on the growth and yield of barley, broad beans and peas. *Annals of Botany* (Lond.), 33: 160 - 84.
- ABRAMI, G. 1969. Optimum mean temperature for plant growth calculated by a new method of summation. *Ecology*, 53: 893 - 900.
- ACKERMAN, T.L. & BAMBERG, S.A. 1974. Phenological studies in the Mojave Desert at Rock Valley (Nevada Test Site). In: LIETH, H. (ed.) Phenology and seasonality modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 215 - 226.
- ACOCKS, J.P.H. 1988. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa*, 57: 1 - 122.
- AITKEN, Y. 1955. Flower initiation in pasture plants. III. Flower initiation in *Medicago tribuloides* Desr. and other annual *Medics*. *Australian Journal for Agricultural Research*, 6: 258 - 64.
- ANDERSON, J.L. 1974. Delaying fruit tree bloom by summer cooling and overhead misting. *Proceedings of the Washington State Horticultural Association*, : 87 - 91.
- ANDERSON, R.C. 1974. Seasonality in terrestrial primary producers. In: LIETH, H. (ed.) Phenology and seasonality modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 103 - 112.
- ANGUS, J.F. & MANCUR, W.M. 1977. Water stress and phenology of wheat. *Australian Journal of Agricultural Research*, 28: 177 - 181.

- ARNOLD, C.Y. 1960. Maximum-minimum temperatures as a basis for computing heat units. **Proceedings of the American Society of Horticultural Sciences**, 76: 682 - 692.
- ARONSON, J., KIGEL, J., SHMIDA, A. & KLEIN, J. 1992. Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. **Oecologia (Berl.)**, 89: 17 - 26.
- ASPINALL, D. & HUSAIN, I. 1970. The inhibition of flowering by water stress. **Australian Journal of Biological Science**, 23: 925 - 936.
- BASKERVILLE, G.L. & EMIN, P. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. **Ecology**, 50: 515 - 517.
- BASKIN, J.M. & BASKIN, C.C. 1972. The ecological life cycle of the cedar glade endemic *Leavenworthia exigua* var. *exigua*. **Canadian Journal of Botany**, 50: 1711 - 1723.
- BASKIN, J.M. & BASKIN, C.C. 1974. Effect of vernalization on flowering of the winter annual *Alyssum alyssoides*. **Bulletin of the Torrey Botanical Club**, 101: 210 - 213.
- BATES, E.M. 1976. Solar radiation a more accurate guide than heat units. **Crops and Soils Magazine**, March: 12 - 15.
- BEATLEY, J.C. 1967. Survival of winter annuals in the northern Mojave Desert. **Ecology**, 48: 745 - 750.
- BEATLEY, J.C. 1974. Phenological events and their environmental triggers in the Mojave desert ecosystem. **Ecology**, 55: 856 - 863.
- BOOT, R., RAYNAL, D.J. & GRIME, J.P. 1986. A comparative study of the influence

- of drought stress on flowering in *Urtica dioica* and *Urtica urens*. **Journal of Ecology**, 74: 485 - 495.
- BOWERS, M.A. 1987. Precipitation and the relative abundance of desert winter annuals: a six year study in the northern Mohave desert. **Journal of Arid Environments**, 12: 141 - 149.
- BROWN, D.M. 1978. Heat units for corn in southern Ontario. Factsheet. Agdex 111/31.
- BUNTING, E.S. 1976. Accumulated temperature and maize development in England. **Journal of Agricultural Sciences**, 87: 577 - 583.
- CAPRIO, J.M. 1974. The solar thermal unit concept in problems related to plant development and potential evapotranspiration. In: LIETH, H. (ed.) Phenology and seasonality modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 353 - 364.
- CAPRIO, J.M., HOPP, R.J. & WILLIAMS, J.S. 1974. Computer mapping in phenological analysis. In: LIETH, H. (ed.) Phenology and seasonal modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 77 - 82.
- CHIEF DIRECTORATE: NATURE AND ENVIRONMENTAL CONSERVATION. Undated. Namaqualand. Hand-bill. Cape Provincial Administration. Private Bag x9086, Cape Town, 8000.
- CLARK, S.C. 1969. Some effects of temperature and photoperiod on growth and floral development in three winter annuals. **New Phytologist**, 68: 1137 - 1144.
- CLARKSON, N.M. & RUSSELL, J.S. 1976. Effect of water stress on the plastic development of annual *Medicago* species. **Australian Journal of Agricultural Research**, 27: 227 - 234.

