POPULATION AND PHYSIOLOGICAL STUDIES OF SELECTED GEOPHYTIC SPECIES OF LOWLAND COASTAL FYNBOS IN THE SOUTHWESTERN CAPE

BY

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I, Cornelius Rivers, declare **Population and Physiological Studies of Selected Geophytic Species of Lowland Coastal Fynbos in the Southwestern Cape** is my own work and that all the sources I have used or qouted have been indicated and acknowledged by means of complete references.

DEDICATION

This thesis is dedicated with humble respect to my **father** (Cornelius Ruiters: 10 -04 - 1934 to 02 - 11 - 1987), my **mother** (Sarah Elizabeth Ruiters) and **sister** (Marjory Elizabeth Kleynhans) for their support and encouragement throughout my academic career and in giving me the most precious gifts that a child could ask, viz. knowledge and wisdom. This work is a small gesture of thanks and love.

REWARDS OF WISDOM

Listen to what is wise and try to understand it. Yes, beg for knowledge, plead for insight. Look for it as hard as you would for silver or some hidden treasure.

Proverbs 2: 2 - 4

PREFACE

Geophytes represent a much neglected segment of the fynbos flora. The taxonomic resource of these plants is not well defined and will remain so until researchers pay more attention to the below-ground parts of plants when conducting vegetation surveys or describing species. Such life-forms indeed are a common and major component of this fire-prone mediterranean-terrestrial biome of Southern Africa, viz. fynbos, where they appear to assume importance, in terms of biomass, in their overall survival and stability as herbaceous "winter annuals" in the understorey.

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My family, especially my **Mother** and **Sister (Marjory)** for their support and enthusiasm.

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SUMMARY

Population and physiological studies were conducted in coastal fynbos in the South-western Cape. Minor ecophysiological studies were also conducted such as the soil moisture content and pH. Two species, viz. **Haemanthus pubescens** L.f. subspecies **pubescens** and **Sparaxis grandiflora** (de la Roche) Ker. subspecies **fimbriata** (Lam.) Goldbl. were selected for the project. **H. pubescens** subsp. **pubescens** is a bulbous geophyte belonging to the family Amaryllidaceae and **S. grandiflora** subsp. **fimbriata** a cormous geophyte a member of the family Iridaceae. The species were classified either as a perennial geophyte with hysteranthous leaves or an annual geophyte with synanthous leaves. Two sites were demarcated on the farm Klein Welmoed at Penhill and near the Blackheath industrial area for the project.

The following population studies were conducted:

1. Age-structure - species with herbaceous above-ground parts develop repeated subterranean markers which offer accurate clues to an individual's age.
2. Age-states - individuals of **H. pubescens** subsp. **pubescens** was not characterized by their age alone, but by their state of development, which has been shown

to be of greater usefulness for a number of species.

3. Seasonal ontogeny, phenology and demography - influence of environmental conditions on the functional performances of the species, i.e. the seasonal growth cycle changes.
4. Germination and seedling establishment - strategies of seed germination and mechanisms in the burial of the storage organs were examined.
5. Life-history and aspects of adaptation to the fire-regime in fynbos.
6. Additional population studies for **S. grandiflora** subsp. **fimbriata** were conducted, such as correlations between parent- and daughter corm and leaf-number, depth of burial versus corm diameter, age versus corm diameter and influence of corm size on floral iniation.

The physiological studies have entitled the following:

1. Seasonal nutrient concentrations of the species constituent parts.
2. Seasonal biomass and resource allocation.
3. Seasonal production, partitioning and efficiency of mobilization of dry matter, mineral nutrients and organic substances.

INTRODUCTION

The habit of bearing fleshy underground storage organs, classified as geophytes (Raunkiaer 1934), features quite prominently in the Fynbos flora both in abundance of species and in the apparent success of indivdual species in this particular biome. Plants exhibiting these features occur most commonly in those regions of the Southwestern Cape where a strong seasonal rainfall pattern is combined with periodic drought (Specht & Moll 1983) and soils of low nutrient status (Day 1983). In these situations a plant is likely to have a competitive advantage if it possesses underground storage organs, such as corms, bulbs, rhizomes, stem tubers or root tubers, which permit it to survive unfavourable conditions, and to carry substantial fractions of its nutrient resources from one growing season to the next (Raunkiaer 1934; Pate & Dixon 1982). Geophytes are also classified as "indirect flowering plants" because of the interpolation of a "rest period" into their life-history, and the fact that floral initiation usually occurs in this period of reduced vegetative growth (Grainger 1939).

Most geophytes in the South-western Cape are monocotyledons belonging to the families Amaryllidaceae, Liliaceae, Iridaceae

and Orchidaceae (Goldblatt 1978; Perry **et al.** 1979: Bond & Goldblatt 1984). There are several dicotyledons, but the petaloid geophytic monocotyledons account for 16% of the Cape flora, and two-thirds of the monocotyledons of this flora (Goldblatt 1978).

Since the inception of the Fynbos Biome Project in the late 1970's which greatly enhanced the knowledge of disturbance dynamics of communities and the mineral nutrient status of the biome (Kruger 1978), only minor research projects have focussed on geophyte communities. Although studies on the physiology, population structure and composition of geophytes have been well documented elsewhere (Barkman 1980a & b; Dafni **et al.** 1981a & b; Pate & Dixon 1982; Keeley 1986; Fitter & Setters 1988), very little information exists on geophyte population dynamics and physiology in South Africa. Past studies on geophyte populations have been largely limited to descriptive accounts of fire ecology (Bean 1962; Le Maitre 1984) and qualitative accounts on flowering rhythms (Kruger 1981). Although the phenology in the Fynbos Biome has been reviewed by Pierce (1984), only a small paragraph was devoted to geophytes. The neglect of this guild in descriptive studies in the Fynbos Biome can be attributed to the following reasons:

1. They do not comprise a large fraction of above-ground plant biomass,
2. They are only visible for a part of the year.
3. Although they will flower in the absence of fire obvious

blooms of many only occur after a fire.

A study of the geophytic guild in the Fynbos Biome was undertaken with the emphasizes on two major fields, viz. population biology and seasonal physiology. The species selected for the study were **Haemanthus pubescens** L.f. subspecies **pubescens** (Amaryllidaceae), a bulbous geophyte, and **Sparaxis grandiflora** (de la Roche) Ker. subspecies **fimbriata** (Lam.) Goldbl. (Iridaceae), a cormous geophyte. Both subspecies are endemic to the Southwestern Cape. Of the 21 **Haemanthus** species, belonging to the family Amaryllidaceae, 15 are endemic to the winter rainfall region of Southern Africa (Snijman 1984). The 15 **Sparaxis** species, belonging to the family Iridaceae, are exclusively found in the Southwestern Cape (Goldblatt 1969).

The reasons for concentrating on the two species were:

1. They are widely distributed and abundant on the coastal fynbos flats and are endemic to the South-western Cape.
2. H. **pubescens** subsp. **pubescens** is restricted to marine and aeoline sand (Snijman, 1984) and is thus easy to collect.
3. S. **grandiflora** subsp. **fimbriata** occurs on fairly damp clay flats and hills around Cape Town and it was possible to select and demarcate a suitable study site.
4. Suitable sites for destructive sampling were available at the farm Klein Welmoed at Lyndoch, and at the Blackheath

industrial area. The chances of these sites being transformed from natural vegetation to housing are high.

5. Coastal lowland sites are rapidly being taken up for industrial and urban development, so it may soon become difficult to study coastal lowland species under natural conditions.

The study was therefore initiated to provide information on the population structure, dynamics and physiology of the two geophytes in the Southwestern Cape. The key objectives identified were:

1. To document and compare the population structure of the two species.
2. To understand seasonal allocation of nutrient resources. This provided an opportunity to compare the nutrient dynamics of geophytes in two different localities with each other and with published data for sclerophyllous plant communities.
3. To determine resource allocation in the different aged leaf-bases of **H. pubescens** subsp. **pubescens**. This section was not originally planned to form part of the thesis, because it was essentially designed for the testing of the methods. After thorough consideration it was included as a chapter to form an integral part of the thesis.

The work has been demarcated into chapters for their dissemination to current journals, with each chapter having a detailed record of the research carried out and relevant literature both local and abroad.

In **Chapter 1**, the results detail the ontogeny and demography of a **H. pubescens** L.f. subspecies **pubescens** population on coastal lowland fynbos. The identification of seasonal ontogeny and phenology, age structure, age states, life history and aspects of the fire regime were the key components of the study and provided a framework for later comparisons (Chapter 3 & 5).

In **Chapter 2**, aspects of population biology of **Sparaxis grandiflora** (de la Roche) subsp. **fimbriata** (Lam.) Goldbl. were investigated and findings are discussed in the light of the species ontogeny, seasonal phenology and biomass, and population parameters.

The results presented in **Chapter 3** provide a comparison of seasonal allocation in flowering (mature) and non-flowering (juvenile) plants representing different stages in population development for **H. pubescens** subsp. **pubescens**. A similar seasonal nutrient allocation study was carried out for **S. grandiflora** subsp. **fimbriata** and the findings are presented in **Chapter 4**.

The final chapter is an analytical account of resource allocation to different aged leaf-bases. In **Chapter 5,** analytical studies conducted on 23 year old bulbs are presented in an attempt to assess allocation patterns, thus providing information of relevance to objective three.

In the conclusion, a brief synopsis of the major findings of the study is given, key points are addressed and areas for future research are identified.

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CHAPTER 1

ONTOGENETIC AND DEMOGRAPHIC STUDIES OF A *HAEMANTHUS PUBESCENS* L.f. SUBSP. *PUBESCENS* POPULATION ON LOWLAND COASTAL FYNBOS IN THE SOUTH-WESTERN CAPE

CONTENTS

1.1 INTRODUCTION

Although the effects of disturbance in the fynbos biome are manifested at the community level it is necessary to conduct studies at the population level to understand the community dynamics (Manders & Cunliffe 1987), and these studies should include an examination of life history strategies. Most population studies in the fynbos biome have concerned taxa belonging to life forms other than geophytes. While the taxonomy of the geophytic guild has been fairly well documented surprisingly little ecological attention has been devoted to the group despite the fact that geophytes comprise some 16% of the Cape Flora; a contribution much greater than in other meditteranean climatic regions of the world (Goldblatt 1978). Even in phytosociological descriptions less emphasis has been placed on the geophytes than other life forms because " they are not visible throughout the year" or "they are not dominant in terms of biomass except perhaps immediately after a fire" (see Macdonald 1985; Boucher 1987).

The fact that the adaptation of subterranean life forms is considered to be primarily concerned with the avoidance of drought (Raunkiaer 1934; Pate & Dixon 1982) is probably the reason for the

lack of detailed studies relating to the fire regime. Fire is however the major disturbance factor in the biome (Cowling 1987) and it follows that the majority of species should have life histories which enable persistence through fire disturbance, and the geophytic guild should, therefore, be no exception. Most references to geophytes and the fire regime are restricted to a few species where qualitative findings indicate that some geophytes exhibit mass flowering after a fire (e.g. Bean 1962; Le Maitre 1984;) while others produce seed only in the first few weeks after a fire (e.g. Levyns 1966). Geophytes are generally expected to be resilient to relatively frequent fires (Keeley 1986) and are capable of extended dormancy in the absence of fire and there is no evidence to suggest they die out (Taylor & Kruger 1978).

This paper is concerned with aspects of the life history of a common hysteranthous geophyte (**Haemanthus pubescens** L.f. subsp. **pubescens**) on a Lowland Fynbos site. This species was chosen for investigation because of its abundance on sandy substrates and its fairly robust nature which made excavation of the bulb a relatively easy task. In addition, the production sequence of leaves, leaf bases and reproductive organs suggested that it would be relatively easy to categorise individual plants in terms of their age states and actual age. Age itself may be a poor indicator of size or reproductive activity (Harper 1977) while the use of age states (Rabotnov 1950) accounts for some of the limitations of calendar age (Harper 1977). The determination of actual age and age states was important in this study because one of the aims was to examine

aspects of the life history of the species in relation to the suggested frequency of the fire regime in lowland fynbos.

1.2 METHODS

The ontogeny and seasonal development of the plant was studied from destructive sampling of 20 individuals of varying sizes at monthly intervals over a period of one year. Plants were selected randomly in a 1 ha site at Lynedoch ($34^{o}65'S$ and $18^{o}46'E$) where the density ranged from one individual per $10m^2$ up to 122 individuals per $10m^2$. Two hundred and forty individuals were marked by means of steel rods so that the bulbs could easily be located when the plants were in their dormant stage. All plants were brought back to the laboratory where they were carefully cleaned and cut through their median longitudinal section. Leaf bases were counted to estimate the age of the plants. Preliminary examinations of over three hundred plants from the field and experimental beds indicated that the plants produce one leaf per annum (therefore one leaf base) in the pre-reproductive phase and two leaves per annum in the reproductive phase. It was thus possible to count the leaf bases prior to the reproductive stage and consider the number obtained to be equivalent to the actual age of the plant. For plants that had reached the reproductive phase, age was determined by counting the leaf bases from the base up to nine (the calender age when over 99% of the test sample first flowered) and then adding this to half the remaining number of leaf bases (to account for the two leaf bases produced per year) to give the calender age (see Figure 1.1).

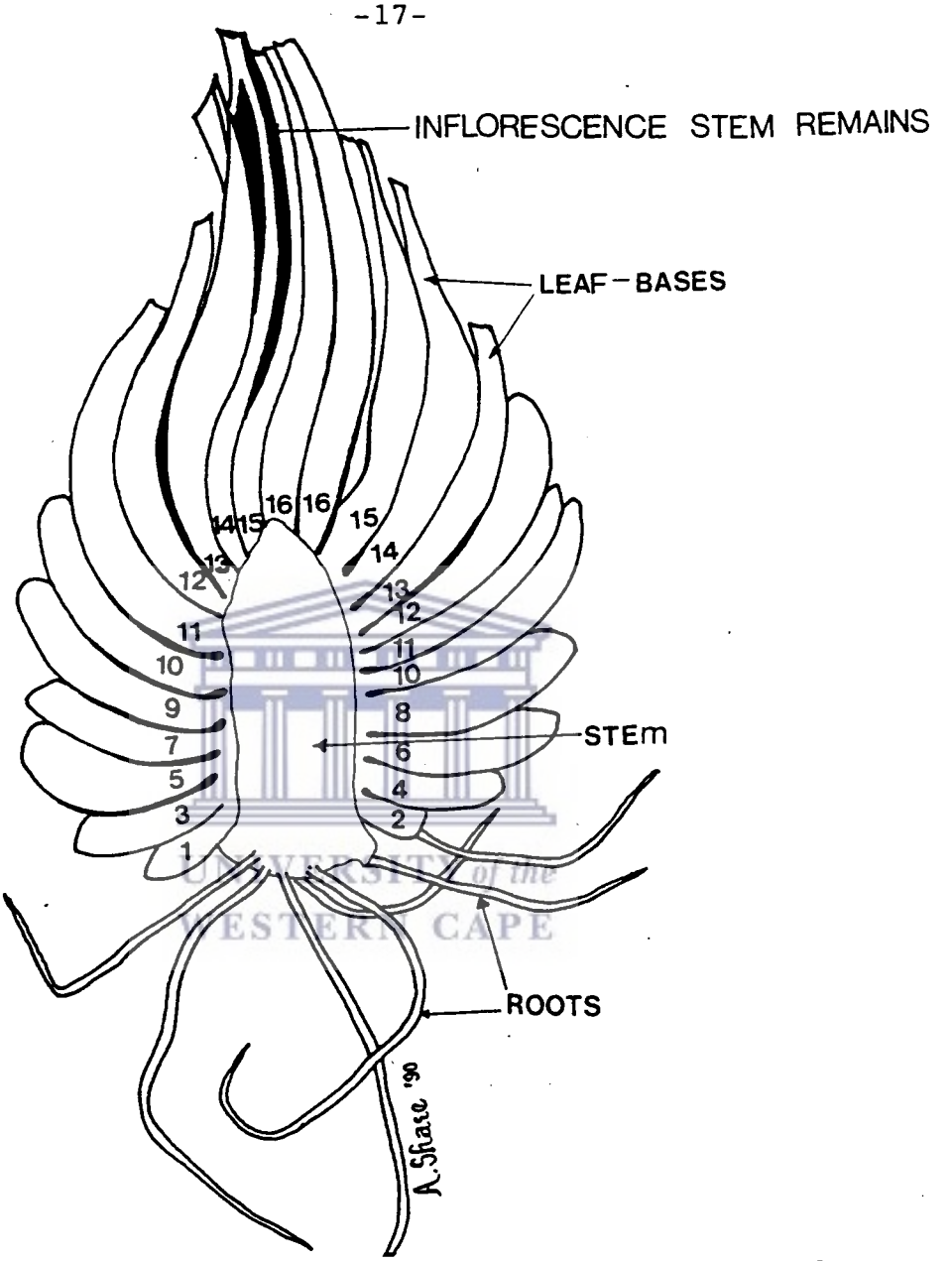


Figure 1.1:Longitudinal section of a 16 year old **H. pubescens** subsp. **pubescens** bulb. Numbers indicating how the plant was aged.

Snijman (1984) reported that occasionaly three leaves are produced per annum in the reproductive phase, but in the study site only two individuals were ever seen in that condition which represented less than 0,005% of the population. In addition to ageing the plants, flowering pattern was determined by searching for the remains of repoductive tissue between the axils of the leaf bases. Seasonal phenological trends were examined by considering not only the above-ground appearance and disappearance of plant parts but also by examining the "dormant bulb" for signs of leaf and flower initiation, and root rejuvenation. The dry mass of the individual bulbs was also determined because it is known that many bulbous geophytes only flower after reaching a "critical bulb mass" (Rees 1969, 1972).

In addition to the 240 plants used for the ontogeny and seasonal study a further 163 plants were selected randomly at the site and used for the determination of age states and estimation of the age structure of the population. Finally, because reproductive allocation is such a vital component of the life history two additional samples were taken from the population. The first of these involved the analysis of 92 flowering individuals from the 1989 season to examine the trends in the number of flowers produced per inflorescence and the fresh weight of individual flowers per age class. Counts of the number of flowers per inflorescence give some idea of the potential magnitude of sexual reproduction (Barkman 1980a) even though the proportion of ovules fertilized varies substantially from year to year and from site to site (Barkman

1980a & b). The second data set consisted of 288 samples from the reproductive age state which were analyzed in terms of the flowering pattern over two years by tracing the remains of the reproductive parts in the axils of the leaf-bases. Unfortunately it was not possible to examine the flowering pattern for a longer period as it was difficult in most cases to determine whether the plants had flowered three or more years previously.

1.3 RESULTS AND DISCUSSION

1.3.1. Seasonal ontogeny and phenology

Figures 1.2 - 1.4 show the seasonal development and phenology of the seed, seedling, pre-reproductive and reproductive stages. The phenology is discussed in terms of calendar months during the period of observation but it must be expected that the actual timing of the events would change depending on the particular conditions of any one season. In the event of fruit (berry) development the peduncle lengthens and finally bends over under the weight of the mature berries (Snijman 1984; personal observation). The large berries (10 to 22 mm in diameter) become detached on the soil surface. During the months of April and May the berries become dehydrated and the seeds (1-5) are exposed and germinate immediately.

The seeds germinate on the surface of the soil and the apical part of the cotyledon remains within the seed, where it

Figure 1.2: Seed germination and seedling establishment patterns of a **Haemanthus pubescens subsp. pubescens** population at Klein Welmoed, Lynedoch.

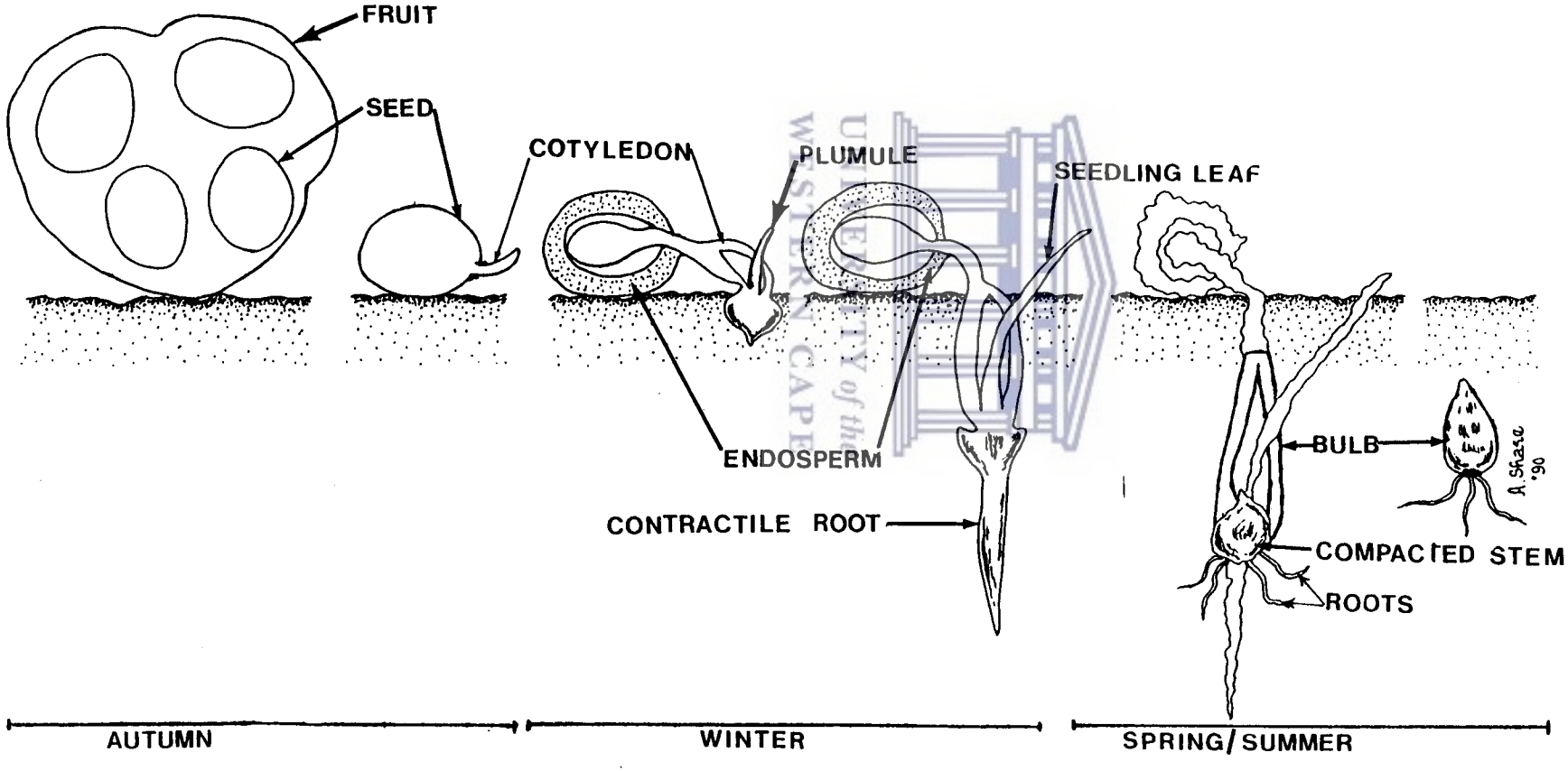


Figure 1.3 Phenological patterns of plants ‹10 years of age of a **Haemanthus pubescens** subsp. **pubescens** population at Klein Welmoed, Lynedoch.