- CONSTABLE, G.A. & ROSE, I.A. 1988. Variability of soybean phenology response to temperature, daylength and rate of change in daylength. **Field Crops Research**, 18: 57 - 69.
- COOK, R. 1980. The biology of seeds in the soil. In: SOLBRIG, O.T. (ed.) **Demography and Evolution in Plant Populations**. Blackwell, Oxford. pp. 107 - 29.
- CRAIGON, J.C., ATHERTON, J.G. & BASHER, E.A. 1990. Flowering and bolting in carrot. II. Prediction in growth room, glasshouse and field environments. **Journal of Horticultural Science**, 65: 547 - 554.
- CROCKER, W. 1938. Life-span of seeds. **Botanical Review**, 4: 235 - 274.
- CROSS, H.Z. & ZUBER, M.S. 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. **Agronomy Journal**, 64: 351 - 355.
- DARLINGTON, H.T. & STEINBAUER, G.P. 1961. The eighty-year period for Dr. Beals' seed viability experiment. **American Journal of Botany**, 48: 321 - 325.
- DIERINGER, G. 1991. Variation in individual flowering time and reproductive success of *Agalinis strictifolia* (Scrophulariaceae). **American Journal of Botany**, 78: 497 - 503.
- DIJKHUIS, F.J. 1971. The use of Heat Units in maize production. Part 1. Literature review. **Fertilizer Society of South Africa**, 1: 39 - 43.
- DOYLE, A.D. 1975. Influence of temperature and daylength on phenology of sunflowers in the field. **Australian Journal of Experimental Agriculture and Animal Husbandry**, 15: 88 - 92.
- DUNGAN, G.H. & KOEHLER, B. 1944. Age of seed corn in relation to seed

infection and yielding capacity. **Agronomy Journal**, 36: 436 - 443.

EICKER, R. 1979. Die ondersoek van die invloed van temperatuur en straling op die blomtyd van mielies te Potchefstroom. M.Sc. dissertation. University of the Orange Free State, Bloemfontein.

ELIOVSON, S. 1972. Namaqualand in flower. Macmillan, Johannesburg.

ELPHINSTONE, E.D. & REES, A.R. 1990. Temperature and development in *Iris x hollandica* during pre-planting storage. II. Floral initiation. **Journal of Horticultural Science**, 62: 185 - 192.

EVANS, L.T. 1975. The discovery and adaptive role of photoperiodism. In: EMLEU, J.M., EPSTEIN, H.T., HASTINGS, J.W., HOPKINS, J.W. & KLEIN, A.O. (eds.) Daylength and the flowering of plants. Benjamin, Menlo Park. pp. 1 - 14.

EVANS, P.M., LAWN, R.J. & WATKINSON, A.R. 1992. Predict the date of flowering in cultivars of subterranean clover (*Trifolium subterraneum* L.). **Australian Journal of Agriculture**, 43: 1547 - 1558.

EVENARI, M. & GUTTERMAN, Y. 1985. Desert plants. In HALEVY, A.H. (ed.) CRC Handbook of Flowering. Vol. 1. CRC Press, Florida. pp. 41 - 59.

EVENARI, M., SHANAN, L. & TADMOR, N. 1982. The Negev: Challenge of a Desert, 2nd edn. Harvard University, Cambridge.

EZCURRA, E. & RODRIGUES, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. **Journal of Arid Environments**, 10: 13 - 28.

FENNER, M. 1985. Seed ecology. Chapman & Hall, New York.

FOX, G.A. 1990a. Components of flowering time variation in a desert annual.