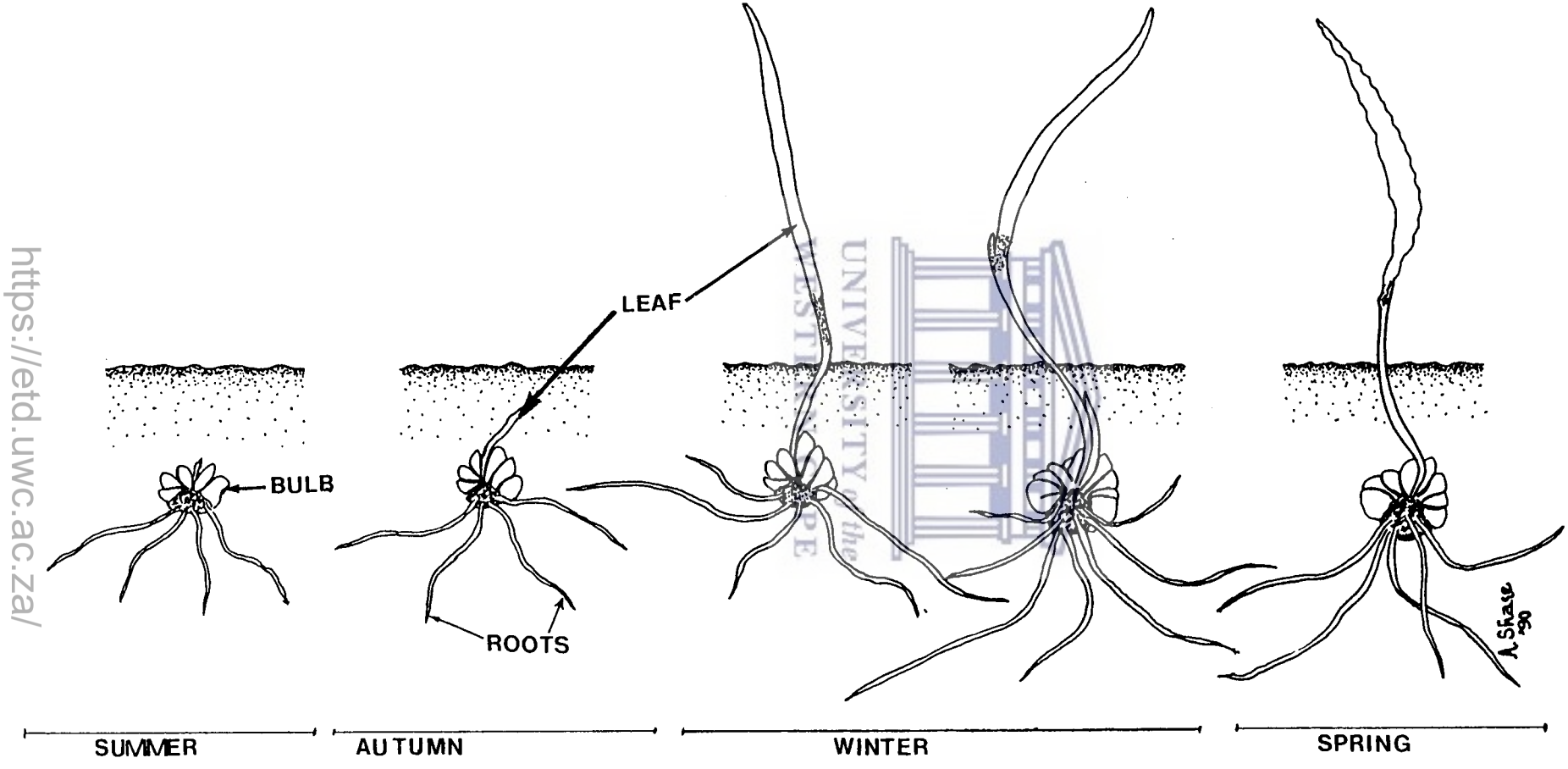
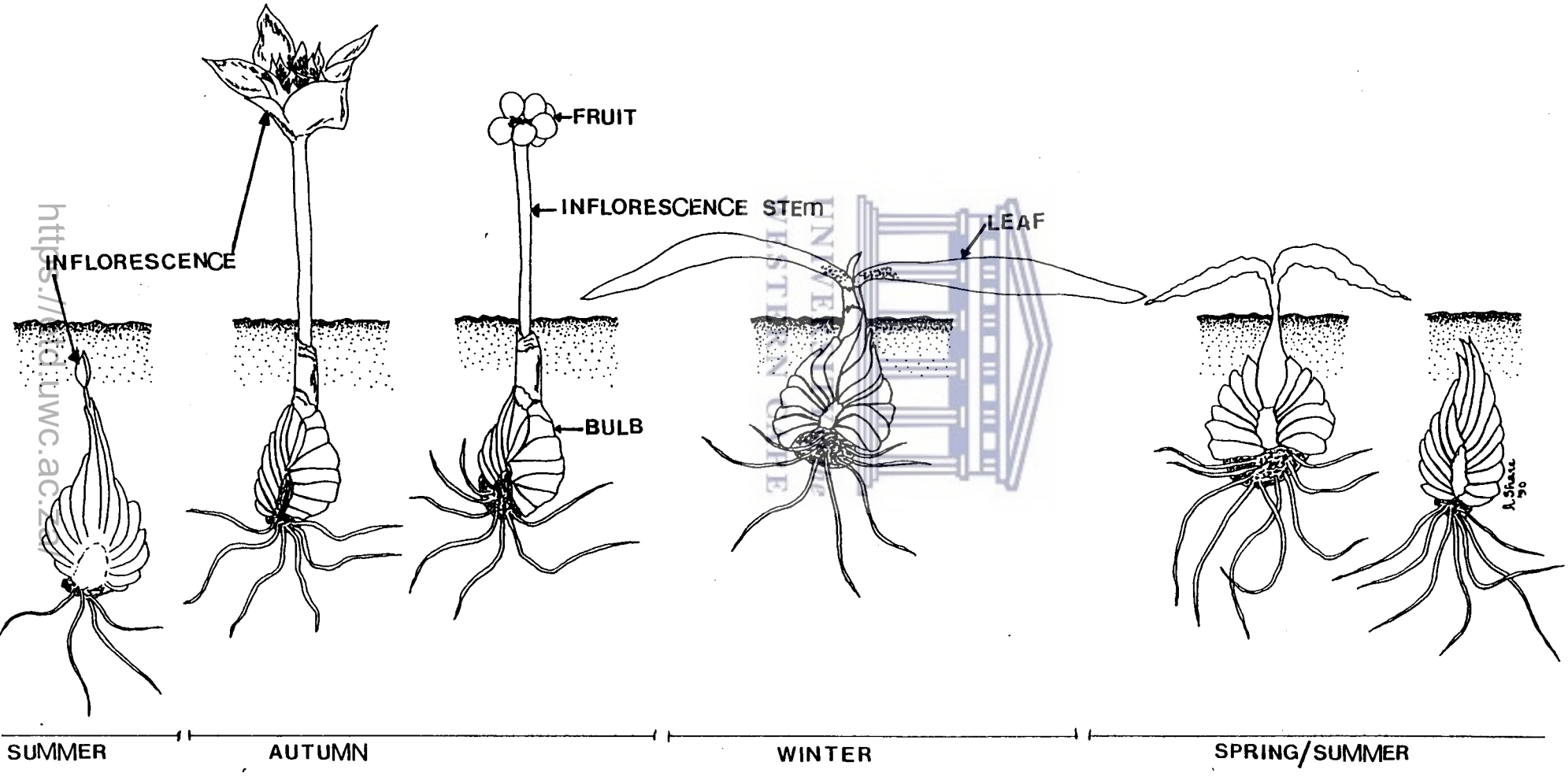


Figure 1.4 Phenological patterns of plants >9 years of age of a **Haemanthus pubescens** subsp. **pubescens** population at Klein Welmoed, Lynedoch.



presumably digests and absorbs the reserves of the endosperm. The radicle and plumule of the seedling are pushed downwards into the rooting medium by the extension of the proximal end of the cotyledonary sheath. During this process the radicle end of the embryo remains as a compacted inverted cone of tissue , and it secretes mucilage which facilitates the downward penetration of the seedling shoot and root into the soil. While the cotyledon expands or swells, the first leaf bursts through the cotyledonary sheath and emerges above the soil. Through the photosynthetic activity of the leaf, reserves are laid down in the first leaf-base of the young bulb. The young bulb is buried 5-10 cm below the surface by the onset of the dormant period. The seedling exhibits contractile properties by means of a deeply-penetrating tap-root which forms during the first year of growth. The contraction which usually precedes the dormancy period pulls the young bulb much deeper into the substrate than the depth which was previously reached through the down-growth of the cotyledonary sheath. Bulbs of young plants become progressively more deeply buried in subsequent seasons due to the contractile activity of the generations of adventitious roots which develop from the stem stock of the bulb. A mature plant may have its bulb buried up to 25 cm below the soil surface.

Leaves of **Haemanthus pubescens** L.f. subsp. **pubescens** are ephemeral structures which are formed annually and they last from approximately April to September whereafter growth ceases

in response to the onset of the dry season. During the pre-reproductive stage the plant develops one leaf per year and the subsequent leaf bases are arranged alternately on the stem stock. Leaf initiation and adventitious root development takes place during March. The leaves emerge above the soil after the first autumn showers during mid-April or early May. Rapid development follows during the month of May and leaf maturity is reached during the early half of June.

The phenological events of leaf development in reproductive plants are the same as described above, except that two leaves are formed on the stem stock of the bulb annually.

The inflorescence begins development at the start of the leaf die-back period and is strongly developed by the beginning of the dormant period. The plants experience slow inflorescence development until the peduncle emerges during late-February. After emergence above the soil the peduncle lengthens rapidly, reaches its maximum length within 3-4 days, and the inflorescence opens. This delayed inflorescence development is typical of the **Urginea**-type geophyte classified by Dafni **et al.** (1981a) which is probably a mechanism to avoid pollinator competition (Dafni **et al.** 1981a).

Simultaneously with the emergence of the inflorescence above the soil the development of new adventitious roots takes place and leaf development commences. Fruit formation starts during the

latter part of March and fruit setting occurs during April. After the lengthening and bending of the penduncle, the fruits become detached on the soil surface and thereafter the peduncle becomes dehydrated and eventually withers away. Only a portion of the peduncle is retained between the leaf-bases.

1.3.2 Age structure

The oldest individual in the sample was 24 years of age with the majority of individuals in the sample being between ten and seventeen years old (Fig. 1.5). This suggests that recruitment to the population was relatively high between 1973 and 1979 and has been considerably reduced since 1980, the reasons for this difference being unknown. However, the alien, **Acacia saligna** has taken over the area in this period. The relatively low numbers found in the ages greater than seventeen years could reflect low recruitment during the years 1965 to 1972, or be a consequence of increased mortality in the older age-classes. There is obviously a wide variation in recruitment from year to year and this could be ascribed to variations in relative annual success of flowering and/or seed production, and germination which may be coupled to particular moisture regimes (Hadley & Levin 1967; Harper 1977). The effects of predation on seed, seedling and adult numbers has not been determined and would obviously also effect the recruitment pattern. The varied recruitment pattern also shows no relationship to two known fire events at the site (Fig. 1.5). In the case of a fire event in

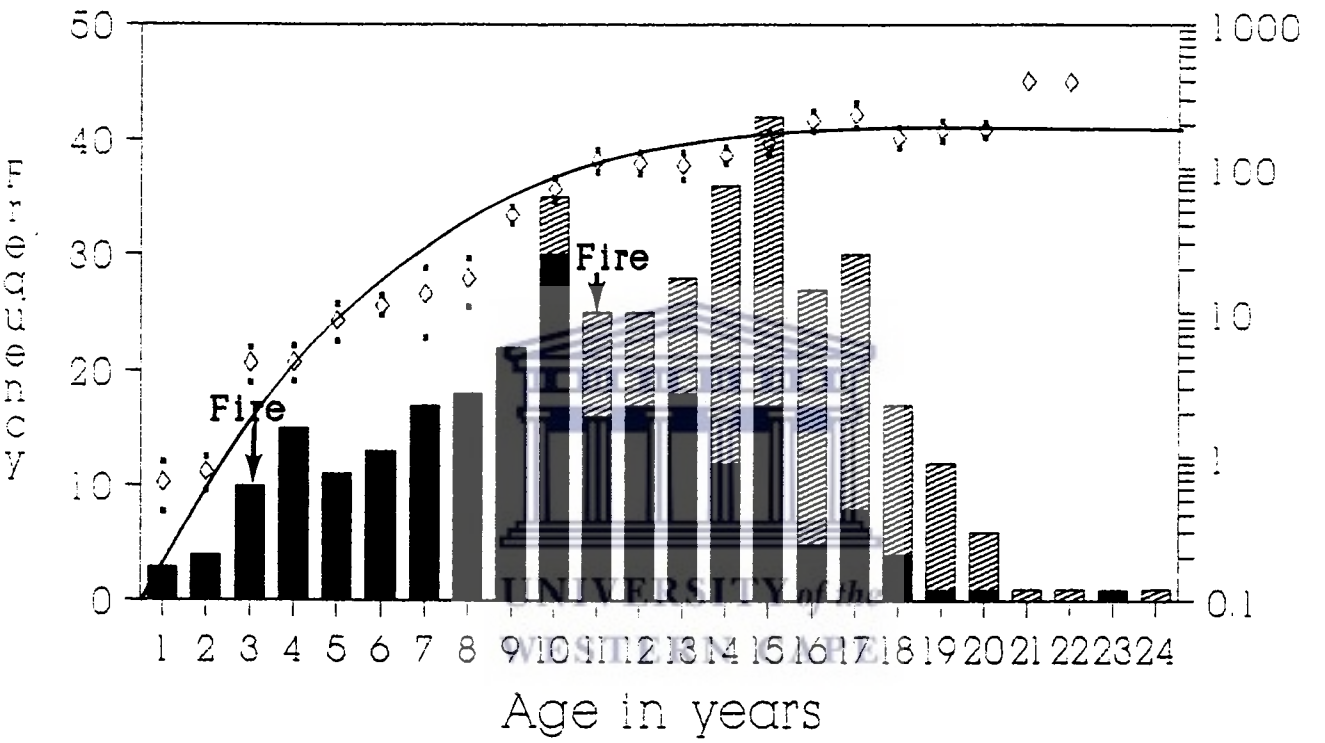


Figure 1.5: Age distribution, flowering and bulb size (log scale) of a **H. pubescens** subsp. **pubescens** population in the 1988/89 season.

the summer of 1977/78 the recruitment was greater in the flowering period (1980) immediately before the fire while in the case of the fire event in the summer of 1985/86 the recruitment in the first flowering season after the fire was lower than the previous year but higher than the second post-fire flowering season. It is possible that there was a greater percentage of flowering and recruitment within the population immediately after the fires but if so this is not reflected in the population profile as analyzed in 1988.

1.3.3 Age States

Of particular interest in Figure 1.5 is the pattern of flowering. None of the individuals younger than ten years of age flowered in 1988, which suggests that the juvenile period for this population of **H. pubescens** subsp. **pubescens** spans nine years. This is confirmed by the graph in Figure 1.5 which indicates that the size of the bulb increased fairly rapidly up to approximately ten years and thereafter showed minimal increase. It is well documented that individuals of most geophytes need to reach a critical minimum mass before they flower (Rees 1969, 1972; Dafni **et al.** 1981b) and this was calculated at 69.1 ± 13.9 g for **Haemanthus**. The flowering pattern was used as a basis for a preliminary classification of the sample population into age states. The age class one to nine years is classified as juvenile, the age class 10-13 years

as young reproductive where less than 50% of the individuals in any age flowered and the age class 14 years and greater as mature reproductive as flowering percentage was greater than 50%. This classification was refined by examining the fresh weight of flowers and the number of inflorescences produced per individual for the different aged plants and these results are presented in Figure 1.6 & 1.7.

Plants in the young reproductive age-class produced a relatively low number of flowers per inflorescence (23.84 ± 6.95) and a relatively low flower fresh weight (2.77 ± 0.67 g) (Figure 1.6 & 1.7). This pattern provides further support for classifying the age-group 10-13 years as young reproductive. The majority of plants in this age-class had thus not yet built up a sufficient "shortage fund" (Dafni et al. 1981b) from which resources could be used to sustain maximum reproductive development.

The highest number of flowers per inflorescence (41.075 ± 4.547) were produced by individuals in the 14-17 year age-group (Fig. 1.6). This pattern was also true for the average fresh weight of flowers (5.271 ± 1.61 g) and is shown in Figure 1.7.

There was great variation in plants older than 17 years in terms of the number of flowers produced per inflorescence and their fresh weight. Plants in this group showed a surprisingly low

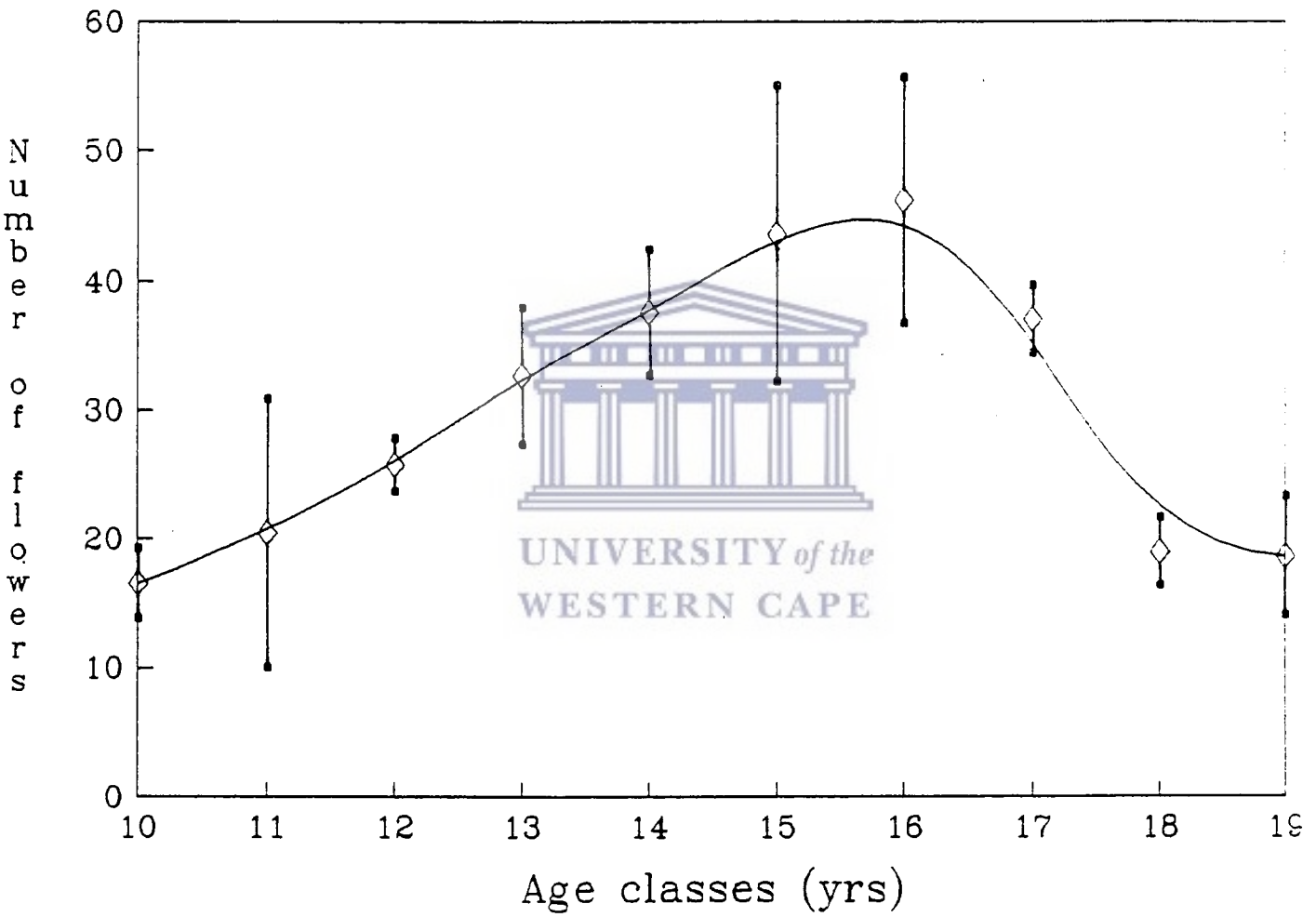


Figure 1.6: Number of flowers produced per inflorescence per age-class of a **H. pubescens** subsp. **pubescens** population at Klein Welmoed, Lynedoch.

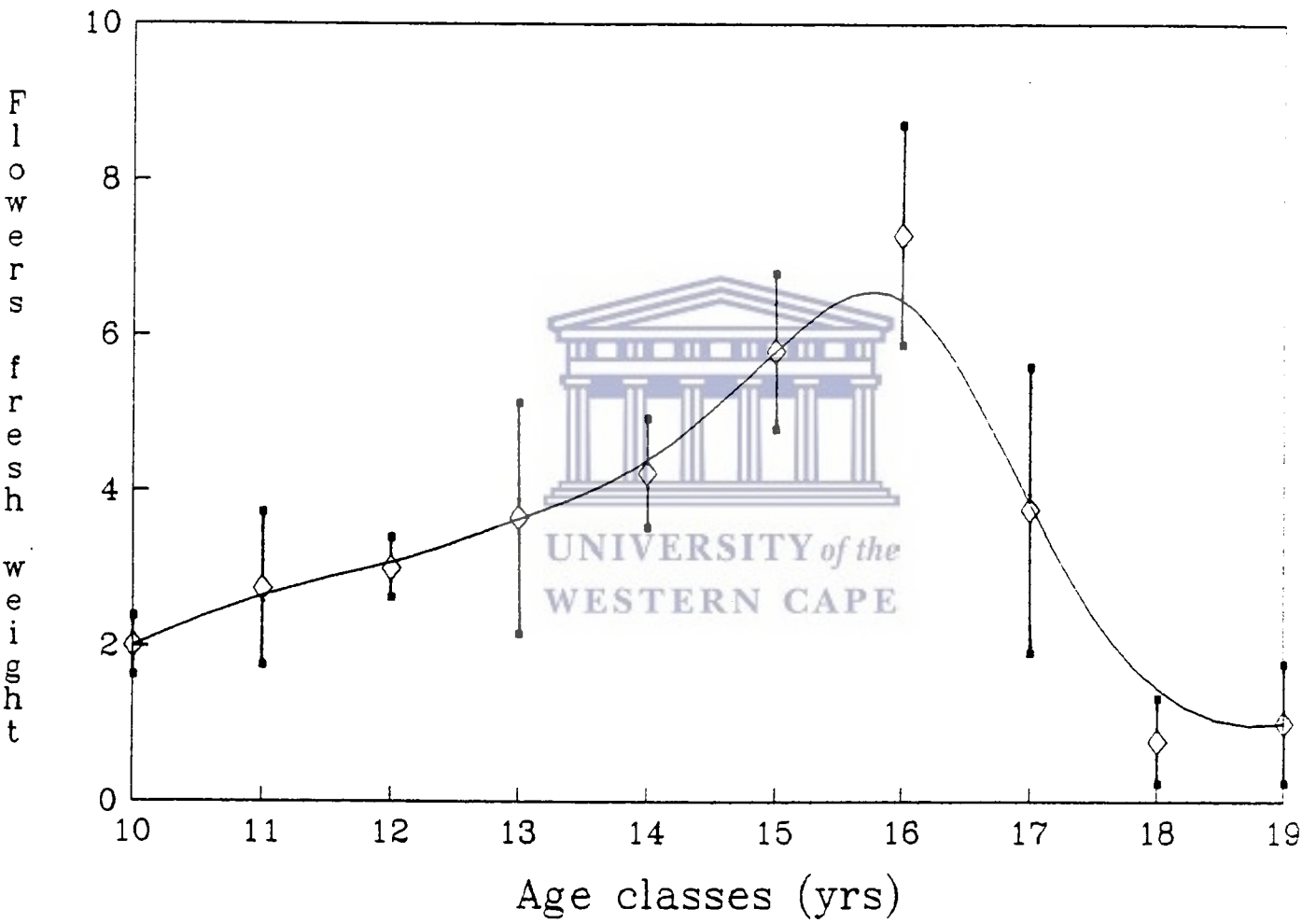


Figure 1.7: Fresh weight (g) of flowers per age-class of a **H. pubescens** subsp. **pubescens** population at Klein Welmoed, Lynedoch.

reproductive capacity as measured by the number of flowers per inflorescence (23.84 ± 6.951) and flower fresh weight (2.77 ± 0.67 g). The above findings enabled the mature reproductive age state to be sub-divided into two categories. The first comprised individuals in the 14-17 year old group for which we retained the term mature reproductive and the second for the group older than 17 years which we refered to as old reproductive. In the latter group the low reproductive allocation (Fig. 1.6 & 1.7) and small numbers of plants recorded (Fig. 1.5) could suggest that plants were entering a subsenile phase. The classification of H. **pubescens** subsp. **pubescens** into age states is summarized in Table 1.1.

The flowering patterns in the various age states over a two year period are presented in Table 1.2. The young reproductive age state (10 - 13 years) is confirmed by this analysis because in both 1987 and 1988 <50 % of individuals flowered and 43% did not flower in any of the two years. It is thus likely that a high percentage of individuals in this age state have not yet reached their critical biomass for flowering and some revert to the juvenile stage after flowering for the first time. The mature reproductive age-state is also confirmed because in both 1987 and 1988 >50 % of individuals flowered. A larger proportion of individuals flowered in both years and only 30% failed to flower in any of the two years. The variation in the flowering pattern

Table 1.1: Life history periods, age states and approximate age for a **H. pubescens** L.f. subsp. **pubescens** population.

Life History Period (After Gatsuk **et al.** 1980)	**Age State**	**Approximate age** (Years)	**Symbol** (After Rabotnov 1985)
I. Latent	(1) Fruit & Seed	0.00 - 0.25	Se
II. Pre-reproductive	(2) Seedling	0.25 - 1	pl
	(3) Juvenile	1 - 9	j
III. Reproductive	(4) Young	10 - 13	g_1
	(5) Mature	14 - 17	g_2
	(6) Old	>17	g_3
IV. Post-reproductive	(7) Subsenile	Not determined	s
	(8) Senile	Not determined	s

Se = seed; pl = seedling; j = juvenile; g_1 = subperiod of generative and vegetative vigour of individuals; g_2 = subperiod of maximal generative and vegetative vigour of individuals (subperiod of life culmination); g_3 = subperiod of senescence; s = senile.

Table 1.2: Flowering pattern in the different age-states for a **H. pubescens** L.f. subsp. **pubescens** for two years (1987 and 1988).

Age State	Percentage Flowering				Total(No of plants)
	1987 Only	1988 Only	1987 & 1988 Both years	None	
Young Reproductive	8.97	20.5	26.92	43.5	78
Mature Reproductive	2.02	16.16	51.52	30.3	99
Old Reproductive	Not sufficient data.				

can probably be explained by insufficient allocation to the "shortage fund" after the plants have reached their critical biomass (Dafni **et al.** 1981b). Dafni **et al.** (1981b) suggested that once the critical biomass has been reached the plants will flower every year and suggested further that in moderate and predictable habitats (like the Mediterranean-type climate of the South-western Cape) the "shortage fund" may be quite small. This means that there are fewer chances for successive bad years and that the "fund" needs only to be sufficient to support years of shortage, so that flowering may be expected to occur every year. This idea is partly supported because plants in the mature- and old reproductive age-states had built-up a large storage organ, with a large "shortage fund," which is reflected by the relatively high percentage of flowering (Table 1.2). Young reproductive plants on the other hand had smaller storage organs (Fig. 1.5) which presumably indicated a small "shortage fund." The "shortage fund" can thus be depleted in the event of floral and leaf development and the plants revert back to their juvenile-stage and must build-up the "shortage fund" once again. Thus flowering will not occur in the subsequent years unless a sufficient "shortage fund" has been built-up and this is reflected by the results in Table 1.2 and Figure 1.5. Even in the mature reproductive age class a relatively high number (30%) did not flower in either of the two years. This does not necessarily mean an inadequate "shortage fund" but could be the

result of other inhibiting influences (eg. temperature, rainfall).

1.3.4. Life History and Aspects of the Fire Regime

The hypothesis that fynbos is adapted to fire intervals between 10 and 30 years is supported by a number of life history studies (Van Wilgen 1987). Juvenile periods of fynbos species seldom exceed eight years (Kruger & Bigalke 1984) and maximum reproductive effort is reached at approximately 15 years (Bond 1980; Boucher 1981; Moll & Gubb 1981; Cowling 1987). Futhermore it is suggested that fire intervals of >30 years could result in the senescence of some **Protea** species (Bond 1980) and in the case of **Staavia dodii** and **Orothamnus zeyheri** between 20 and 30 years (Moll & Gubb 1981; Boucher 1981).

Most of the life history studies have concentrated on mountain fynbos where the present mean fire frequency is suggested to be 15 years (Van Wilgen 1987). Hoffman **et al.** (1987) suggest that a longer fire-return interval is the norm in lowland fynbos communities. Their findings were based largely on species richness where the richness did not drop significantly in the oldest post-fire age sample (20 years) and geophytes in fact showed an increase in richness in the 20 year old sample.

Although **H. pubescens** L.f. subsp. **pubescens** in common with

other geophytes is able to survive fires because of the presence of the underground storage organ, aspects of its life history tend to support the findings of life history patterns of other species in relation to the fire frequency.

The juvenile period for **H. pubescens** L.f. subsp. **pubescens** spans nine years which fits the suggested juvenile period mentioned above. The species reaches maturity at ±16 years which indicates synchronization with the fire frequency suggested for fynbos. Although the population shows low numbers for individuals >17 years where reproductive allocation is also low this does necessarily mean senescence and it is possible that plants will survive for many years.

Furthermore this geophyte did not show massive recruitment in early post-fire periods as evident in some mountain fynbos geophytic species (eg. **Watsonia pyrimadata, Oxalis purpurea**) following an early autumn burn (Kruger & Bigalke 1984; Le Maitre 1987). Findings by Hoffman **et al.** (1987) also illustrated that geophytes on coastal lowland fynbos do not exhibit massive recruitment in early post-fire periods.

1.4 CONCLUSION

Aspects of the life history of **H. pubescens** L.f. subsp. **pubescens** was successfully determined by using age and age states. The juvenile period (<9 years) is similar to many fynbos species and reproductive maturity is reached at about 16 years which suggests that the life history of the species is well synchronized with the suggested fire frequency for lowland fynbos and a minimum critical bulb biomass is a prerequisite for flowering. Massive recruitment does not appear to take place immediately after a fire event; a strategy which would not be essential as the plant can survive fires easily in its dormant state. The life history pattern of the species is thus well synchronized with fire frequency but appears not to be dependent on fire for recruitment. Seed germination and seedling establishment occur immediately after seed setting in autumn which can be regarded as a strategy to avoid the adverse environment dry summer environment. The fruit and contained seeds are soft and fragile and would thus easily be dessicated during the hot summer months.

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CHAPTER 2

ONTOGENETIC AND POPULATION BIOLOGY STUDIES FOR *SPARAXIS GRANDIFLORA* (da la Roche) Ker. SUBSPECIES *FIMBRIATA* (Lam.) Goldbl.

CONTENTS

2.1 INTRODUCTION

Sparaxis grandiflora (da La Roche) Ker. subspecies **fimbriata** (Lam.) Goldblatt, is a cormous member of the family Iridaceae, endemic to the Southwestern Cape (Goldblatt 1969) where it is confined to fairly damp clay flats and hills in the Cape Town vicinity (Goldblatt 1969). It is a synanthous geophyte (Dafni **et al** 1981) which possesses an annual storage organ.

In this region with its strongly seasonal rainfall pattern combined with periodic drought and soils of low nutrient status (Day 1983), a plant is likely to be at a competitive advantage if it possesses an underground storage organ which permits it to survive unfavourable conditions, and allows the plant to carry a substantial fraction of its nutrient resource from one growing season to the next.

Knowledge of longevity, population age structure, and generation span is lacking for most geophytic species in their natural habitat for the fynbos, and with the increasing disruption of indigenous populations by sprawling industrialization and urbanization it may

become even more difficult to study the species under natural conditions. This paper examines the life form, phenology and reproductive behaviour and these are examined in relation to factors such as depth of burial, size and age of the corms, the number of leaves produced per corm, and the number of individuals per age-class.

2.2 MATERIALS AND METHODS

2.2.1 Study Site and Sampling Methods

The study site was located near the Blackheath industrial area ($34^{o}62'E$ and $18^{o}43'S$). This site is the remains of a natural habitat of **Sparaxis grandiflora** subsp. **fimbriata** disrupted as a result of sprawling industrial development in the area (Fig. 2.1 & 2.2). This micro-habitat is a flat area on the Cape flats which is waterlogged during the winter growing season (Fig. 2.3).

A 144 m^2 block was demarcated in the study area. This was subdivided into 12 quadrats of 12 m^2 each and sampling was done monthly using random permutations (Moses & Oakes 1963). Five sods (20 x 24 cm) were removed each month (by destructive digging) from the quadrat and the plants in the sod were carefully seperated in the laboratory for analysis. Five soil samples were taken to determine the soil moisture content as a percentage of the soil dry mass, dried at 80 ^{o}C until a constant mass was reached.

Figure 2.1: Natural habitat of **S. grandiflora** subsp. **fimbriata** near Blackheath, in the Southwestern Cape, during the dry, hot summer months.

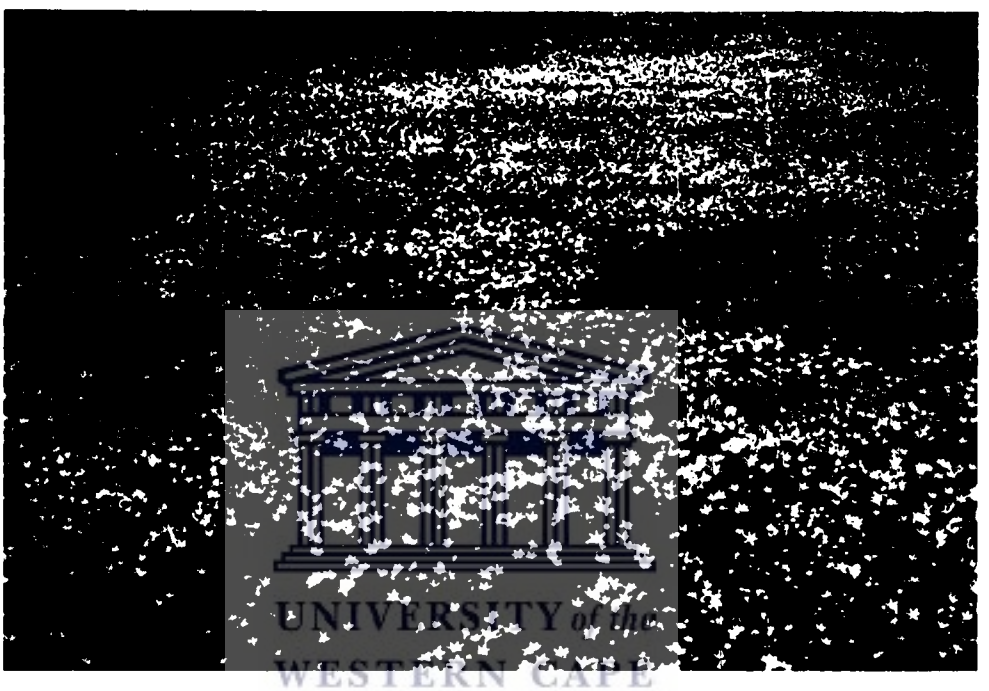


Figure 2.2: Natural habitat of **S. grandiflora** subsp. **fimbriata** near Blackheath, in the Southwestern Cape, during spring with the species in flower.

Figure 2.3: Natural habitat of **S. grandiflora** subsp. **fimbriata** near Blackheath, in the Southwestern Cape, during the winter growing season.

2.2.2 Plant Material and Harvesting of Plants

A total of 2880 plants were excavated from the site during the study period over the 1988/89 season. Records were taken of leaf number, width and length, number of cormlets produced per plant, number and length of stems, number of flowers and fruits produced per plant, diameter and depth of burial of corms, and the number of epidermal tunics around the corms. This latter feature is of great relevance to the ageing of plants because these epidermal tunics are highly resistant to decay (Dixon & Pate 1978), and the parent corm is replaced in situ by the daughter corm, which suggests that tunic counts could be used as an indicator of plant age. Hence with time a series of concentric layers build up around a corm; the outermost of these layers being the epidermal remnant from the season of recruitment (Pate & Dixon 1982) as a new daughter corm and, the innermost layer being the epidermis of the previous-season's corm in which the present-season's replacement corm is currently developing. Tunic number was taken as a direct measurement of plant age in years, year one in the life of a plant was defined as a 12-month period following its appearance as a corm from seed or cormlet.

The count of 18 tunics, the result of in situ replacement of the parent corm, indicated the resistance of these dead layers of tissue to decay, and how long certain plants can continue to replace their corms in situ under natural conditions. It seemed reasonable to assume, therefore, when examining populations whose members proved to

be much smaller and possessed fewer epidermal tunics than mentioned above, that errors due to loss of outer tunics by decay would be relatively unimportant. Goldblatt (1985) stated that although the actual age of **Geissorhiza** was difficult to determined they found plants with up to 12 annually produced corm tunic layers. In **Hesperantha** corms are covered by specialized layers of tunics which are woody in texture and a single layer is produced annually (Goldblatt 1982).

The sampled plants were seperated into their constituent organs (see Fig. 2.4), viz.: parent corms, replacement or daughter corms, roots, stem, leaves, flowers, and fruit and seed. The respective plant organs of each sod were pooled and dry weight was then determined.

Investigations were made of the ontogeny, phenology of growth and reproduction, age structure and age states of the species. The monthly collections were carried out to follow seasonal changes in dry matter content of plant parts and to examine the filling of the season's new corms with dry matter and mineral elements.

2.3 RESULTS AND DISCUSSION

2.3.1 Ontogeny

This species has a form of germination in which the cotyledon extends greatly in length both above and below the ground after germination (Fig. 2.5). The plumule (P) is then pulled underground by the

Figure 2.4: The geophytic life form and morphology of the constituent plant parts of **S. grandiflora** subsp. **fimbriata**.

combined action of the downgrowth of the basal region of this cotyledon and the contractile activity of the primary root (R, CR) (Figure 2.5). The latter is the only root to form in the first season of growth. One to three leaves (L) are formed in the first season. By the time of dormancy (mid-November) at or near the end of the first growing season, stem tissue has swollen below the apex to form a diminutive corm (CO) and all the other parts of the seedling, including the contractile root (CR), have withered and died.

2.3.2 Seasonal Phenology and Biomass

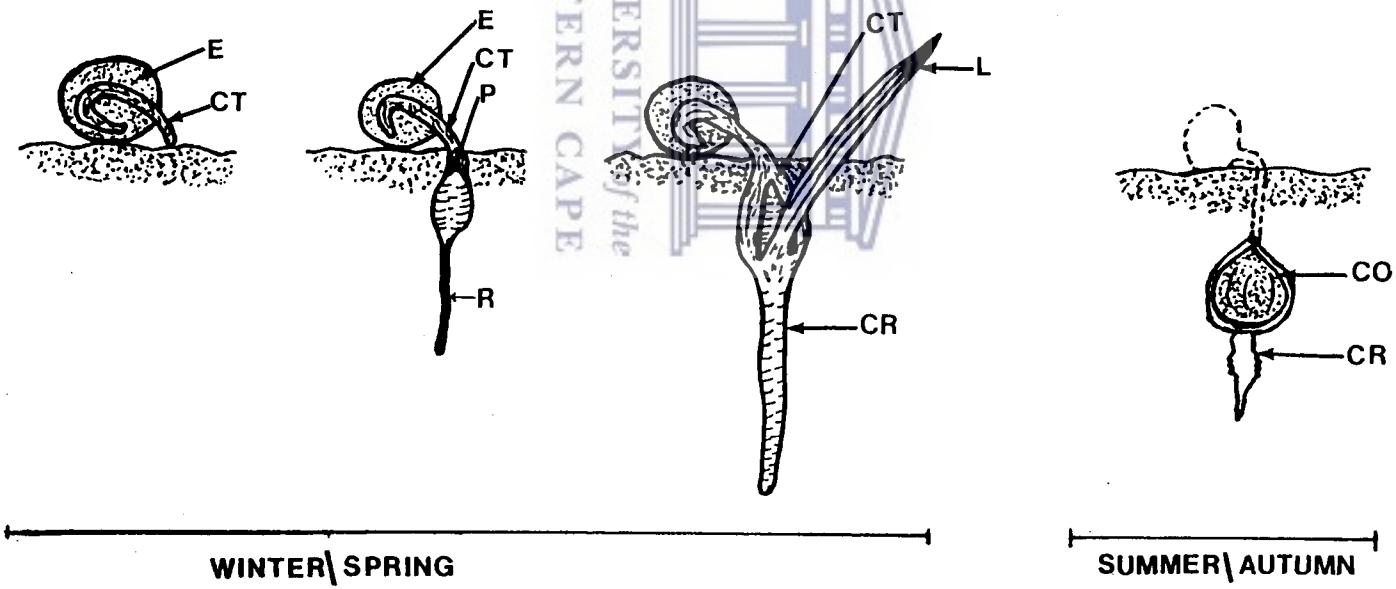
Measurements of the seasonal phenology of plant organs proved to be highly variable within populations and between seasons (eg. Harper 1977) and were therefore regarded as unreliable estimators of vigour and age of the population.

Seasonal changes in distribution of dry matter is illustrated in Figure 2.6. Corm dormancy spanned the five hot dry months (Fig. 2.7). The parent corm broke dormancy during late March, coincident probably with lower soil and air temperatures during autumn but before the soil was fully drenched by the autumn rains.

Data for the mean monthly soil moisture content of the study site (Fig. 2.8) illustrates the essentially Mediterranean-type climate with which the species is typically associated.

Figure 2.5: Ontogenic patterns in the development and burial of the underground storage organ in **S. grandiflora** subsp. **fimbriata**. The timing of the principal events is related to a calender year.

E = Endosperm, CT = Cotyledon, R = Radicle, L = Seedling Leaf, CR = Contractile Root, P = Plumule, CO = Corm.



The leaves grew to the soil surface in early April and had expanded by mid-April above the soil surface. Development of new adventitious roots took place in association with leaf development. Establishment of the above-ground plant parts in the early season of growth involved expenditure of dry matter from the previous season's storage organ (parent corm) (Fig. 2.6). By June a substantial portion of the parent corm dry matter had been exhausted. This species initially produces two to three leaves during autumn but as the season progresses more leaves were produced to a maximum of twelve in some plants. The leaves remain green and active until senescence in October (Fig. 2.6 & 2.7). Allocation of dry matter to the daughter corm and reproductive structures was the major assignment from June to November. The newly-formed photosynthate must have been the major source of filling the daughter corm, since the above-ground vegetative and reproductive parts did not show net losses of dry matter over the period when maximum accumulation of dry matter was made to the daughter corm. The parent corm initially showed a slow decline in dry matter during the second half of the growing season, dropped abruptly from September to October and was totally exhausted by November. By August the dry matter of the daughter corm had become greater than the initial dry matter of the parent corm. Maximum dry matter allocation in the plant was achieved during September to November.