- Evolution**, 44: 1404 - 1423.
- FOX, G.A. 1990b. Drought and the evolution of flowering time in desert annuals. **American Journal of Botany**, 77: 1508 - 1518.
- GILMORE, E.C. & ROGERS, J.S. 1958. Heat Units as a method of measuring maturity in corn. **Agronomy Journal**, 50: 611 - 615.
- GOYNE, P.J., WOODRUFF, D.R. & CHURCHETT, J.D. 1977. Prediction of flowering in sunflowers. **Australian Journal of Experimental Agriculture and Animal Husbandry**, 17: 475 - 481.
- GUTTERMAN, Y. 1985. Flowering, seed development and the influences during seed maturation on seed germination of annual weeds. In: DUKE, S.D. (ed.) *Seed Physiology I*. Boca Raton, Florida. pp. 1 - 25.
- GUTTERMAN, Y. 1988. Day-neutral flowering in some desert *Blepharis* spp.. **Journal of Arid Environments**, 14: 157 - 167.
- HADLEY, P., ROBERTS, E.H., SUMMERFIELD, R.J. & MINCHIN, F.R. 1984. Effects of temperature and photoperiod on flowering in Soya bean (*Glycine max* (L.) Merrill): a quantitative model. **Annals of Botany**, 53: 669 - 681.
- HARI, P., KELLOMAKI, S. & VUOKKO, R. 1977. A dynamic approach to the analysis of daily height growth of plants. **Oikos**, 28: 234- 241.
- HARPER, J.L. 1977. *The population biology of plants*. Academic Press, London.
- HEWITT, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.
- HURD, R.G. 1969. Effect of tomato seed age on germination and seedling growth.

Annual Report of the Glasshouse and Crops Research Institute (Littlehampton),:
151 - 54.

IDSO, S.B., JACKSON, R.D. & REGINATO, R.J. 1978. Extending the "Degree day" concept of plant phenological development to include water stress effects. *Ecology*, 59: 431 - 433.

KALISZ, S. 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology*, 72: 575 - 585.

KATZ, Y.H. 1952. The relationship between heat unit accumulation and the planting and harvesting of canning peas. *Agronomy Journal*, 44: 74 - 78.

KLIKOFF, L.G. 1966. Competitive responses to moisture stress of a winter annual of the Sonoran Desert. *American Midland Naturalist*, 75: 383 - 391.

KREKULE, J. & HAJKOVA, L. 1972. The developmental pattern in a group of therophytes. II. Vernalization and photoperiodic induction. *Flora*, 161: 121 - 128.

LANG, A. 1963. Achievements, challenges and limitations of phytotrons. In: EVANS, L.T. (ed.) *Environmental control of plant growth*. New York. pp. 405 - 419.

LARCHER, W. 1983. *Physiological Plant Ecology*. Second edition. Springer-Verlag, New York.

LE HOUEROU, H.N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments*, 7: 213 - 247.

LE ROUX, A. & SCHELPE, E.A.C.L.E. 1988. *Namakwaland. Veldblomgids van Suid-Afrika 1*. Revised edition. Botanical Society of South Africa, Cape Town.

- LETTAU, K. 1965. A new method for predicting the blooming date of spring flowers. **Wisconsin Academy of Sciences Arts and Letters Transactions**, 54: 135 - 142.
- LEVITT, J. 1956. The hardiness of plants. Academic Press, New York.
- LEWIS, H. & WENT, F.W. 1946. Plant growth under controlled conditions. 4. Response of California annuals to photoperiod and temperature. **American Journal of Botany**, 32: 1 - 12.
- LIETH, H. 1974. Purposes of a phenology book. In: LIETH, H. (ed.) Phenology and seasonality modeling. Ecological Studies 8. Springer-Verlag, New York. pp. 3 - 22.
- LINDSEY, A.A. & NEWMAN, J.E. 1956. Use of official weather data in spring time temperature analysis of an Indian phenological record. **Ecology**, 37: 812 - 823.
- LOSS, S.P., PERRY, M.W. & ANDERSON, W.K. 1990. Flowering times of wheat in South-western Australia: a modelling approach. **Australian Journal of Agricultural Research**, 41: 213 - 223.
- LOWRY, W.P. 1970. Weather and life. An introduction to biometeorology. Academic Press, New York.
- MAJOR, D.J., JOHNSON, D.R. & LUEDDERS, V.D. 1975. Evaluation of eleven thermal unit methods for predicting soybean development. **Crop Science**, 5: 172 - 174.
- MAJOR, D.J., JOHNSON, D.R., TANNER, J.W. & ANDERSON, I.C. 1975. Effects of daylength and temperature on soybean development. **Crop Science**, 15: 174 - 179.
- MATTHEE, G.W. 1982. Koue-eenhede in die winterreëgebied van Suid- Afrika.

Government Printer, Pretoria.