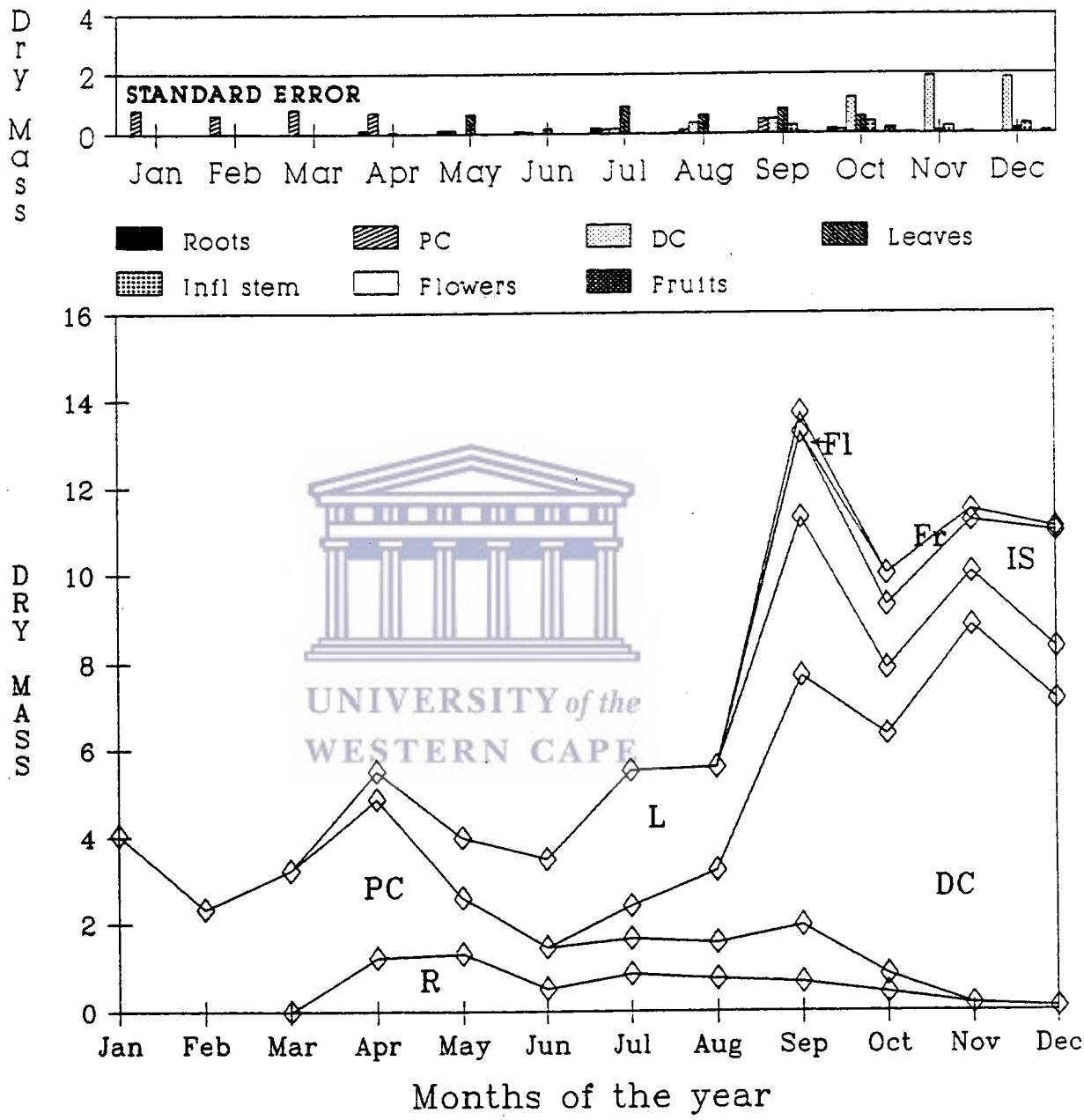
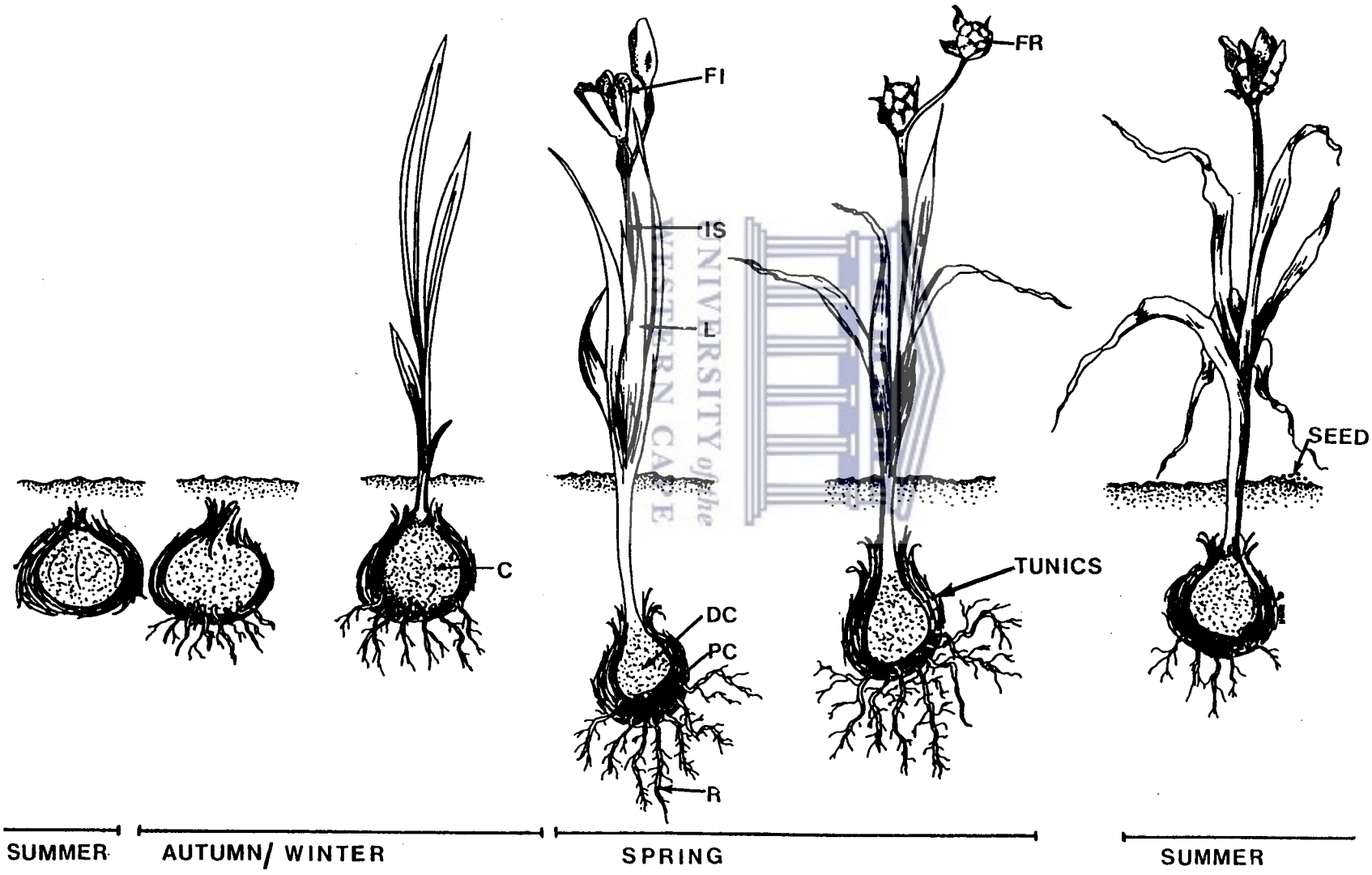


Figure 2.6: Seasonal dry weight (g) changes in plant parts of a **S. grandiflora** subsp. **fimbriata** population during a calendar year in a natural habitat at Blackheath. C = corm, DC = daughter corm, Fl = flowers, Fr = Fruit, IS = Inflorescence stem, L = leaves, PC = parent corm, R = adventitious roots.

Figure 2.7: Seasonal phenology and growth cycle of a **S. grandiflora** subsp. **fimbriata** population in a natural habitat at Blackheath. See Fig. 2.6 for symbols.



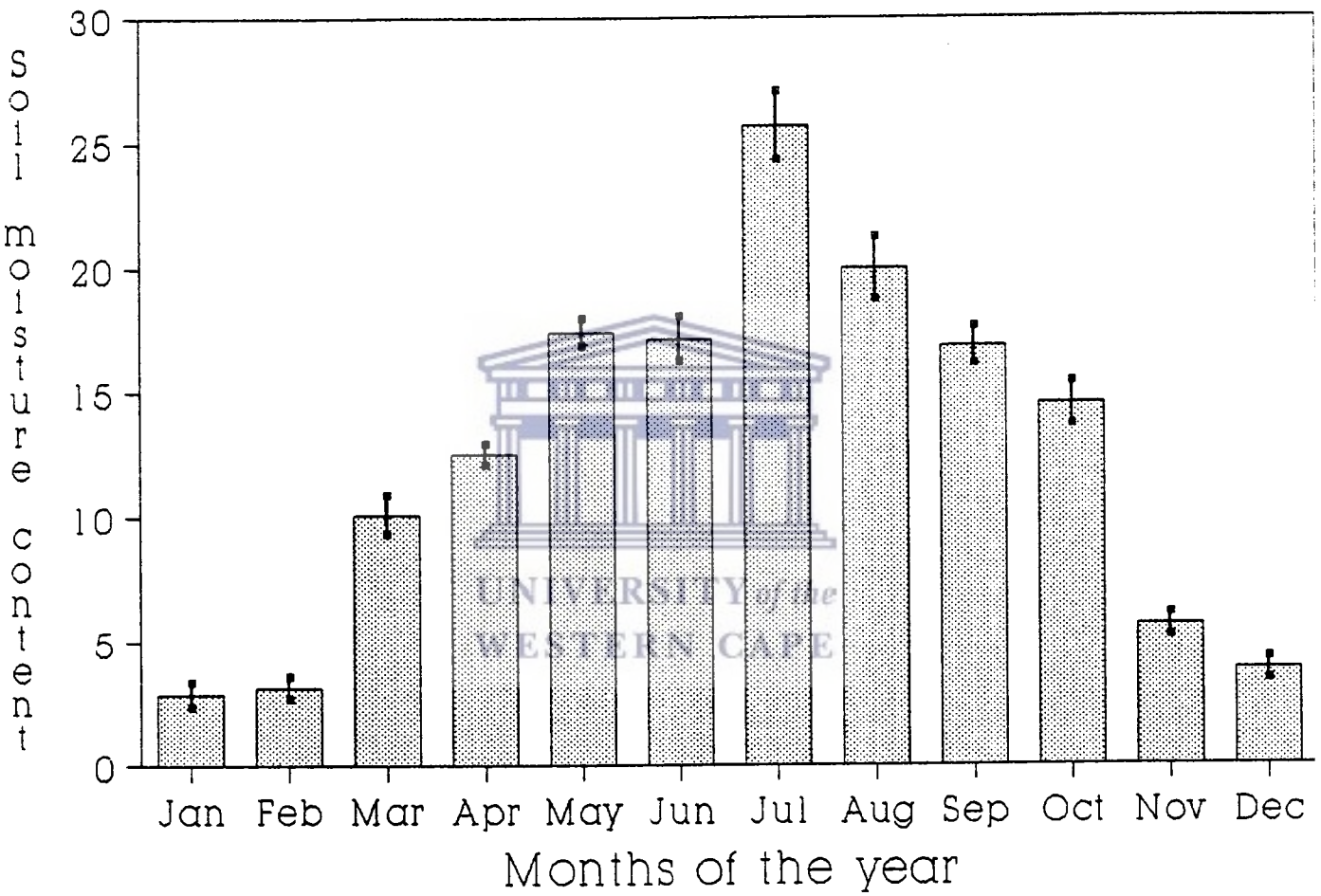


Figure 2.8: Mean monthly soil moisture content (%) for the study site at Blackheath.

This species, which flowers from August to September, partitioned some of its dry matter to flower and fruit formation while still in the process of filling the daughter corm. Thus competition exists for photosynthate between young fruit and the daughter corm and it might well be an important factor affecting a season's seed production and the underground reserves of the species (Pate & Dixon 1982). This would happen in October (Fig. 2.6).

The above-ground vegetative and reproductive plant parts senesce by mid-November and in December the only living plant part remaining is the daughter corm which becomes the parent corm of the new-season. On entering dormancy the combined season's production of dry matter for seed and daughter corm accounts for some 78.0% of the total dry matter production. Only small amounts were incorporated into seed production (2.3%) in comparison with the amount laid down in the storage organ (75.7%) (Fig. 2.6). The filling of the seeds might have been implemented by mobilization of dry matter from the vegetative parts and flowers since these organs lost substantial greater amounts of dry matter during the senescence period than was required for growth of seeds (Fig. 2.6 & 2.7). Thus this species employed a highly efficient mechanism of retrieving dry matter for its daughter corm and seeds.

2.3.3 Population Parameters

A series of instructive relationships emerged between depth of burial of the plant's corm, size of daughter corm, number of leaves

produced, age of plants and flowering of plants in the distinct age classes in the season of study.

The depth at which the storage organ of the species was buried was found to be shallow, a burial highly charateristic of compact clay soils. The following conclusions were drawn:

1. Corms were restricted to 1.5 - 8 cm below the soil surface. Approximately sixty percent (59.5%) of the plants were concentrated in the depth zone 1.5 to 2.5 cm, and 37.7% occurred in the 3-4 cm zone. Only 2.8% occurred in the 5-8 cm depth zone of the soil profile. The corms in the soil profile are exposed to dessication during summer and to waterlogging or drenching during winter (Fig. 2.1 & 2.3; 2.8).

2. The organic layer of the soil profile extends to 3cm and 80% of the sampled plants were located within this depth. Since the species does not possess an extensive root system it is important for the plants' roots to exploit the organic layer for nutrient absorption.

Applying the data from tunic counts the folowing conclusions were made from the presumed age distribution (Figure 2.9):

1. The maximum age found was 18 years.
2. The shape of the age distribution histogram suggests that 18 years may be near the maximum age attained on the Blackheath study site.

3. The histogram shows strong skewness to the left which indicates that the bulk of the population (86.1%) was found in the 1-7 year classes.
4. Most of the variation in size of the adjacent year classes is probably due to variations in initial germination and seedling survival success; both stages are sensitive to the moisture regime (Kerster 1968).

From the data on presumed age versus depth of burial of corms in the soil profile the following conclusions were made:

1. A progressive increase in the mean depth per age-class for the first seven years was found.
2. An even distribution for depth of burial was attained for the 8-16 year age classes (3.4 cm).
3. About one-quarter (27.8%) of the population's plants were located within the range of the mean depth of the 8 - 16 year old plants.
4. The lower mean depth of burial which is exemplified in the 18 year age-class was due to a low number of plants sampled in the respective age-class.
5. There was some evidence that older plants were located in the 4-8 cm zone range, but otherwise age has apparently little effect on the mean depth of corm burial and mean age per corm.
6. From the data presented it can be suggested that plants in this population reached their final depth after 8 years.

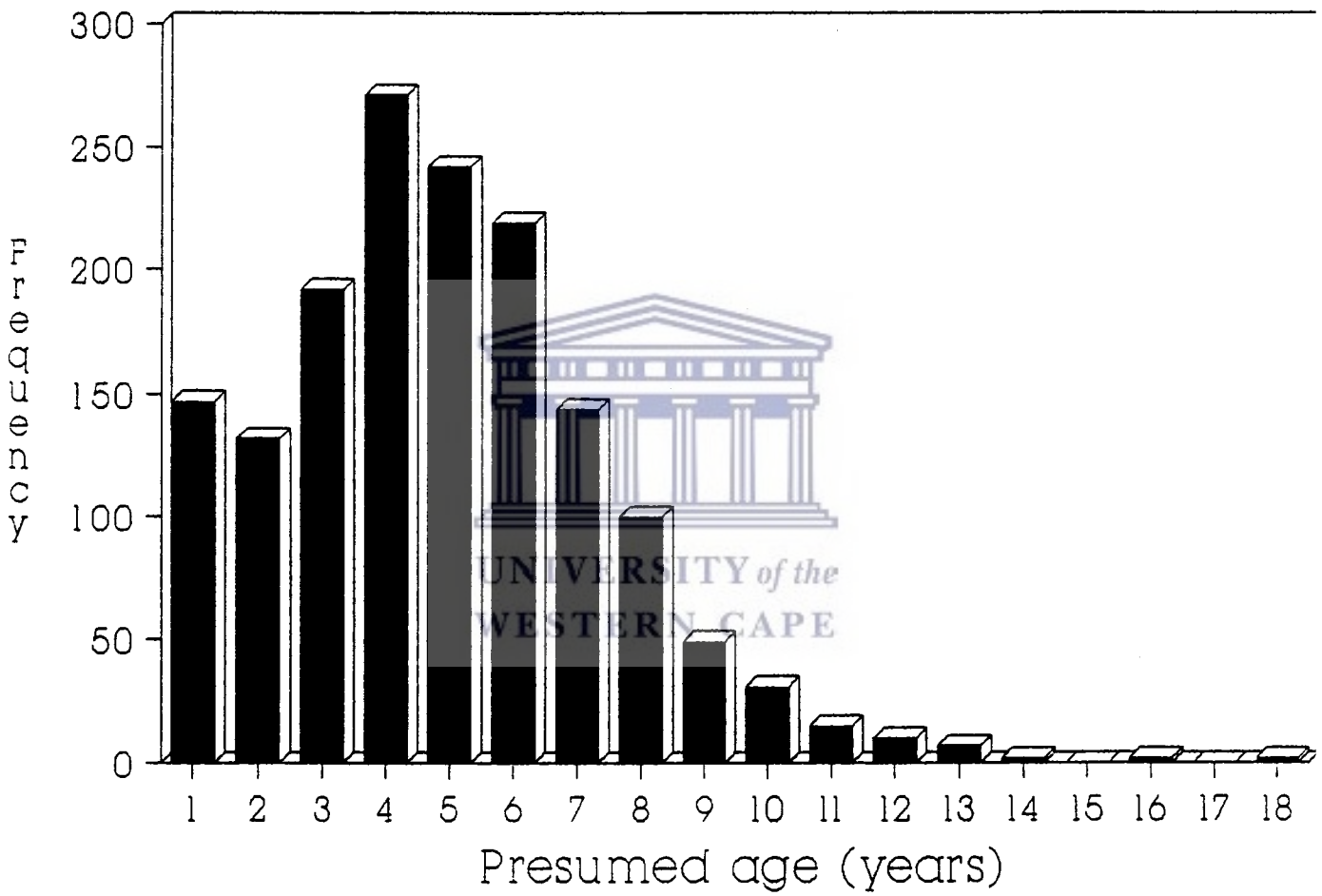


Figure 2.9: Frequency distribution (N) of the number of individuals per age-class in a **S. grandiflora** subsp. **fimbriata** population.

Corm diameter for the various age-classes was determined for the population and is presented in Figure 2.10. The data exemplified the following:

1. The calculated mean corm diameter for the population was 0.839 ± 0.347 cm.
2. A progressive increase in corm diameter was found for the first four years.
3. The population exhibits uniformity in the mean corm diameter after four years.
4. Only minor fluctuations showed in the 9-12 year age-classes.

From the data comparing corm diameter with depth of burial the following conclusions were made:

1. Largest corm diameter was obtained in the 2-4 cm zone of the soil profile.
2. The smallest corm diameter, as expected, was obtained in the 1.5 cm zone.
3. Considerable variation is evidence for the 5-8 cm zone which indicated that corm diameter was not positively correlated with depth of burial in the soil profile, perhaps only once "mature" depth and size attained.

The number of leaves produced per corm increased progressively with corm diameter. The maximum of twelve leaves was produced by corms with a diameter of >1 cm.

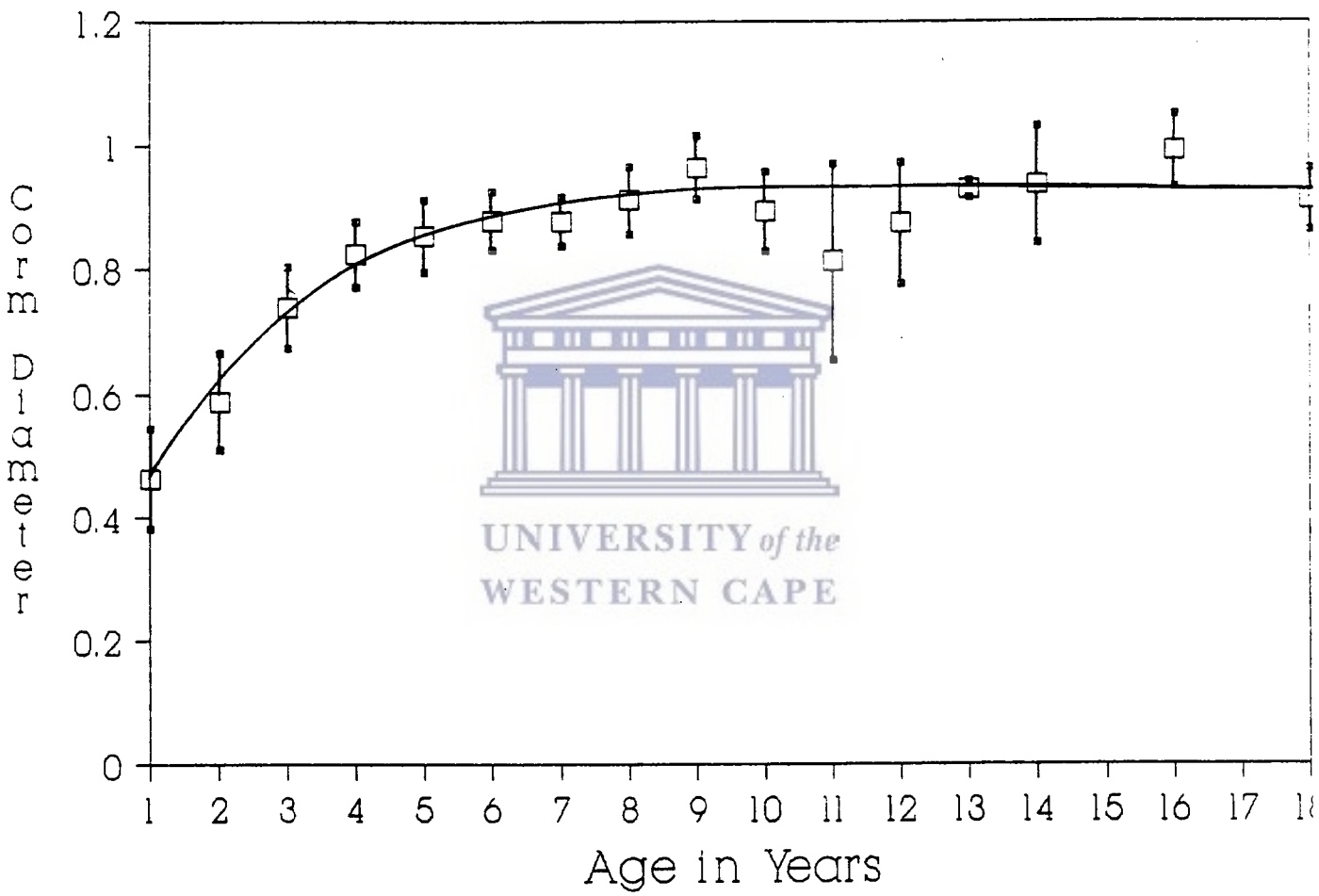


Figure 2.10: Corm diameter (cm) for the various age-classes of a **S. grandiflora** subsp. **fimbriata** population.

Production of new individuals in **S. grandiflora** subsp. **fimbriata** occurred asexually through the vegetative formation of cormlets and sexually through flowering and seed development. The relationship between vegetatively reproducing and flowering individuals are interrelated as cormlets are formed in the axils of the inflorescence stem.

1. There was no evidence that sexual and vegetative reproduction was determined during the preceding season, but presumably factors such as corm depth, size and weight of the perennating organ are important determinants along with environmental conditions.
2. In other species there is apparently a density related influence on the relationship between vegetative and sexual reproduction (Muller 1979). In dewberry under conditions of high population density the proportion of biomass allocated to reproduction is increased in favour of sexual reproduction (Abrahamson 1975). It is not known how the occurrence of flowering or biomass allocation in flowering plants is influenced by population density, but it seems likely that density is less important in determining characteristics of flowering and vegetative reproduction.
3. It was found that 77.4% of plants with a corm size greater than 0.78cm and a biomass of >0.37g, sampled during the flowering season of the species, did flower (n= 199).
4. It was found that 86.6% of plants with a corm size below 0.76 cm (0.37 g d.m.) did not flower (n = 238).
5. It was found that plants younger than 4 years did

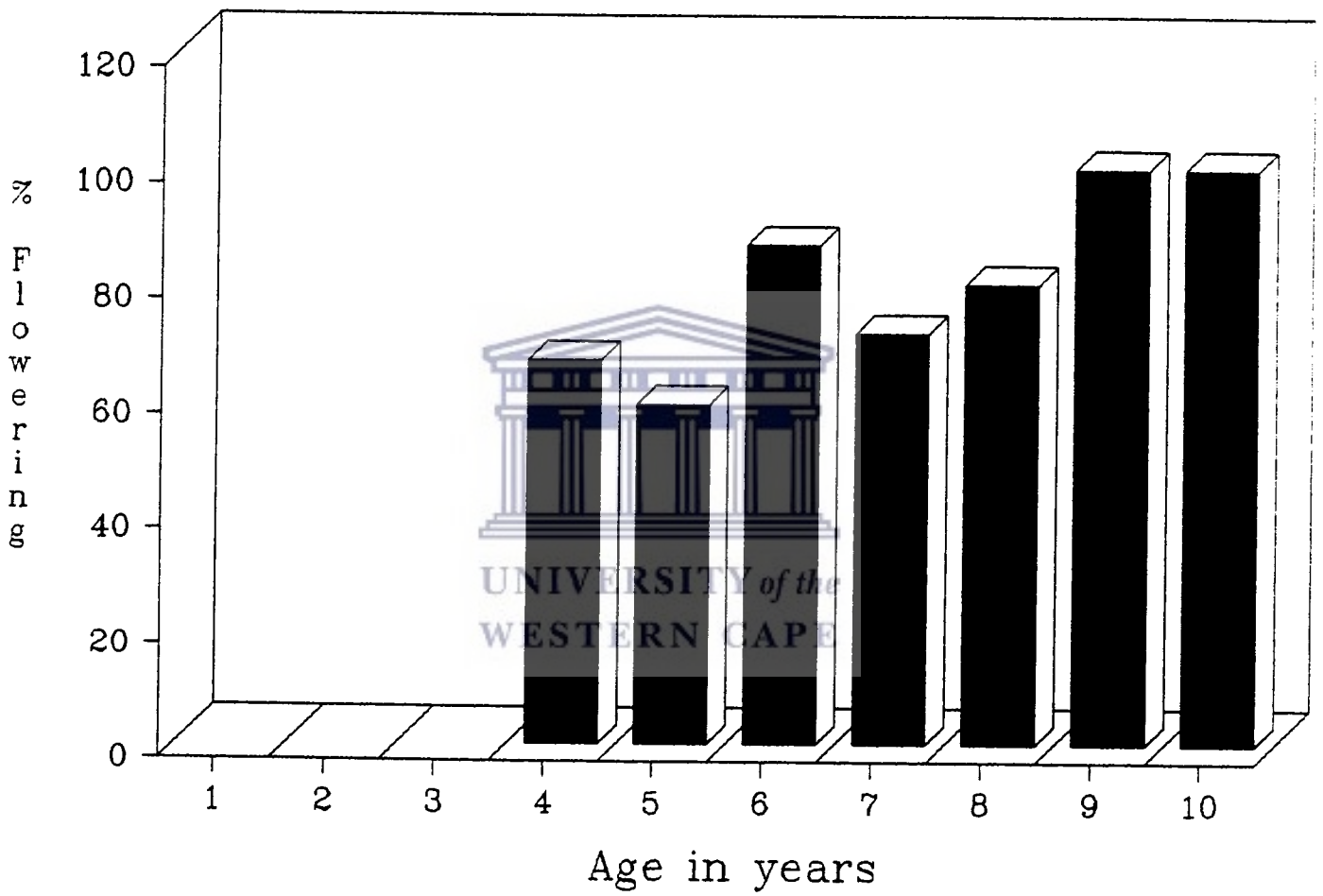


Figure 2.11: Percent of individuals of each age class that flowered in a **S. grandiflora** subsp. **fimbriata** population for the 1988/89 season (n = 199).

not flower (Fig. 2.11). It suggested that this synanthous species required a "minimum critical" corm biomass and size (Rees 1969, 1972) before flowering could occur.

6. Age and biomass were equally important predictors of flowering status, but for a number of species total biomass is emphasized as a better predictor for flowering than age (Pritts & Hancock 1983).

7. The reproductive structures accounted for a small amount of production. Maximum fruit production of 0.43g d.m. per plant occurred during October. Production of mature seed averaged 14.29 ± 0.69 seeds per fruit.

8. Total reproductive effort, including biomass allocation to inflorescence stalk, floral parts and fruit development, amounted to about 19.72 - 42.94 % of the observed net production between September and October. Biomass in mature seeds accounted for 4.92 - 11.24 % of net production, 25.9 - 38.4 % of the reproductive effort.

2.4 CONCLUSION

The phenology, demography and utilization of resources for reproduction in **S. grandiflora** subsp. **fimbriata** resembles that of many annual synanthous geophytic species, i.e. annual die-back of above-ground herbaceous plant parts and that a large proportion of the annual biomass production is invested in filling the storage organ and reproduction. The development of an underground annual storage organ coupled with the annual die-back of above-ground herbaceous plant parts in **S. grandiflora** subsp. **fimbriata** can be regarded as an adaptative strategy to cope with the low nutrient status and climatic conditions of the mediterranean-type ecosystem in the Southwestern Cape.

The counting of corm tunics appeared to be a reliable tool for establishing the age of the species. Sexual maturity in this species was found to be reached after seven years. Population parameters such as mean corm size, mean corm depth, age and biomass were found to be equal important predictors of flowering status. The reproductive strategy which the species employs, viz. sexual production of a large number of seeds and vegetative production of cormlets, is indicative of a r-strategist although density is less important in determining reproduction. The acquisition of a "minimum critical biomass" for the corm is an important prerequisite for flowering. It can also be suggested that the dense soil in which the species occurs is an important determinant of corm size.

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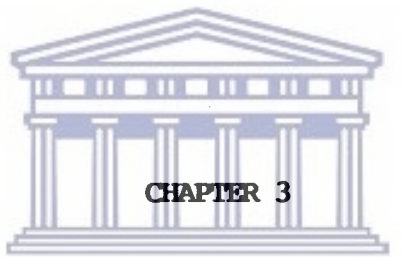
SECTION TWO

PHYSIOLOGICAL STUDIES



CHAPTER 3

SEASONAL BIOMASS AND RESOURCE ALLOCATION IN A *HAEMANTHUS PUBESCENS* L.f. SUBSPECIES *PUBESCENS* POPULATION IN THE SOUTHWESTERN CAPE

CONTENTS

3.1 Introduction

The bulbous plant, **H. pubescens** L.f. subsp. **pubescens**, is a prominent member of the winter ground flora of the nutrient-poor sands of the Southwestern Cape. It aestivates during spring and summer in the form of a dormant bulb and spreads vegetatively by means of bulblets, and sexually by means of berries (Snijman 1984).

The concept of allocation implies the movement of materials differentially to and from various organs (Fitter & Setters 1988) and most workers have illustrated that mineral elements and biomass are not allocated synchronously (eg. Abrahamson & Caswell 1982; Gross **et al.** 1983; Whigham 1984; Hume & Cavers 1983; Nault & Gagnon 1988). It is also well documented that nutrient concentrations vary greatly between plant organs and at different growth stages (eg. Abrahamson & Caswell 1982; Gross **et al.** 1983; Whigham 1984; Hume & Cavers 1983; Nault & Gagnon 1988) and that nutrient and biomass allocation do not necessarily show similar responses to environmental conditions (eg. Doust 1980; Van Andel & Vera 1977). The bulbous habit allows for the potential carry-over of substantial amounts of nutrients and food reserves from one growing season to the next. Furthermore, in geophytes with hysteranthous leaves an accumulation of storage

materials is a prerequisite for flowering (Burt 1970; Rees 1969, 1972; Frontiaer 1973; see also Chapter 1). In this way flowering can be completed even if there is a shortage of reserves in the current year (Dafni **et al.** 1981). Dafni **et al.** (1981) postulated that in moderate and predictable habitats the "shortage fund" (the reserves above the consumption of one year) may be quite small since there is a low probability of successive dry years. They suggested further that if a storage organ is large enough, which indicates a large " shortage fund", flowering is likely to occur almost every year. Other workers have indicated that other triggers such as temperature can be very important (Hartsema 1961; Rees 1966).

The objective of the study was to examine how the species allocated biomass and resources to its constituent parts and how resources were manipulated from season to season. The allocation and partitioning of biomass, phosphorus, potassium, calcium, magnesium, sodium, nitrogen, zinc, copper, iron, manganese, soluble carbohydrates and starch to the different structures of the plant were examined over a period of one year.

The study attempted to ascertain whether there were differences between the allocation patterns of biomass and the various nutrients, and if so, which resources differ from biomass, and which follow the same pattern. Allocation patterns were examined seperately for flowering and non-flowering plants.

3.2 Study Site

See chapter 1 for the description of the study site.

3.3 Methods

3.3.1 Collection of Specimens

A plot of 192 m^2 was selected which included a large, well-protected population of **H. pubescens** subsp. **pubescens**. The plot was subdivided into 16 quadrats of 12 m^2 each and sampling was done according to a random permutation method (Moses & Oakes 1963) for a full calendar year. Fifteen to twenty plants were excavated monthly. Of these five non-flowering (<9 years) and five flowering plants (see Chapter 1) were selected each month for chemical analysis. The flowering plants were selected as those which would flower or had flowered in the calendar year. The non-flowering plants included only "medium-sized" plants, while flowering plants were "large sized" (see Chapter 1). The interpretation of biomass and resource allocation patterns necessitated the careful consideration of the fact that the five plants selected randomly each month for analysis would be expected to vary considerably in size. It is not always possible to use such data to draw firm conclusions about the movement of materials, because an increase or decrease in the total amount in an organ can come about by (i) import or export, (ii) a change of identity (eg. leaves can die), (iii) loss, particularly of roots and fruits, or (iv) simple sampling error (Fitter & Setters 1988). The term inflorescence was

used for the reproductive structures from November to February because it was difficult to distinguish between the different floral parts at all times. The floral parts were only seperated during March, but for the allocation patterns they were combined to avoid confusion.

3.3.2 Chemical Analysis

The plants and soil were dried in an oven at 60 ^{o}C until a constant mass was reached. Water content was expressed as percentage of both the fresh and the dry mass. The dry material was ground with a Wiley mill to pass through a forty mesh prior to chemical analyses. Concentrations of macro- and micro-elements were determined on sulphuric-peroxide digests with a Pye Unicam SP9 atomic absorption spectrophotometer (Allen **et al.** 1986). Phosphorous was determined in the same digests as the phosphomolybdate blue-complex (Allen **et al.** 1986) while soluble carbohydrates and starch were determined according to the anthrone reagent and perchloric acid methods respectively (Allen **et al.** 1974). They were then determined colorimetrically with a Varian Techtron model 635 double beam spectrophotometer. Nitrogen was determined by Kjedahl analysis (Allen **et al.** 1986).

3.3.3 Resource Concentrations and Allocation

Resource concentrations were determined as the amount present in 0.5g dry mass of the constituent plant parts. Concentration trends were

identified for the plant parts and levels of significance were computated according the **student-t** test. Thus the allocation of resources was calculated as the product of the dry mass and the concentrations of the resources. The values used for plotting the biomass graphs are mean values for total plant weight; and thus demonstrate temporal changes in component weights which are independent of differences in the total weight of plants. Seasonal soil moisture content was determined as a percentage of the soil's dry mass.

3.4 RESULTS AND DISCUSSION

3.4.1 Biomass

The seasonal distribution of biomass for reproductive and non-reproductive plants is shown in Figures 3.1 & 3.2 respectively. The mean percentage monthly soil moisture content (Fig. 3.3) for the study region illustrates the essentially Mediterranean-type climate with which the species is typically associated.

The leaf-bases accounted for the largest percentages (70.3 - 90.7%) for both flowering and non-flowering plants of the total biomass throughout the year. However, the entire bulb (leaf-bases and stem) attained and maintained over 80% of the total plant biomass. The mean bulb biomass, 6.737 ± 0.837g dry mass, for non-flowering plants was considerably lower than the "minimum critical biomass"

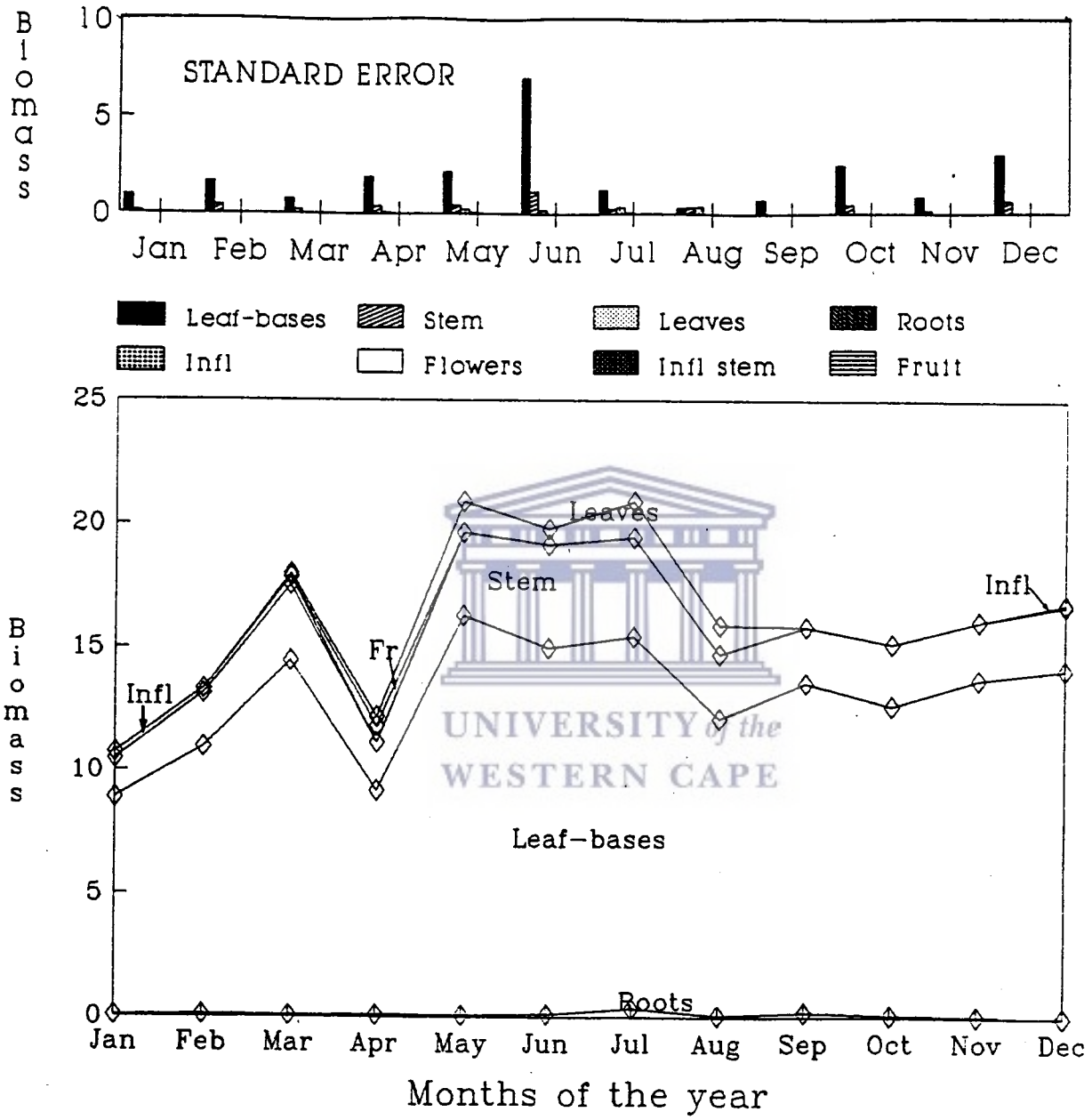


Figure 3.1 Seasonal biomass (g. dry mass) changes in reproductive plants of a **H. pubescens** subsp. **pubescens** population sampled from a large natural population of plants inhabiting aeolian sands at Klein Welmoed, Lynedoch. Infl = Inflorescence, Fr = Fruit.

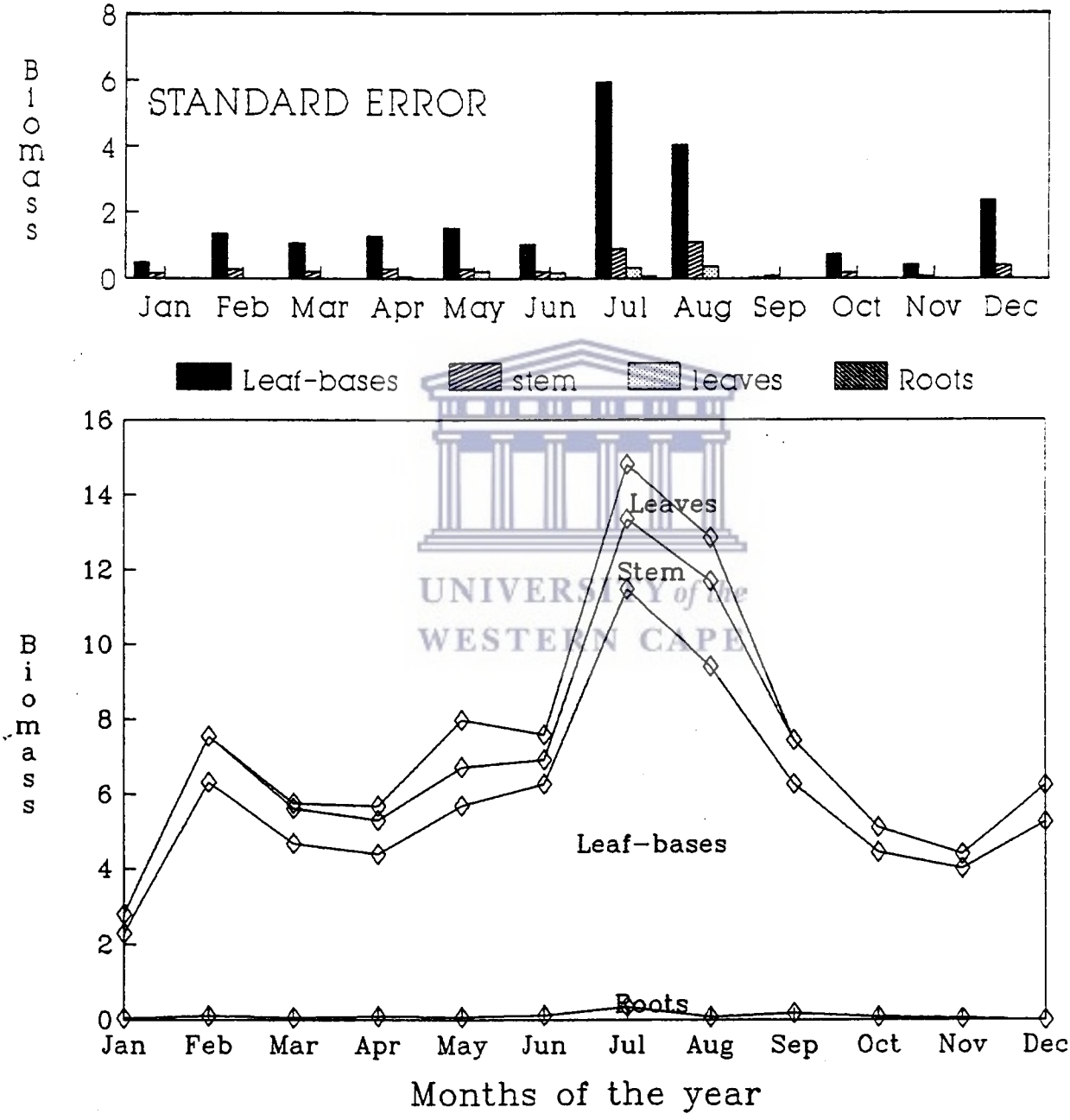


Figure 3.2: Seasonal biomass (g. dry mass) changes in non-reproductive plants of a **H. pubescens** subsp. **pubescens** population sampled from a natural population at Klein Welmoed, Lynedoch.