- McGIFFEN, M.E.Jr. & MASIUNAS, J.B. 1992. Prediction of black and eastern black nightshade (*Solanum nigrum* and *S. ptycanthum*) growth using degree-days. *Weed Science*, 40: 86 - 89.
- MEDERSKI, H.J., MILLER, M.E. & WEAVER, C.R. 1973. Accumulated heat units for classifying corn hybrid maturity. *Agronomy Journal*, 65: 743 - 747.
- MORTENSEN, L.M. 1991. Effects of temperature, light and CO₂ level on growth and flowering of miniature roses. *Norwegian Journal of Agricultural Sciences*, 5: 295-300.
- MOTT, J.J. & CHOUARD, P. 1979. Flowering, seed formation and dispersal. In: PERRY, P.A. & GOODALL, D.W. (eds.) *Arid-land Ecosystems: Structure, Functioning and Management*. Cambridge University Press, Cambridge. pp. 627 - 645.
- MOTT, J.J. & McCOMB, A.J. 1975. The role of photoperiod and temperature control in the phenology of three annual species from an arid region of Western Australia. *Journal of Ecology*, 63: 633 - 641.
- MULROY, T.W. & RUNDEL, P.W. 1977. Annual plants: adaptations to desert environments. *BioScience*, 27: 109 - 114.
- NEWMAN, E.I. 1965. Factors affecting seed production of *Teesdalia nudicaulis*. II. Soil moisture in spring. *Journal of Ecology*, 53: 211 - 232.
- NEWMAN, J.E., BLAIR, B.O., DALE, R.F., SMITH, L.H., STIRM, W.L. & SCHAAL, L.A. 1968. Growing degree days. *Crops and Soils Magazine*, 21 : 9 - 12.
- NUTTONSON, M.Y. 1955. Wheat-climate relationships and the use of phenology in

ascertaining the thermal and photothermal requirements of wheat. American Institution for Crop Ecology, Washington, D.C..

ODUM, E.P. 1971. Fundamentals of Ecology. Saunders, Philadelphia.

PEMADASA, M.A. & LOVELL, P.H. 1974. Factors controlling the flowering time of some dune annuals. *Journal of Ecology*, 62: 869 - 880.

PENG, S., KRIEG, D.R. & HICKS, S.K. 1989. Cotton lint yield response to accumulated heat units and soil water supply. *Field Crops Research*, 19: 253 - 262.

PERRY, M.W., SIDDIQUE, K.H.M. & WALLACE, J.F. 1987. Predicting phenological development for Australian wheats. *Australian Journal of Agricultural Research*, 38: 809 - 819.

PETITT, F.L., ALLEN, J.C. & BARFIELD, C.S. 1991. Degree-day model for vegetable leafminer (Diptera: Agromyzidae) phenology. *Environmental Entomology*, 20: 1134 - 1140.

PILBEAM, C.J., HEBBLETHWAITE, P.D., RICKETTS, H.E. & HASSAN, O.A. 1990. Effects of autumn sowing dates on growth and yield of indeterminate and determinate field beans (*Vicia faba*). *Journal of Agricultural Science*, 114: 339 - 352.

PRIESTLEY, D.A. 1986. Seed aging: Implications for seed storage and persistence in the soil. Cornell University Press, New York.

PRIMACK, R.B. 1979. Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). *American Naturalist*, 114: 51 - 62.

RAJBHANDARY, K.L. 1971. Yield potentialities of aged wheat seed. *Nepalese*

Journal of Agriculture, 6: 165 - 69.

RATHCKE, B. & LACEY, E.P. 1985. Phenological patterns of terrestrial plants. **Annual Review of Ecology and Systematics**, 16: 179 - 214.

RICHARDSON, E.A., SEELEY, S.D. & WALKER, D.R. 1974. A model for estimating the completion of rest for "Redhaven" and "Elberta" peach trees. **Horticultural Science**, 9: 331 - 332.

RIDDELL, J.A. & GRIES, G.A. 1958. Development of spring wheat: III. Temperature of maturation and age of seeds as factors influencing their response to vernalization. **Agronomy Journal**, 50: 743 - 746.

ROBERTS, N.J. & MENARY, R.C. 1989. Environmental interaction between daylength, night temperature, and photon flux density on growth and flowering in *Boronia megastigma* Nees.. **Journal of Horticultural Science**, 64: 597-604.

ROBINSON, R.G. 1971. Sunflower phenology - year, variety, and date of planting effects on day and Growing Degree-day summations. **Crop Science**, 11: 635 - 638.

ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York.

ROZIIN, N.A.M.G. & VAN DER WERF, D.C. 1986. Effect of drought during different stages in the life-cycle on the growth and biomass allocation of two *Aira* species. **Journal of Ecology**, 74: 507 - 523.