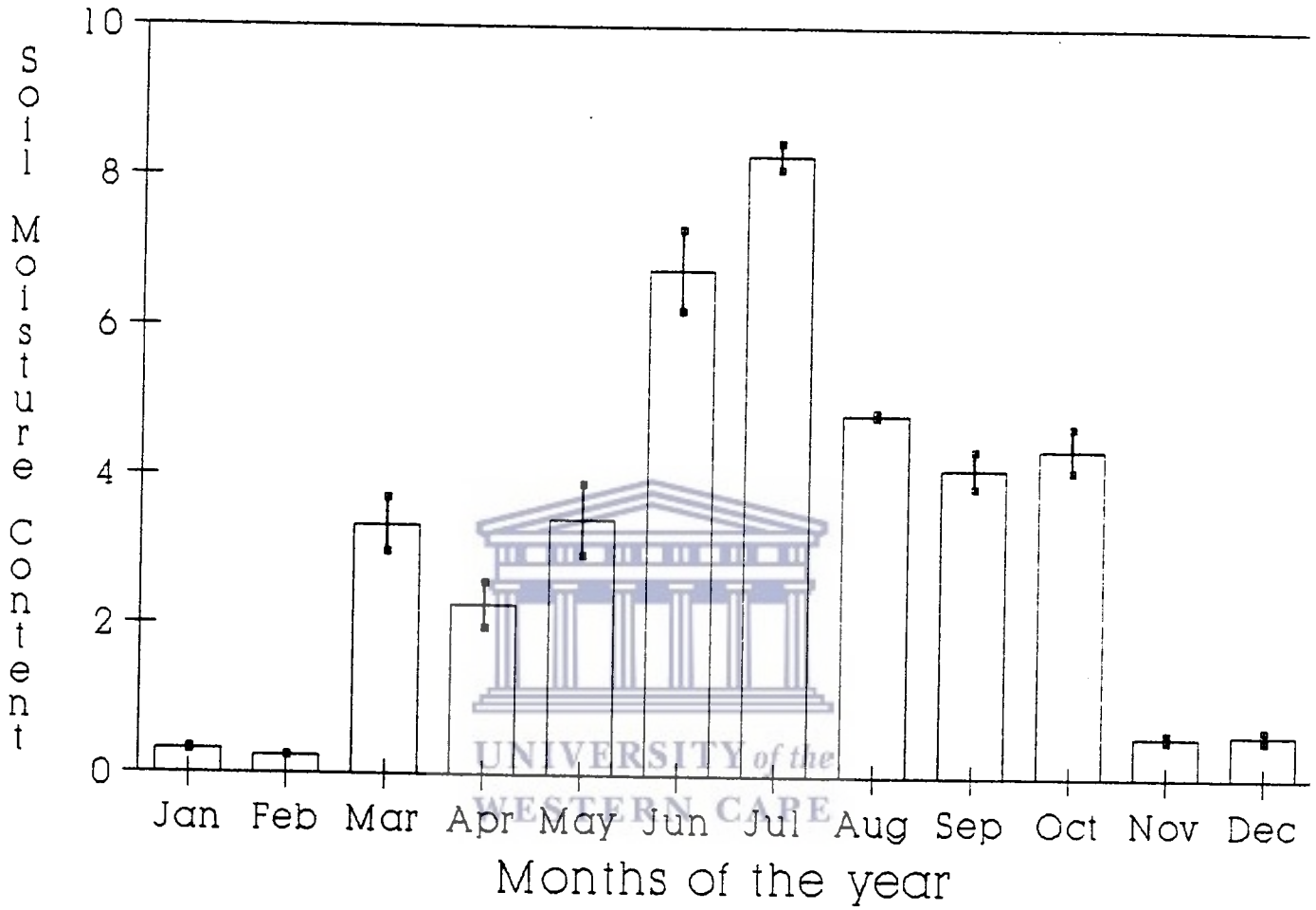


Figure 3.3: Mean monthly soil moisture content (%) (± standard error) of the study site at Lynedoch for a **H. pubescens** subsp. **pubescens** population.

suggested for flowering plants (see Chapter 1). Leaves began development in March and accounted for 1.0 - 15.8% of the total plant biomass between March and August (Figs. 3.1 & 3.2). The inflorescence developed slowly between September and March and reached relative peak biomass during April when the percentage allocation to the inflorescence was the highest. Total reproductive effort (i.e. all the reproductive structures) was maintained between 2% and 6% of the total plant biomass from November until April (Fig. 3.1). The roots in both cases represent only a small fraction of the total plant biomass, with percentages ranging between 0.59 and 2.39%.

The bulb dry mass does not show any major increases for both flowering and non-flowering plant during the period of rapid growth between April and September although one would expect an increase in bulb dry mass as a result of the addition of new leaf-bases. Increases in bulb dry mass during this period must indicate transfer of material from the leaves to the leaf-bases and stem. Changes in dry weight of the non-photosynthetic inflorescence stalk increases from November to March.

3.4.2 Nutrient Concentrations

Concentration patterns of the macronutrients, organic substances and micronutrients which are described for vegetative phases of

flowering plants are also applicable to the non-flowering plants (see Table 3.1; Appendix 3.7.1 - 3.7.4) so only those for flowering plants are presented. The concentration ranges for the reproductive structures, viz. inflorescences, flowers, fruit and inflorescence stalk, were not included in Table 3.1 but are to be found in Appendixes 3.7.1 & 3.7.2. The overall concentration ranges will be discussed in relation to other findings. The calendar year was divided into four phenological periods and the results are discussed in relation to these. Where resource concentrations and allocations have similar patterns significance levels are only presented for one or two resources.

3.4.2.1 Apparently dormant period with marked reproductive development below ground (January - February)

During this period all macro-nutrients, except Na, have relatively high concentrations in the reproductive structures. The concentration levels for Na were significantly higher in the roots than elsewhere {$t(4) = 316.703$, $p < 0.00005$} with the ranking order being roots (R) > reproductive structures (RS) > stem (St) > leaf-bases (LB). Equally high relative concentrations of soluble carbohydrates were present in the reproductive structures, leaf-bases and stem, but starch had significantly lower concentrations in the reproductive structures than the stem and leaf-bases {$t(6) = -4.275$, $p = 0.0052$} with the ranking order being LB > St > RS. The micro-nutrients have generally low concentrations in all plant parts.

3.4.2.2 Reproductive period (March - April)

The macro-nutrient concentrations were varied in all the constituent plant parts, but were significantly higher in the leaves (L) than elsewhere {eg. K: $t(21) = 22.376$, $p < 0.00005$) with the ranking order being L > Reproductive structures (Flowers, fruit and inflorescencee stalk) (RS) > R > St > LB. The total nonstructural carbohydrates (TNC), soluble carbohydrates and starch, were much higher in the leaf-bases and stem than elsewhere {eg. Sol. CHO: $t(18) = 3.413$, $p = 0.0031$} with the ranking order being LB > St > L > RS > R. The micro-nutrients Cu, Mn and Fe were generally higher in the roots and reproductive structures than elsewhere, but were not significant {eg. Fe: $t(19) = 1.422$, $p = 0.235$} with the ranking order being R > RS > L > St > LB. The concentration levels of Zn were generally constant in all the plant parts although the following ranking order was identified: St • LB • R > RS > L.

3.4.2.3 Vegetative period (May - August)

During this period the macro-nutrients N, Mg and phosphate (P) were significantly higher in the leaves than in any other plant part {eg. N: $t(32) = 4.746$, $p < 0.00005$) with the ranking being L > R > St > LB. The concentration levels for K and Na were much higher in the leaves and roots than elsewhere, but higher concentrations were found in the leaves than the roots {eg. K: $t(32) = 4.562$, $p = 0.0001$}. The ranking order is L > R > St > LB. No distinct differences in Ca concentrations were found for all the plant

parts. The TNC concentration levels were significantly higher in the stem and leaf-bases than elsewhere {eg. Sol. CHO: $t(38) = 14.284$, $p < 0.00005$} with the ranking order being St > LB > L > R. The micro-nutrients Mn and Cu have significant high concentrations in the roots than in any other plant part {eg. Cu: $t(36) = 13.463$, $p < 0.00005$} with the ranking order being R > LB > L > St. During this time of the year it appears that the leaf-bases have higher concentrations of Zn and Fe than other plant parts but these are not significant {eg. Zn: $t(35) = 1.227$, $p = 0.2413$}. The ranking order is LB > R > St > L.

3.4.2.4 Leafless period (September - December)

During this period the roots have significantly higher concentration levels of the macro-nutrients N, Mg and P than elsewhere {eg. N: $t(33) = 13.919$, $p < 0.00005$} with the ranking order being R > LB > St. The concentrations for Na and K were also significantly higher in the roots than the other constituent plant parts {eg. K: $t(39) = 19.369$, $p < 0.00005$} with the ranking order being R > St > LB. Ca concentrations were not significantly higher for any of the plant parts {$t(39) = 0.432$, $p = 0.6681$}. The stem and leaf-bases have significantly higher concentrations of TNC than the roots {eg. Sol. CHO: $t(33) = 18.829$, $p < 0.00005$} with the ranking order being LB > St > R. The roots have significantly higher concentrations of the micro-nutrients Mn and Cu {eg. Cu: $t(39) = 10.956$, $p < 0.00005$} with a ranking order R > LB > St, but differences for Zn and Fe where not significant {eg. Zn: $t(27) =$

0.724, p = 0.4947} although the ranking order LB > St > R was identified.

The concentration ranges for all the macro-nutrients, except K, were comparatively low to the proposed "typical" ranges for plants (Table 3.1). The micro-nutrients compare favourably with the ranges, but for the roots the concentration ranges were generally higher. The ranges for starch were higher than those found in other storage organs, but the values for soluble carbohydrates compares favourably. The stipulated ranking orders were the dominant patterns for the resources for the phenological periods, however minor deviations were present.

The leaves and reproductive structures had the highest concentration for most of the macronutrients (Table 3.1; Appendix 3.7.1) and temporal differences between components were particularly striking for N, P, K, soluble carbohydrates, and starch, all of which have been demonstrated elsewhere to be translocated or leached from senescing structures, particularly leaves (Staaf 1982). Leaf N averaged 1.524 ± 0.201 $g.kg^{-1}$ from March-July and remained high until the the leaves senesced in August when N concentrations declined. N concentrations for the inflorescences (inflorescence stalk and flowers inclusive) were relatively high for the entire flowering period and, unlike the leaves, did not decline as the inflorescence matured. It seems likely that N remained high in the reproductive structures because of the high N requirement of developing seeds where it is stored (Whigham 1984). Except for high values during the months of March and May for the stem,

Table 3.1: Concentration ranges of mineral elements (macronutrient: $g.kg^{-1}$; micronutrients: $mg.kg^{-1}$) and carbohydrates ($g.kg^{-1}$) in the constituent plant parts of a **H. pubescens** subsp. **pubescens** population.

Resource	Concentration ranges				
	Leaf-bases	Stem	Leaves	Roots	Typical ranges for plants
N	1.68 - 5.17	3.15 - 12.33	10.75 - 21.87	7.54 - 12.66	10 - 50 [1;2]
P	0.30 - 0.97	0.61 - 1.46	1.01 - 3.19	0.80 - 1.63	1 - 8 [1;2]
K	7.37 - 14.63	9.08 - 18.29	21.60 - 49.09	15.78 - 34.38	5 - 50 [1;2]
Ca	2.30 - 6.17	3.31 - 8.69	3.04 - 6.11	0.16 - 8.16	5 - 50 [1;2]
Mg	1.00 - 1.61	1.26 - 2.19	1.67 - 3.73	1.63 - 4.13	1 - 10 [1;2]
Na	0.61 - 1.30	0.85 - 1.55	0.51 - 15.30	7.27 - 12.25	0.2- 2 [3]
Zn	0.005 - 0.047	0.016 - 0.026	0.004 - 0.012	0.008 - 0.011	0.01 - 0.1 [1]
Mn	0.016 - 0.201	0.013 - 0.069	0.021 - 0.279	0.033 - 0.077	0.02 - 0.3 [1]
Cu	0.027 - 0.074	0.019 - 0.082	0.032 - 0.072	0.093 - 0.129	0.002 - 0.02 [1]
Fe	0.060 - 0.709	0.023 - 0.132	0.143 - 0.423	0.088 - 1.645	0.05 - 1 [1;2]
Sol. CHO	110.5 - 237.2	98.1 - 236.9	29.9 - 78.3	33.5 - 67.2	40 - 377 *
Starch	117.1 - 217.3	149.8 - 209.6	9.2 - 31.0	13.9 - 39.6	25 - 170 *

1 = Larcher (1980); 2 = Epstein (1972); 3 = Hewitt & Smith (1974)
* = Grainger (1941), Fonda & Bliss (1966).

N in the bulbs showed no distinct temporal patterns. The high root N concentrations might be attributed to the presence of vesicular arbuscular micorrhizae in the roots, a common feature of plants inhabiting environments with a low nutrient status, which thus fascilitate uptake of inorganic nitrogen (N. Allsopp pers. comm.; Lamont 1982).

There were no temporal trends for any of the macro-nutrients in the stem and leaf-bases. Like N, P and K concentrations were highest in new leaves and declined in senescing leaves. Mg, Ca and Na concentrations were also high in new leaves and their concentrations were still relatively high in senescing leaves. Guha & Mitchel (1966) have demonstrated that concentrations of immobile elements like Ca increase or remain high in senescing structures primarily because they are retained in cell walls.

Micronutrient concentrations (Zn, Fe, Mn and Cu) were more variable than the macronutrient concentrations and seasonal patterns were also apparent. Micronutrient concentrations were generally high in the leaf-bases, stem, leaves and reproductive structures and all had a tendency to increase late in the year (July and August). The high leaf values for July and August suggest that they are not translocated nor leached from senescing leaves and are thus retained in the cell walls (Guha & Mitchell 1966). The data for the micronutrients suggest that they might be stored throughout the plant in quantities sufficiently large enough to mask any clear patterns of translocation.

Soluble carbohydrate and starch concentrations in the roots and leaves were generally low and varied considerably for all the seasons. The leaf-bases and stem contained high concentrations of soluble carbohydrates probably because they serve as major sinks for storage and as major sources from which TNC are translocated during vegetative and reproductive development. This implies that the main function of the bulb might be to build up surplus resources and that the aerial parts develop at the expense of these resources in the bulb but in return the leaves produced photosynthate. The reproductive structures (inflorescences, inflorescence stalk, flowers and fruits) contained high concentrations of TNC. This indicates that a considerable amount of reserves are required for the initiation of reproductive organs.

3.4.3 Seasonal Nutrient Allocation

Although the leaf-bases were regarded as the major storage plant part, four general allocation patterns were identified and are as follows:

1 Relatively large amounts of the resources N, P, K and Cu are allocated to the leaves and stem from May to August (Fig. 3.4). The major reserves remains in the leaf-bases.

2 Major storage of Ca, Mg and Mn occurs in the leaf-bases, but considerable allocation to the stem throughout the year and minor allocations to the leaves and reproductive structures (Fig. 3.5).

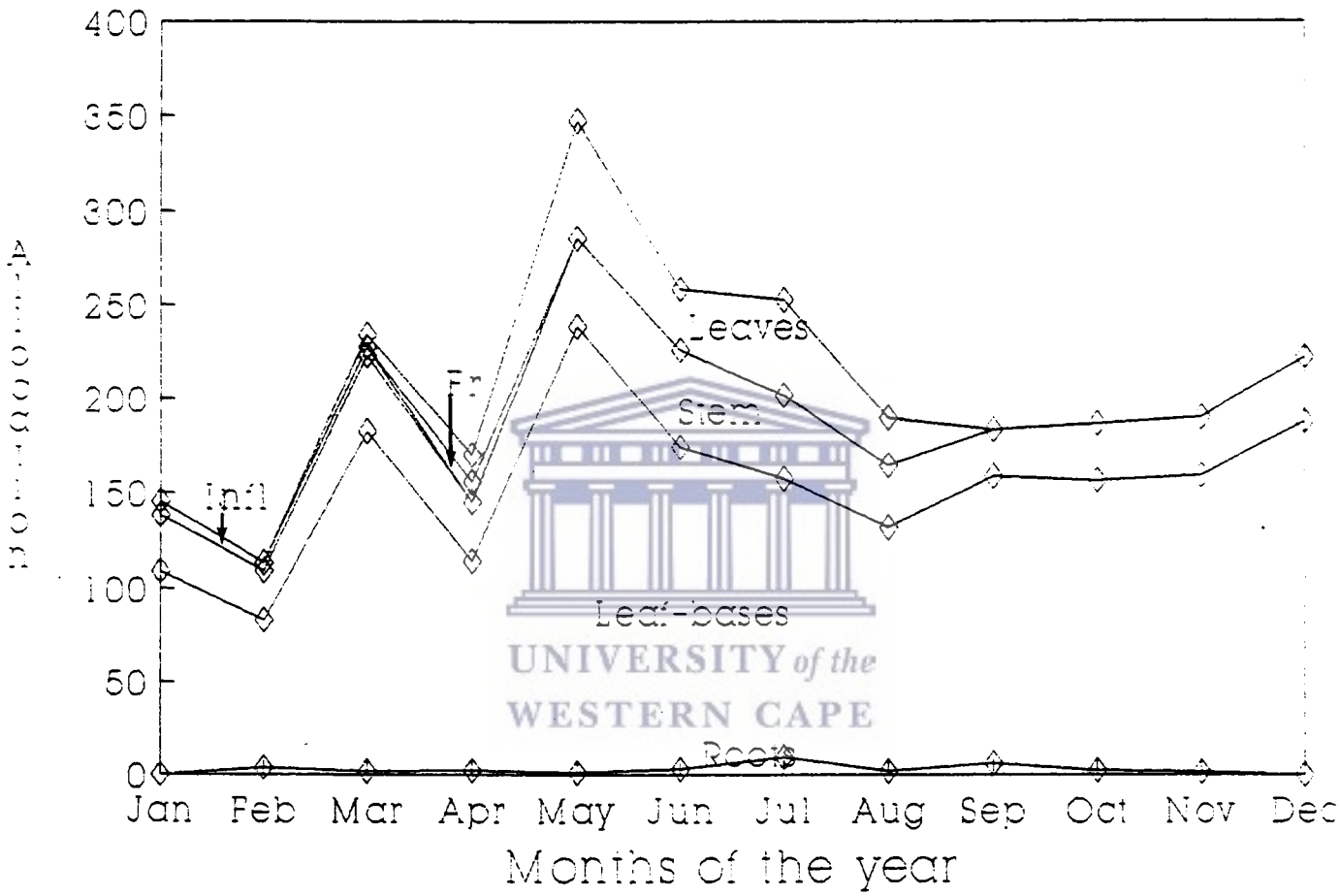


Figure 3.4: Seasonal allocation of potassium (mg) in a **H. pubescens** subsp. **pubescens** population sampled at Klein Welmoed, Lynedoch.

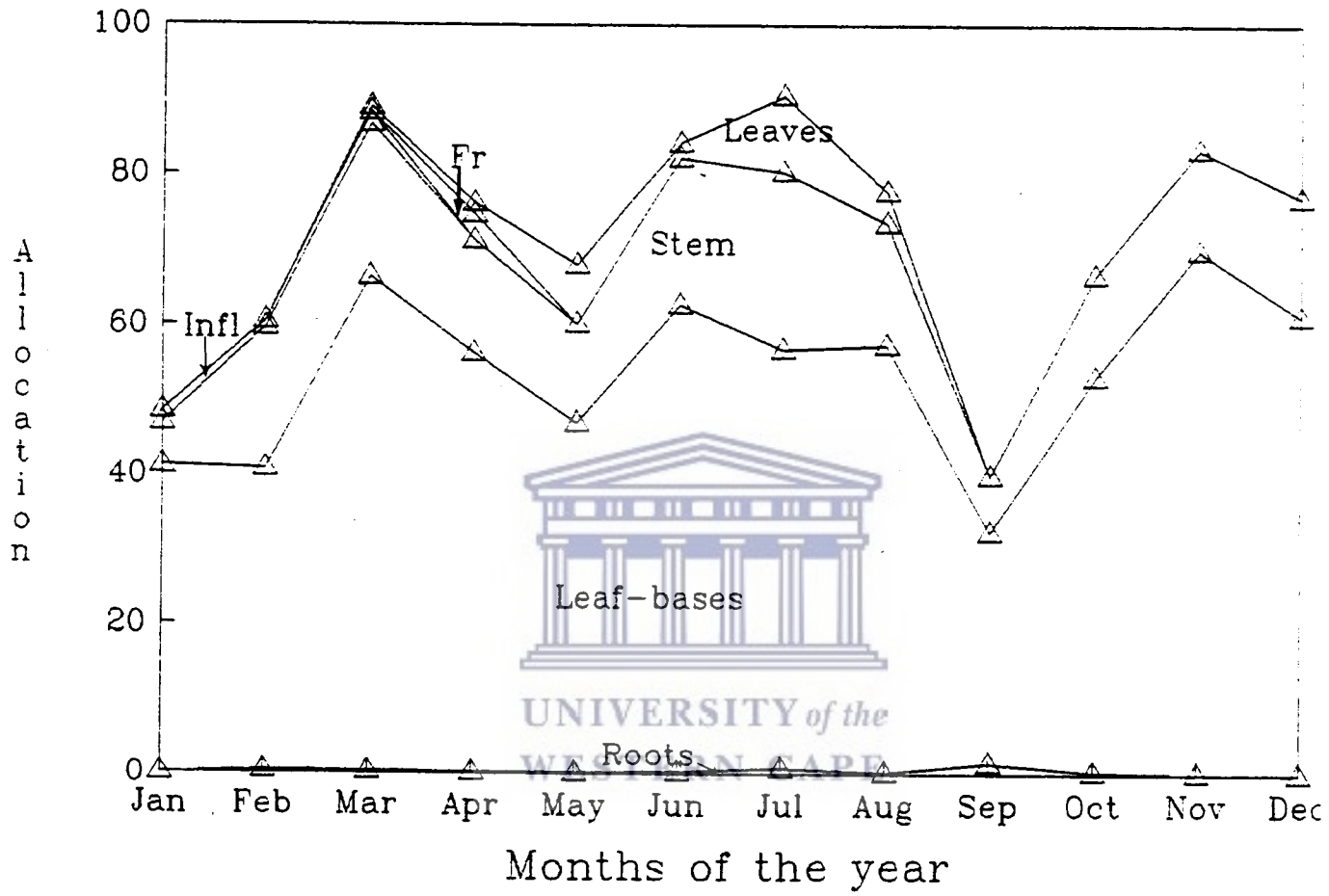


Figure 3.5: Seasonal allocation of calcium (mg) in a **H. pubescens** subsp. **pubescens** population sampled at Klein Welmoed, Lynedoch.

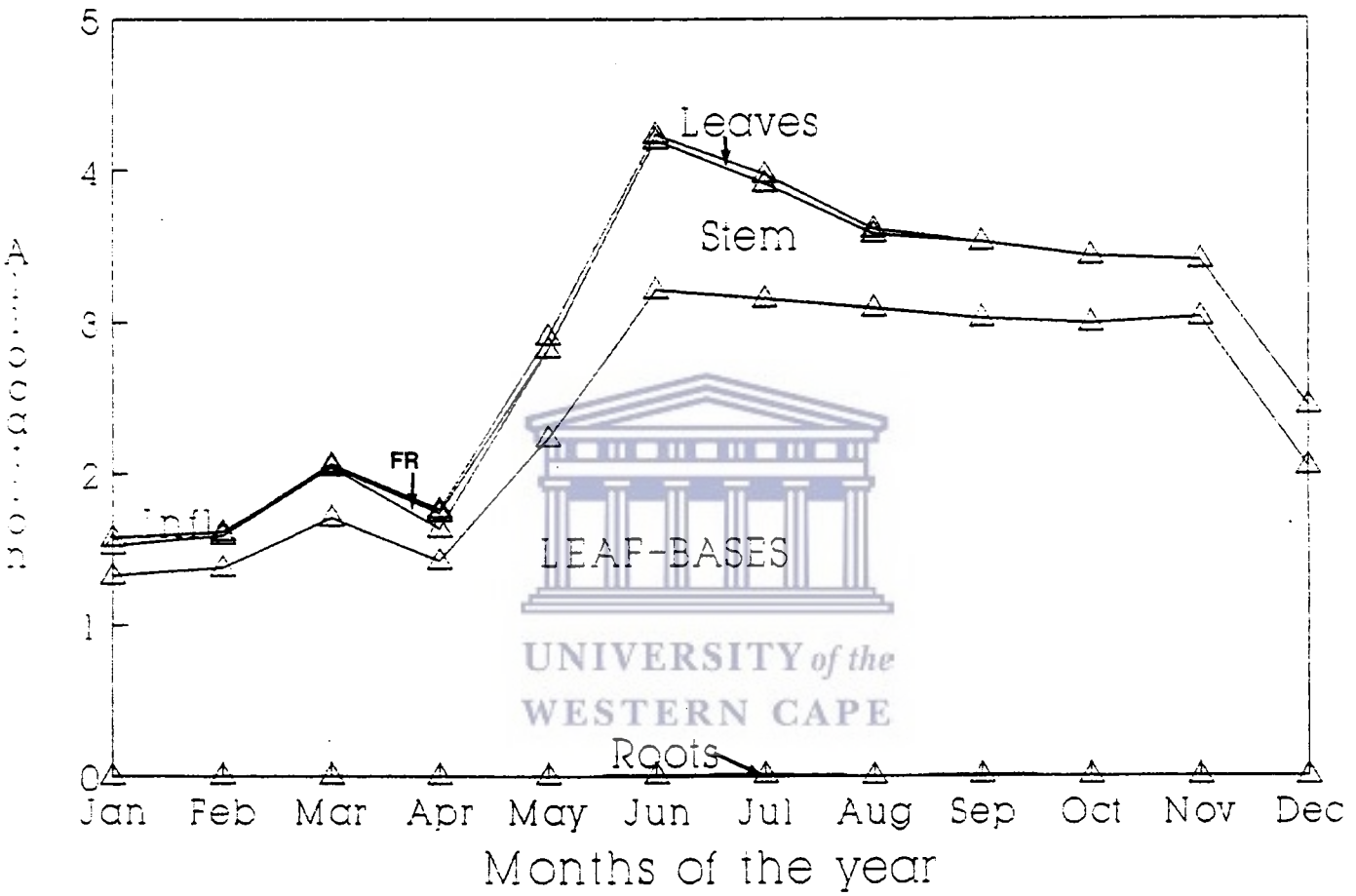


Figure 3.6: Seasonal allocation of soluble carbohydrates (mg in thousands) in a **H. pubescens** subsp. **population at Klein Welmoed, Lynedoch.**

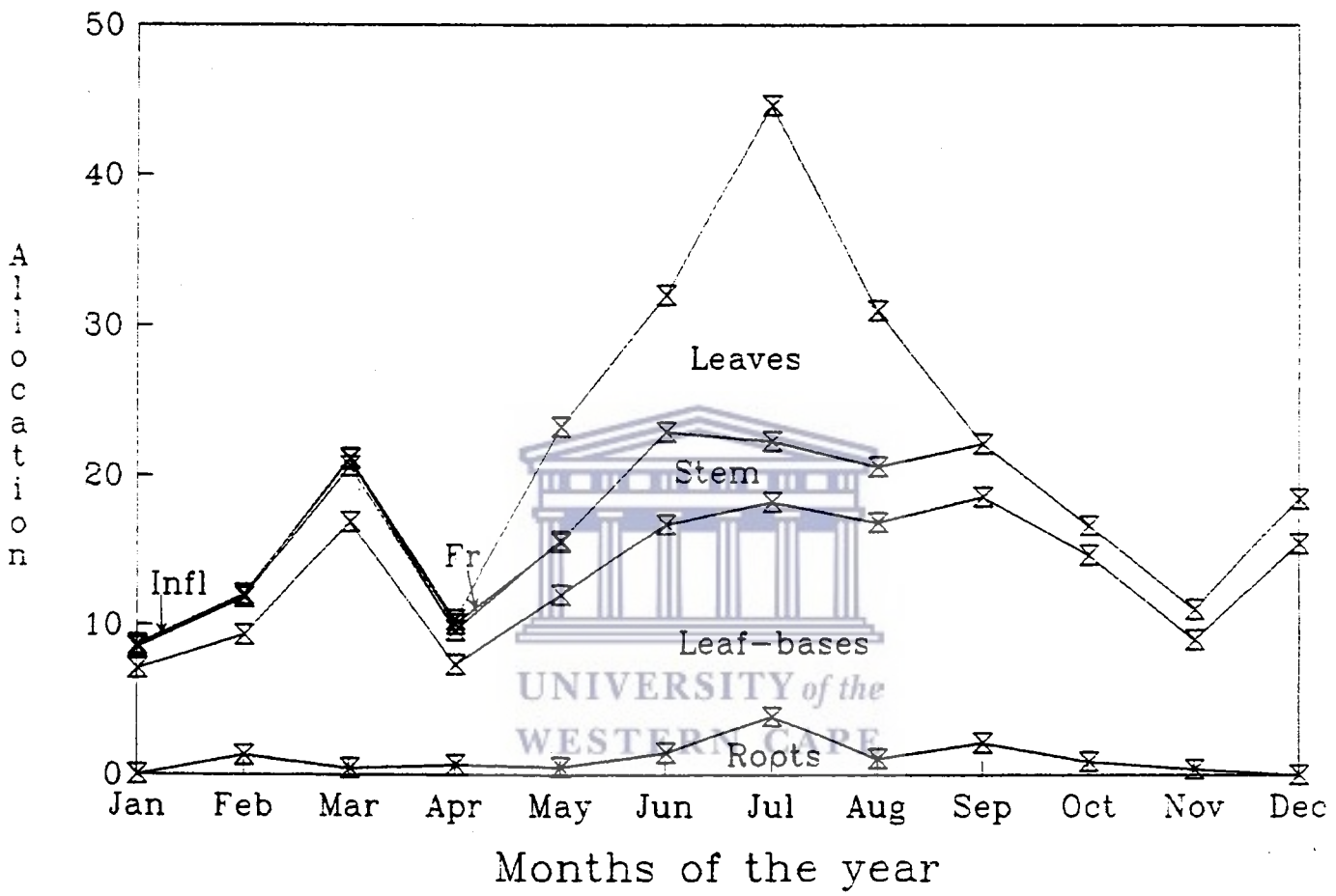


Figure 3.7: Seasonal allocation of sodium (mg) in a **H. pubescens** subsp. **pubescens** population at Klein Welmoed, Lynedoch.

3 Major storage occurs in the leaf-bases throughout the year although the stem also serves as a sink, eg. soluble carbohydrates, starch, Zn and Fe. Relatively small amounts are allocated to the leaves (April - August), roots (throughout the year) and reproductive structures (Jan - April) (Fig. 3.6).

4 Major storage of Na in the leaves which serve an important storage compartment for the element during the growth season. Amounts allocated to the roots and stem are moderate throughout the year. Negligible amounts are allocated to the reproductive structures (Jan - April) (Fig. 3.7).

For the non-flowering plants allocation patterns mirrored those of reproductive plants and are therefore not discussed seperately.

The seasonal allocation of resources will be discussed in the four periods as identified in the previous section. The storage organs were found to contain 82.2 - 88.3% of the fresh weight as water throughout the year which indicates that water storage remains constant through the seasons and it is thus not discussed seperately for each period.

3.4.4.1 Apparently dormant period with marked reproductive development below ground (Jan - Feb)

The bulb (leaf-bases and stem) accounted for the entire nutrient bulk during this period (Fig. 3.4 - 3.7). Considerable amounts

of macro-nutrients, TNC and micro-nutrients would be expected to be allocated to reproductive structures development. The reproductive structures accounted for 1.4 to 5.7% of the macro-nutrients, 0.4 to 3.4% of the TNC and 0.7 to 5.3% of the micro-nutrients of the total standing nutrient stock. The leaf-bases contained the largest amount of macronutrients present in the plants. This represented greater than 80% of the total macronutrient content of the plants. The general trend for the macronutrient contents was that exhibited by potassium (Fig. 3.4). Only sodium is different (Fig. 3.7).

3.4.4.2 Reproductive period (March - April)

The bulb also accounted for the largest nutrient bulk during this period. A large amount of the macro-nutrients, TNC and micro-nutrients would also be expected to be allocated to reproductive structures and seed development and for the initiation of new leaves (Fig. 3.4 - 3.7) although the reproductive structures accounted for only 6% of the total plant biomass. It is commonly supposed that flowering and fruiting make a drain upon the food resources of a plant (Grainger 1941). Reproductive organs (inflorescences, inflorescence stalk, flowers and fruit) accounted for a small amount (0.2 to 8.2%) of the total macronutrient, 0.2 to 5.9% of the TNC and 0.9 to 12.8% of the micronutrient standing stock which demonstrate the metabolic demands of these reproductive organs. The reproductive organs were particularly enriched in K, soluble carbohydrates and to a lesser extent P (see Appendix 3.7.1)

while N, Ca, Mg and starch showed minor changes except in April when fruit development was completed. The fruits contained considerable amounts of macronutrients (8.2%), organic substances (5.9% soluble carbohydrates and 0.8% starch) and micronutrients (2.4 to 12.8%) at the end of their development. Leaf initiation accounted for 0.2 to 1.4% of the TNC, 0.3 to 9.2% of the macronutrient and 0.5 to 5.5% of the micronutrient standing stock which also demonstrate metabolic demands.

3.4.4.3 Vegetative period (May - August)

The bulbs served as a major food and nutrient source for resource consumption during the establishment of herbaceous above-ground organs and roots. At the beginning of the growing season, the amount of TNC increased rapidly which may have been a result of active photosynthesis or starch, the storage material during the unfavourable leafless period, being hydrolized to mono- and disaccarides. Carbohydrates stored in the bulb provided for rapid growth of leaves during winter. As the leaves expanded above-ground the newly produced matter accumulated in the bulbs through translocation, which guaranteed higher net productivity. The most prominent feature of this period was that the leaves served as strong sinks for K (12.4 to 20.1%), N (10.9 to 21.8%), Mg (6.9 to 16.1%) and particularly for Na (28.4 to 50.1%), but for Cu (7.2 to 10.6%) and Mn (7.3 to 9.9%) only during the latter part of winter. Moderate amounts (1.5 to 17.1%) of P, Ca, Zn and Fe were allocated to the leaves, but correspondingly lower levels (0.4 to 2.9%) were found for soluble carbohydrates and starch. Compared

with macronutrients, lower percentages in terms of allocation for the micronutrients were found in the leaf-bases, stem and leaves.

Compared with the macronutrients no major differences in percentages of Fe (approximately 53.68 - 90.76%), Cu (approximately 74.01 - 84.03%), Zn (approximately 51.35 - 85.76%) and Mn (approximately 56.55 - 85.61%) were found in the leaf-bases. The stem accumulated 0.0034 to 0.2900 ug (0.84 to 43.45%) of the micronutrients present in the plants (Fig. 3.4 - 3.7; see Appendix 3.7.1 and 3.7.5).

The roots were under-represented in terms of the allocation of TNC and 0.30 to 14.39% of the total macronutrient stock of the plants were allocated to the roots.

3.4.4.4 Leafless period (Sept - Dec)

During this period the leaf-bases and stem are the major storage sites (see Appendix 3.7.5). Stored food for unfavourable conditions is usually in the form of starch (Mooney & Billings 1960, 1961, 1965; Fonch & Bliss 1966; Risser & Cottam 1968; Ho & Rees 1975). The decrease in starch from the end of the growing season, if any, can be attributed to respiration (Risser & Blisser 1968), because all active cells respire continously and carbohydrates serve as respiratory substrates (Salisbury & Ross 1985). Starch is the primary reserve material and is stored almost

immediately when assimilation starts, apparently at the beginning of winter, and reaching a maximum at the conclusion of the growing season.

An important feature of the TNC results presented is that in **H. pubescens** subsp. **pubescens** floral formation begins at the time of maximum carbohydrate content of the bulb, viz. during the latter part of this period (Fig. 3.6; see also Chapter 1). It is also the time of the highest ratio between total nitrogen and total carbohydrate (1 : 117). Chael & Winsor (1965) stated that nitrogen deficiency delayed flower bud differentiation and also decreased the size of the leaves, flowers and reduced bulb yield (Nishii & Tsutsui 1963). Although the authors stress the importance of nitrogen for floral development they haven't supplied data to back their statements, but for this particular population the ratio 1: 117 was sufficient for the plants to flower. The acquisition of a sufficient nitrogen to TNC ratio combined with a minimum "critical biomass", can be regarded as an important adaptation for floral initiation of plants inhabiting nutrient poor ecosystems. Flower initiation certainly appears in general to take place only when there are adequate supplies or stores of resources, eg. TNC, and the bulb has reached an initial "critical minimum biomass" (see Chapter 1). The present results show that this species, making its inflorescence initial at the beginning of the dormant period, when it has the highest content of TNC in the bulb compared to other times of the year (Fig. 3.1 & 3.6).

During the leafless months the leaf-bases constituted 63.91 to 89.81% of the total macronutrient contents. The stem accounted for 3.55 to 34.32% of the plant's macronutrients. It can be said that the stem serves as the second largest sink for the macronutrients. The results presented for the micro-nutrients in the previous period (May - August) are also applicable to this period.

The changes of dry weight are fairly closely reflected by similar changes in the total carbohydrate (Grainger 1941) as might be expected, since this kind of resource accounts for such large percentages of the dry weight - nearly 90% when above-ground growth ceases in August (Fig. 3.1 & 3.6). The total nitrogen in this species conversely is in general low due to the high total carbohydrate and dry weight (Figs. 3.1; 3.2; 3.4 & 3.6).

Chmielewski & Ringius (1987) stated that dry weight can be used as measure for biomass-allocation patterns for the following reasons:

1. it reflects the integration of all physiological processes throughout the season (Abrahamson & Caswell 1982);
2. it is simple and fast to use;
3. biomass reflects the functional aspects of all assimilations;
4. it is the best available measure of resource allocation for comparing species growing in different environments when the availability of and species requirements for, particular nutrients are unknown (Gross **et al.** 1983); and
5. energy content and dry weight equally reflect energy

allocation patterns in plants (Hickman & Pitelka 1975).

As a measure of resource allocation, the proportion of biomass (dry weight) in various structures was used. Although the use of dry weight as a measure of resource allocation in plants has been criticized (Thompson & Stewart 1981), it has been shown that biomass is the best available measure of resource allocation concerning the species requirements for particular nutrients (Gross **et al.** 1983) if they have not been determined.

As described **H. pubescens** subsp. **pubescens** allocated a considerable proportion of its biomass to its below-ground structure. Resource allocation patterns that were calculated on the basis of total plant weight may be biased by the inclusion of the perennial below-ground structures that represent several years accumulation of biomass (Gross **et al.** 1983). In contrast, above-ground structures in herbaceous perennials represent only one year's or few months growth. This species shows a relatively constant annual allocation of biomass to its bulbs, particularly with the addition of leaf-bases, in both reproductive and non-reproductive plants. The reproductive structures accounted for a small amount of plant production. The leaves showed a particularly moderate proportional investment in biomass and resources at the time of maximum photosynthesis. Leaves were rich in potassium, calcium and particularly sodium. They also contained considerable amounts of iron and copper.

The change from vegetative to reproductive phase in this species appears to be determined by the accumulation of reserve food in the

bulb as described for **Allium victorialis** ssp. **platyphyllum** (Kawano & Nagai 1975). This is perhaps an optimal behaviour in an environment which generally has high stability and predictability. Pitelka **et al.** (1980) regarded sexual reproduction as a luxury in which a plant indulges in to the extent that resources permit, as was the case in **Aster acuminatus.** In particular the very high mineral cost of sexual reproduction may dictate this behaviour pattern, and this is supported by the increased element allocation to sexual reproduction in **H. pubescens** subsp. **pubescens.** Van Andel & Vera (1977) stated that the allocation of mineral nutrients to reproductive tissues rose with increasing nutrient level (Appendix 3.7.1 & 3.7.2; Figures 3.4.1 - 3.4.4), but not in a manner proportional to the amount of nutrients absorbed per plant.

The bulb is the storage organ of **H. pubescens** subsp. **pubescens** and contains a substantial fraction of total biomass and resources throughout the year. The full development of reproductive structures occurs in March, using reserves accumulated in the bulbs. Allocation patterns of biomass and resources in reproductive plants were found to be considerably different. The fact that the flowering and non-flowering plants exhibit the same relative dry matter allocation to various vegetative organs, suggests that this species possesses a rather fixed programme of dry matter allocation to varying vegetative component parts of the plants.

The mechanisms governing the differentiation and expression of reproduction in this species are not well understood at present. The individuals with somewhat larger biomass appear to express reproduction (Fig. 3.1 & 3.2), since the dry matter economy of this species is of a typical perennial type. Rodrigues-Pereira (1964) has demonstrated the presence of gibberellin-like substances in **Iris** which are translocated to the apex during cold treatment which normally precedes flower initiation. He suggested that the failure of flowering in small bulbs might be due to an insufficient total amount of gibberellin-like substances in the bulb-scales. He stated that the concentration of gibberellin in the bulb scales is relatively constant, but that a large bulb would contain a larger total amount; it is therefore more likely to flower than a smaller bulb. If these substances are shown to be implicated in floral initiation in bulbs, it would partially explain the dependence of flowering on bulb size. A similar mechanism might operate to influence bulb-size in **H. pubescens** subsp. **pubescens** and a "shortage fund" could regulate floral initiation.

According to van Andel & Vera (1977) resource allocation patterns differ from species to species, thus the dissimilarities between biomass allocation patterns and resource allocation patterns found in one population of a species cannot be generalized or extrapolated to other species. Different intraspecific patterns have been observed between populations of **Verbascum thapsus** and different interspecific patterns between species of **Solidago** (Abrahamson & Caswell 1982). Similar allocation patterns were found in different populations of

Tipularia discolor (Whigham 1984). Thus the data presented here for H. **pubescens** subsp. **pubescens** must be treated with caution as it represents only one population.

The concentrations of nutrients in rapidly developing structures, such as the leaves in March, corresponds to patterns of other species (Whigham 1984; Nault & Gagnon 1988). The temporal displacement between flowering and leaf formation may allow optimal utilization of resources. The rapid senescence and decomposition of the leaves releases the nutrients to the soil, where they may be reabsorbed by the roots.

Biomass allocation patterns in non-reproductive plants were found to be irregular and to vary considerably from month to month (Fig. 3.2) and can be ascribed to the variation in sizes of the bulbs selected. This is also applicable to flowering plants, but biomass allocation patterns in mature and old reproductive plants are expected to be relatively uniform and stable (Fig. 3.1; see Chapter 1). It is not known how the occurrence or biomass allocation in flowering plants is influenced by population density.

The main survival strategy of the species appears to be centered on maintaining reserves accumulated in the bulb. H. **pubescens** subsp. **pubescens** showed a relatively fixed biomass allocation strategy for the majority of individuals within the population. Similar regularity has been observed in **Allium victorialis** subsp. **platyphyllum** (Kawano & Nagai 1975). The ability of the species to

mobilize and re-use restricted resources is an important property when coping with soils of a low nutrient status (Bowen 1984) characteristic of Fynbos soils (Groves **et al.** 1983). Efficient re-usage means the withdrawal of large proportions of nutrients such as K, P and N from leaves just before they senesce. Although elements present in fallen leaves represent a net loss to the plant, the release of immobile ions such as Ca, Na, Mg, Cu and Zn would occur only through decomposition (Bowen 1984). Bowen (1984) stated that the ability to store appreciable quantities of nutrients when not required for growth is undoubtedly a most important attribute in coping with low nutrients. Westman & Rogers (1977) suggested that the development of large underground biomass, such as the bulb, is a response to poor nutrition, and partly a strategy for protecting mineral and dry matter resources from fire. The advantage in the development of an underground storage organ is its substantial capacity for storing nutrients, an ability which should buffer the plant against variations in supply and demand of nutrients from season to season and after fire (Read **et al.** 1983). The nutrients are used for the establishment of herbaceous above-ground structures and roots which in turn are involved in the assimilation of photosynthate and the absorption of elements which contribute towards the replenishment of the nutrient stock. At the conclusion of the growth season the nutrients are retrieved from the senescing structure for storage. This functional behaviour of geophytes is regarded as luxury consumption (Witkowski & Mitchell 1989). The leaves and reproductive parts have rapid decomposition rates and thus the nutrients are released easily and leached into the soil and thus are available for reabsorption.

3.5 CONCLUSIONS

The results confirm that resource and biomass allocation patterns were distinct. Thus in estimating the allocation strategy within populations of this species, it would not be prudent to measure biomass and assume that it reflected allocation of all resources. The bulbs showed variable storage capacities for handling the resources. The development of an underground storage organ in **H. pubescens** subsp. **pubescens** might be regarded as a mechanism to cope with the low nutrient status of the fynbos biome. Thus the development of underground storage organs can be considered as an advantage compared to other life forms in fynbos. When compared with sclerophyllous species the nutrient stock of geophytes are safe-guarded against disturbances whereas in sclerophyllous species nutrient stocks are concentrated in the above-ground phytomass and can thus be lost during disturbance, eg. fire, through the volatilization of certain nutrients and also the run-off of nutrients deposited as ash during the rainy season.

3.6 REFERENCES

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3.7 APPENDIX

APPENDIX 3.7.1: Macronutrient (g.kg^{-1} d.m.) and carbohydrates (g.kg^{-1} d.m) concentrations in the plant parts of **H. pubescens** subsp. **pubescens** (reproductive plants).