SALISBURY, F.B. 1981. Responses to Photoperiod. In: LANGE, O.L., NOBEL, P.S., OSMOND, C.B. & ZIEGLER, H. (eds.) **Physiological Plant Ecology 1. Responses to the physical environment**. Springer- Verlag, New York. pp. 135 - 167.

- SARUKHAN, J. 1974. Studies in plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. II. Reproductive strategies and seed population dynamics. *Journal of Ecology*, 62: 151 - 177.
- SCHULZE, B.R. 1965. Climate of South Africa. Part 8. WB 28. Government Printer, Pretoria.
- SEDDIGH, M., JOLLIFF, G.D. & ORF, J.H. 1989. Night temperature effects on soybean phenology. *Crop Science*, 29: 400 - 406.
- SOLBRIG, O.T., BARBOUR, M.A., CROSS, J., GOLDSTEIN, G., LOWE, C.H., MORELLO, J. & YANG, T.W. 1977. The strategies and community patterns of desert plants. In: ORIAN, G.H. & SOLBRIG, O.T. (eds.) *Convergent evolution in warm deserts*. Hutchinson & Ross, Stroudsburg. pp. 68 - 106.
- SPARKS, D. 1989. Predicting nut maturity of the pecan from heat units. *Horticultural Science*, 24: 454 - 455.
- STEYN, H.M. 1993. Namaqualand ephemerals: phenology and thermal units. M.Sc. dissertation. University of Pretoria, Pretoria.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. a). The influence of temperature and sowing date on the phenology of two Namaqualand ephemeral species under controlled conditions.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. b). The influence of sowing date on the phenology of five Namaqualand ephemeral species.
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. c). The influence of water stress on the phenology of five Namaqualand ephemeral species.

- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. d). The effect of achene age on the phenology of a Namaqualand ephemeral species: *Dimorphotheca sinuata* DC..
- STEYN, H.M., VAN ROOYEN, N., VAN ROOYEN, M.W. & THERON, G.K. (In prep. e). The prediction of phenological stages in five Namaqualand ephemeral species using thermal unit indices.
- TAYLOR, F.G. 1969. Phenological records of vascular plants at Oak Ridge, Tennessee. Oak Ridge National Laboratory, Tennessee.
- TEVIS, L. Jr. 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, 39: 681 - 688.
- TEVIS, L. Jr. 1958b. A population of desert ephemerals germinated by less than one inch of rain. *Ecology*, 39: 688 - 694.
- VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis. University of Pretoria, Pretoria.
- VAN ROOYEN, M.W., GROBBELAAR, N. & THERON, G.K. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. 2. The therophyte population. *Journal of South African Botany*, 45: 433 - 452.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1991. The ephemerals of Namaqualand: effects of photoperiod, temperature and moisture stress on development and flowering of three species. *Journal of Arid Environments*, 20: 15 - 29.
- VAN ROOYEN, M.W., GROBBELAAR, N., THERON, G.K. & VAN ROOYEN, N. 1992. The ephemerals of Namaqualand: effect of germination date on

development of three species. **Journal of Arid Environments**, 22: 51 - 66.

VAN ROOYEN, M.W., THERON, G.K. & GROBBELAAR, N. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 1. General observations. **Journal of South African Botany**, 45: 279 - 293.

VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeerspesies. M.Sc. dissertation. University of Pretoria, Pretoria.

WANG, J.Y. 1960. A critique of the heat unit approach to plant response studies. **Ecology**, 41: 785 - 790.

WATKINSON, A.R. 1982. Factors affecting the density response of *Vulpia fasciculata*. **Journal of Ecology**, 70: 149 - 161.

WENT, F.W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. **Ecology**, 39: 695 - 704.

WENT, F.W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. **Ecology**, 30: 1 - 13.

WENT, F.W. 1953. The effect of temperature on plant growth. **Annual reviews of Plant Physiology**, 4: 347 - 358.

WENT, F.W. & WESTERGAARD, M. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. **Ecology**, 30: 26 - 28.

WERGER, M.J.A. 1986. The Karoo and southern Kalahari. In: EVENARI, M., NOY-MEIR, I. & GOODALL, D.W. (eds.) *Hot Deserts and Arid Shrublands*. Elsevier Science Publishers, Amsterdam. pp. 283 - 358.

WILSON, J.W. 1967. Effects of seasonal variation in radiation and temperature on net assimilation and growth rates in an arid climate. *Annals of Botany*, 31: 41-57.