LEAF-BASES

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Jan	149.86	11.89	166.00	22.62	0.44	0.07	4.85	0.91	12.32	0.97	1.00	0.10	4.65	0.53	0.81	0.24
Feb	126.40	16.98	174.83	13.70	0.58	0.06	3.93	0.38	7.37	0.44	1.01	0.11	3.72	0.35	0.75	0.10
March	118.59	8.77	156.72	6.75	0.77	0.17	4.55	0.56	12.55	1.04	1.61	0.35	4.57	0.56	1.14	0.18
April	207.70	12.66	152.04	12.28	0.57	0.21	4.17	0.53	12.37	0.74	1.25	0.04	6.17	0.60	0.74	0.07
May	137.82	9.58	182.03	11.54	0.70	0.10	4.90	0.41	14.63	0.80	1.39	0.05	2.88	0.18	0.71	0.14
June	215.65	25.45	117.08	17.42	0.47	0.08	3.34	0.34	11.57	2.05	1.44	0.15	4.21	1.03	1.03	0.30
July	206.83	7.06	150.22	32.10	0.58	0.18	3.71	0.55	9.81	0.49	1.31	0.05	4.13	0.68	0.94	0.25
August	255.60	30.10	209.06	26.44	0.30	0.04	2.95	0.12	10.77	0.34	1.20	0.02	4.73	0.62	1.30	0.29
Sept.	225.70	14.22	188.85	14.61	0.37	0.01	1.68	0.10	11.44	2.15	1.26	0.20	2.30	0.42	1.23	0.16
Oct.	237.17	11.54	212.02	16.86	0.35	0.03	3.69	0.46	12.13	0.62	1.19	0.12	4.19	0.64	1.05	0.09
Nov	221.60	8.24	217.32	12.59	0.54	0.06	3.58	0.14	11.57	0.62	1.15	0.06	5.10	0.44	0.63	0.05
Dec	145.04	7.92	190.73	7.63	0.44	0.07	5.17	0.66	13.32	0.68	1.04	0.11	4.33	0.58	1.09	0.15

STEM

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Jan	124.57	8.13	173.48	22.71	0.84	0.08	5.87	1.06	18.29	2.10	1.71	0.14	3.60	0.67	0.85	0.22
Feb	98.10	9.57	149.79	10.85	1.61	0.19	5.61	0.51	12.16	0.91	2.02	0.11	8.69	0.71	1.14	0.15
March	108.33	4.56	179.82	8.78	1.43	0.24	12.33	1.31	13.23	0.75	1.96	0.08	6.61	0.44	1.22	0.16
April	107.00	8.51	152.50	11.95	1.68	0.21	10.60	0.89	15.56	1.26	2.19	0.04	7.53	0.65	1.14	0.06
May	170.47	27.35	205.81	13.98	1.96	0.17	9.40	1.32	13.94	0.91	1.61	0.24	3.93	0.98	1.03	0.29
June	236.85	30.45	199.06	1.44	0.65	0.04	4.10	0.91	12.36	1.27	1.77	0.05	4.64	0.60	1.49	0.49
July	187.94	5.73	181.21	12.59	1.46	0.20	3.15	0.22	11.04	0.67	1.70	0.08	5.89	0.43	1.02	0.10
August	185.80	15.09	209.58	16.76	0.64	0.12	3.23	0.08	12.56	0.59	1.39	0.08	6.21	0.75	1.45	0.17
Sept.	216.20	13.30	165.82	17.46	0.70	0.11	3.30	0.51	9.08	0.08	1.46	0.22	3.31	0.66	1.55	0.06
Oct.	176.26	17.63	152.36	7.82	0.61	0.06	3.39	0.37	11.95	0.66	1.26	0.09	5.42	0.37	1.16	0.07
Nov	157.05	13.20	165.62	10.06	0.53	0.13	3.76	0.18	12.89	1.54	2.05	0.16	5.73	0.59	0.85	0.17
Dec	153.73	9.73	204.81	21.48	0.97	0.17	4.65	0.68	13.10	1.31	1.50	0.05	5.97	0.45	1.16	0.05

FRUIT

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
April	152.38	5.26	133.24	7.89	1.65	0.04	8.81	0.68	16.03	0.36	1.59	0.22	5.92	0.45	0.67	0.06

APPENDIX 3.7.1: Continues

LEAVES

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
March	73.30	10.41	30.99	2.99	3.19	0.13	21.87	0.06	43.10	0.39	2.47	0.09	4.84	0.55	3.51	0.05
April	67.63	4.42	30.73	2.61	2.10	0.08	17.90	0.69	38.92	0.20	2.47	0.10	4.09	0.88	0.76	0.06
May	67.96	14.89	23.30	1.85	1.35	0.04	12.35	0.75	49.09	2.99	3.73	0.11	6.11	0.68	6.15	0.73
June	54.60	1.61	17.97	2.48	1.21	0.04	12.46	0.22	48.71	5.13	3.27	0.08	3.04	0.56	10.20	1.17
July	40.24	7.85	9.21	1.56	1.41	0.10	11.40	1.09	34.82	3.23	3.59	0.24	7.04	0.73	15.20	1.48
August	29.98	6.11	12.57	1.66	1.01	0.12	10.75	1.10	21.60	7.44	1.67	0.35	3.63	1.43	9.99	3.11

ROOTS

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Feb	4.42	1.05	2.90	0.16	1.40	0.04	11.08	1.00	29.81	0.07	1.90	0.01	3.50	0.21	12.25	0.14
March	4.86	0.10	3.96	0.15	1.46	0.08	8.75	3.13	23.44	0.62	1.76	0.12	4.77	1.10	7.87	0.23
April	3.91	0.13	2.78	0.21	0.20	0.01	10.20	0.11	25.14	0.10	4.13	0.04	0.16	0.10	7.74	0.13
May	3.74	0.22	1.84	0.19	1.11	0.12	10.17	1.37	15.78	2.34	1.63	0.06	2.87	0.57	6.44	0.11
June	5.13	0.16	3.24	0.55	1.05	0.01	8.40	0.70	35.37	0.14	2.05	0.01	2.00	0.09	11.56	0.25
July	4.27	0.23	1.39	0.28	1.50	0.13	8.52	0.51	33.88	1.11	2.03	0.07	2.04	0.17	11.15	0.44
August	6.78	0.53	3.73	0.20	1.63	0.01	7.54	1.56	24.37	0.38	2.18	0.04	2.43	0.69	14.48	0.29
Sept.	3.96	0.45	2.51	0.30	1.57	0.00	11.85	1.75	34.38	0.19	1.85	0.00	2.16	0.02	12.13	0.04
Oct.	3.92	1.22	2.52	0.33	1.24	0.02	12.56	0.36	27.37	0.07	1.85	0.04	3.78	0.17	12.00	0.35
Nov	3.35	0.94	3.80	0.10	1.19	0.01	8.91	0.43	32.72	0.48	3.01	0.02	2.72	0.20	9.58	0.30

INFLORESCENCES

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Jan	205.83	2.39	ND	ND	1.56	0.08	8.84	0.25	27.65	0.31	2.70	0.01	5.93	0.14	0.70	0.00
Feb	117.33	3.98	47.77	12.10	1.62	0.09	8.98	0.13	20.50	0.41	3.86	0.17	4.29	0.31	0.88	0.01

INFLORESCENCE STALK

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
March	36.60	3.56	19.21	2.97	0.46	0.01	5.32	0.36	17.21	0.51	3.60	0.07	3.89	0.22	2.16	0.03

FLOWERS

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
March	10.41	2.99	13.55	0.37	0.45	0.02	5.81	0.25	11.18	0.17	2.89	0.05	5.86	0.21	0.85	0.01

APPENDIX 3.7.2: Micronutrient ($mg.kg^{-1}$ d.m) concentrations in the plant parts of **h. pubescens** subspecies **pubescens** (reproductive plants).

LEAF-BASES

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Jan	0.005	0.001	0.078	0.012	0.049	0.004	0.021	0.001
Feb	0.007	0.001	0.276	0.100	0.064	0.002	0.028	0.010
March	0.013	0.004	0.119	0.030	0.071	0.004	0.033	0.002
April	0.007	0.001	0.085	0.007	0.071	0.009	0.034	0.000
May	0.015	0.001	0.107	0.010	0.074	0.002	0.033	0.001
June	0.047	0.004	0.390	0.042	0.033	0.003	0.031	0.001
July	0.009	0.001	0.348	0.084	0.040	0.001	0.031	0.004
August	0.016	0.002	0.709	0.340	0.048	0.002	0.027	0.002
Sept.	0.019	0.005	0.348	0.040	0.061	0.002	0.038	0.005
Oct.	0.010	0.001	0.255	0.047	0.056	0.009	0.025	0.010
Nov	0.006	0.001	0.060	0.004	0.027	0.001	0.016	0.001
Dec	0.008	0.001	0.101	0.019	0.038	0.008	0.201	0.002

STEM

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Jan	0.018	0.002	0.099	0.054	0.062	0.004	0.069	0.001
Feb	0.020	0.002	0.124	0.052	0.070	0.006	0.077	0.004
March	0.021	0.003	0.111	0.030	0.071	0.002	0.013	0.001
April	0.024	0.003	0.105	0.020	0.082	0.003	0.021	0.002
May	0.016	0.001	0.131	0.050	0.022	0.003	0.019	0.002
June	0.026	0.007	0.059	0.001	0.019	0.003	0.018	0.000
July	0.020	0.001	0.102	0.040	0.025	0.002	0.022	0.004
August	0.012	0.003	0.049	0.003	0.040	0.006	0.019	0.001
Sept.	0.019	0.004	0.037	0.008	0.024	0.004	0.029	0.002
Oct.	0.017	0.001	0.083	0.024	0.039	0.004	0.042	0.003
Nov	0.023	0.004	0.023	0.004	0.044	0.003	0.051	0.006
Dec	0.020	0.003	0.092	0.033	0.050	0.002	0.065	0.000

LEAVES

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
March	0.009	0.001	0.221	0.007	0.069	0.002	0.279	0.001
April	0.012	0.006	0.191	0.010	0.066	0.002	0.021	0.001
May	0.008	0.002	0.184	0.006	0.069	0.001	0.031	0.001
June	0.004	0.000	0.143	0.014	0.032	0.002	0.034	0.003
July	0.005	0.000	0.202	0.014	0.040	0.001	0.031	0.003
August	0.008	0.002	0.423	0.125	0.072	0.025	0.037	0.009

ROOTS

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Feb	0.015	0.000	0.169	0.001	0.118	0.001	0.051	0.001
March	0.014	0.001	0.169	0.026	0.116	0.003	0.050	0.004
April	0.017	0.000	0.486	0.001	0.121	0.001	0.054	0.001
May	0.008	0.000	0.142	0.003	0.109	0.001	0.043	0.000
June	0.009	0.000	0.112	0.003	0.093	0.001	0.042	0.001
July	0.018	0.003	0.110	0.003	0.111	0.003	0.058	0.007
August	0.014	0.000	0.132	0.001	0.116	0.002	0.033	0.001
Sept.	0.014	0.000	0.088	0.001	0.129	0.001	0.047	0.001
Oct.	0.011	0.000	0.109	0.001	0.109	0.002	0.040	0.000

INFLORESCENCE

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Jan	0.005	0.000	0.165	0.003	0.108	0.001	0.017	0.000
Feb	0.008	0.000	0.203	0.001	0.105	0.002	0.216	0.000

INFLORESCENCE STALK

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
March	0.005	0.000	0.187	0.002	0.106	0.001	0.032	0.000

FLOWERS

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
March	0.006	0.000	0.239	0.007	0.122	0.001	0.031	0.001

FRUIT

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
April	0.008	0.001	0.242	0.050	0.111	0.002	0.018	0.005

APPENDIX 3.7.3: Macronutrient ($g.kg^{-1}$ d.m.) and carbohydrates ($g.kg^{-1}$ d.m.) concentrations in the plant parts of **H. pubescens** subspecies **pubescens** (non-reproductive plants).

LEAF-BASES

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Jan	164.95	7.60	226.43	10.68	0.64	0.11	5.39	0.43	18.31	0.62	1.05	0.04	5.15	0.30	0.83	0.06
Feb	132.14	13.49	181.93	5.74	0.60	0.15	4.62	0.50	18.61	0.64	0.94	0.15	4.60	0.76	0.90	0.07
March	130.13	12.06	158.50	15.71	0.48	0.11	3.77	0.54	18.19	1.22	1.36	0.17	5.63	0.92	1.14	0.15
April	124.05	28.04	154.01	14.55	0.62	0.27	3.74	0.58	17.66	1.02	1.02	0.05	3.85	0.76	0.73	0.11
May	166.31	7.24	166.40	7.61	0.91	0.08	4.23	0.30	18.27	0.92	1.23	0.10	4.34	0.61	0.99	0.06
June	191.20	19.94	143.27	8.79	0.91	0.04	3.94	0.28	18.56	0.55	1.36	0.05	3.68	0.68	1.13	0.14
July	151.63	30.90	154.43	1.42	0.45	0.18	4.54	0.72	17.78	2.16	1.42	0.11	5.07	1.67	0.95	0.07
August	159.24	15.75	174.85	9.87	0.50	0.04	5.55	0.83	17.68	0.69	1.05	0.10	4.83	0.54	1.04	0.05
Sept.	256.63	21.37	155.63	10.41	0.73	0.10	4.16	0.91	19.63	1.11	1.25	0.15	3.34	0.36	1.21	0.16
Oct.	226.45	17.16	71.20	15.32	0.36	0.59	4.59	0.41	12.56	0.72	1.15	0.15	3.78	0.52	1.17	0.15
Nov	217.70	9.96	221.88	3.58	0.65	0.09	3.56	0.70	11.93	0.80	1.22	0.14	4.01	0.06	0.61	0.05
Dec	142.03	8.02	130.99	21.58	0.44	0.13	3.85	0.67	13.84	0.48	0.85	0.01	4.80	0.23	1.09	0.07

STEM

	SOL CHO X	SE	STARCH X	SE	PHOSPHATE X	SE	NITROGEN X	SE	POTASSIUM X	SE	MAGNESIUM X	SE	CALCIUM X	SE	SODIUM X	SE
Jan	132.98	16.25	190.51	10.23	0.91	0.02	5.56	0.66	17.49	1.32	2.03	0.09	5.98	1.26	1.75	0.29
Feb	108.64	10.33	180.61	19.01	1.25	0.15	5.34	0.60	19.97	1.12	1.53	0.07	6.12	1.05	1.55	0.19
MARCH	114.05	7.90	156.45	19.90	0.44	0.11	10.39	3.67	13.54	0.63	1.76	0.19	7.95	1.03	1.19	0.21
April	121.30	11.16	174.69	9.90	1.83	0.61	11.00	1.90	16.09	0.86	2.07	0.10	7.16	1.04	1.05	0.14
May	184.16	16.49	150.08	11.21	0.74	0.15	8.06	1.22	14.26	0.75	1.45	0.10	5.56	0.48	1.34	0.12
June	217.50	24.16	204.12	7.85	0.50	0.02	3.23	0.20	7.97	0.25	1.86	0.01	4.45	0.38	1.09	0.08
July	177.75	16.15	136.07	23.76	1.84	0.22	4.95	0.50	12.96	1.25	2.09	0.23	6.66	0.35	0.73	0.08
August	192.28	2.86	171.62	18.60	0.95	0.16	2.58	0.35	10.37	0.99	1.49	0.09	5.59	0.39	1.10	0.15
Sept.	150.05	2.89	122.45	17.91	1.20	0.41	4.34	0.80	12.30	5.26	1.36	0.33	2.77	0.85	1.28	0.52
Oct.	132.18	11.17	152.03	16.33	0.66	0.04	3.95	0.69	14.08	0.81	1.47	0.01	3.92	1.30	1.52	0.29
Nov	123.08	2.82	176.06	9.95	0.84	0.14	3.63	0.27	15.08	0.50	1.71	0.07	4.61	0.52	0.84	0.10
Dec	128.87	5.77	187.34	13.15	0.81	0.02	4.72	0.66	13.51	0.82	1.61	0.06	6.34	0.79	1.56	0.02

APPENDIX 3.7.4: Micronutrient ($mg.kg^{-1}$) concentrations in the plant parts of **H. pubescens** subspecies **pubescens** (non-reproductive plants).

LEAF-BASES

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Jan	0.007	0.001	0.148	0.053	0.049	0.002	0.021	0.002
Feb	0.006	0.000	0.151	0.040	0.057	0.002	0.037	0.010
March	0.011	0.003	0.136	0.030	0.067	0.009	0.049	0.010
April	0.008	0.001	0.081	0.014	0.072	0.001	0.030	0.001
May	0.011	0.001	0.189	0.010	0.078	0.002	0.038	0.001
June	0.008	0.001	0.198	0.020	0.030	0.002	0.029	0.006
July	0.010	0.002	0.215	0.032	0.041	0.006	0.034	0.008
August	0.009	0.001	0.481	0.270	0.055	0.001	0.032	0.003
Sept.	0.025	0.007	0.345	0.040	0.060	0.003	0.039	0.005
Oct.	0.010	0.002	0.153	0.023	0.041	0.017	0.021	0.010
Nov	0.007	0.001	0.084	0.020	0.025	0.001	0.014	0.001
Dec	0.007	0.002	0.137	0.074	0.039	0.002	0.016	0.001

STEM

	ZINC X	SE	IRON X	SE	COPPER X	SE	MANGANESE X	SE
Jan	0.021	0.002	0.126	0.034	0.061	0.004	0.071	0.001
Feb	0.023	0.002	0.144	0.037	0.070	0.004	0.024	0.003
March	0.020	0.004	0.226	0.081	0.076	0.005	0.033	0.006
April	0.027	0.002	0.332	0.200	0.089	0.001	0.033	0.009
May	0.019	0.001	0.122	0.050	0.027	0.002	0.025	0.001
June	0.018	0.005	0.072	0.021	0.015	0.002	0.015	0.002
July	0.023	0.002	0.098	0.033	0.033	0.006	0.025	0.005
August	0.018	0.003	0.081	0.029	0.033	0.010	0.028	0.006
Sept.	0.019	0.001	0.249	0.114	0.041	0.003	0.055	0.002
Oct.	0.016	0.002	0.088	0.053	0.042	0.004	0.050	0.004
Nov	0.019	0.001	0.009	0.004	0.040	0.002	0.052	0.001
Dec	0.014	0.002	0.137	0.091	0.047	0.001	0.065	0.001

APPENDIX 3.7.5: Biomass (g. dry mass) changes in the plant parts of reproductive plants of **H. pubescens** subspecies **pubescens**.

LEAF-BASES

	X	SE
JAN	9.84	0.75
FEB	10.95	1.57
MARCH	13.11	0.74
APRIL	9.10	1.69
MAY	15.24	2.10
JUNE	14.27	7.01
JULY	16.13	1.26
AUGUST	12.09	0.72
SEPTEMBER	13.40	0.72
OCTOBER	12.61	2.60
NOVEMBER	13.69	0.69
DECEMBER	14.12	3.05

STEM

	X	SE
JAN	1.50	0.69
FEB	2.17	0.41
MARCH	3.08	0.13
APRIL	1.97	0.10
MAY	3.36	0.47
JUNE	4.19	1.46
JULY	4.00	0.25
AUGUST	2.61	0.33
SEPTEMBER	2.30	0.71
OCTOBER	2.50	0.46
NOVEMBER	2.36	0.13
DECEMBER	2.62	0.52

LEAVES

	X	SE
MARCH	0.15	0.02
APRIL	0.37	0.06
MAY	1.26	0.20
JUNE	0.66	0.17
JULY	1.46	0.34
AUGUST	1.16	0.37

ROOTS

	X	SE
JAN	0.04	0.01
FEB	0.10	0.02
MARCH	0.06	0.01
APRIL	0.08	0.00
MAY	0.08	0.05
JUNE	0.13	0.04
JULY	0.35	0.07
AUGUST	0.08	0.02
SEPTEMBER	0.18	0.03
OCTOBER	0.07	0.02
NOVEMBER	0.04	0.00

INFLORESCENCE

	X	SE
JAN	0.26	0.04
FEB	0.20	0.04
NOV	0.04	0.01
DEC	0.07	0.02

FLOWERS

	X	SE
MARCH	0.18	0.02

INFLORESCENCE STAL

	X	SE
MARCH	0.15	0.02

FRUIT

	X	SE

APPENDIX 3.7.6: Biomass (g. dry mass) changes in the plant parts of non-reproductive plants of **H. pubescens** subspecies **pubescens.**

LEAF-BASES

	X	SE
JAN	[illegible]	[illegible]
FEB	[illegible]	[illegible]
MARCH	[illegible]	[illegible]
APRIL	[illegible]	[illegible]
MAY	[illegible]	[illegible]
JUNE	[illegible]	[illegible]
JULY	[illegible]	[illegible]
AUGUST	[illegible]	[illegible]
SEPTEMBER	[illegible]	[illegible]
OCTOBER	[illegible]	[illegible]
NOVEMBER	[illegible]	[illegible]
DECEMBER	[illegible]	[illegible]

STEM

	X	SE
JAN	[illegible]	[illegible]
FEB	[illegible]	[illegible]
MARCH	[illegible]	[illegible]
APRIL	0.91	0.30
MAY	0.94	0.39
JUNE	[illegible]	[illegible]
JULY	[illegible]	0.90
AUGUST	[illegible]	[illegible]
SEPTEMBER	1.17	0.09
OCTOBER	0.56	0.18
NOVEMBER	0.37	0.07
DECEMBER	0.79	0.41

LEAVES

	X	SE
MARCH	0.15	0.02
APRIL	0.37	0.05
MAY	[illegible]	0.29
JUNE	0.56	0.17
JULY	[illegible]	0.34
AUGUST	[illegible]	0.37

ROOTS

	X	SE
JAN	0.04	0.01
FEB	0.10	0.02
MARCH	[illegible]	[illegible]
APRIL	[illegible]	[illegible]
MAY	[illegible]	0.05
JUNE	[illegible]	0.04
JULY	[illegible]	0.07
AUGUST	[illegible]	[illegible]
SEPTEMBER	[illegible]	[illegible]
OCTOBER	[illegible]	[illegible]
NOVEMBER	[illegible]	[illegible]

CHAPTER 4

SEASONAL ECONOMY OF MINERAL NUTRIENT AND ORGANIC SUBSTANCE ALLOCATION IN *SPARAXIS GRANDIFLORA* SUBSP. *FIMBRIATA* DURING GROWTH AND REPRODUCTION IN RELATION TO BIOMASS

Contents

4.1 INTRODUCTION

Since leaf and shoot growth, flowering and fruiting require nutrients over and above those necessary for plant maintenance, it is obvious that the seasonality of these activities must be related to patterns of absolute and seasonal availability of nutrients.

At the commencement of each new growth season, mineral nutrients and organic substances carried over in the corm from the previous season are used for production of a new generation of leaves and roots, and flowers if the plant has reached reproductive age. These organs then become engaged in uptake of further mineral nutrients from the environment and assimilation of organic substances which comprise a pool from which the new season's corm and seed will draw.

In this paper the seasonal changes in allocation patterns for certain mineral nutrients and organic substances are described. Nitrogen, potassium, magnesium, calcium, phosphorus, sodium, zinc, manganese, copper and iron and the organic substances starch and soluble carbohydrates (CHO) were investigated. Seasonal changes in allocation patterns for each of these nutrients were plotted in a manner that was described for dry weight in Chapter 2.

4.2 METHODS

4.2.1 Study Site and Sampling

See Chapter 2 for a detailed account of the study site and the sampling methods employed.

4.2.2 Plant Material and Harvesting of Plants

See Chapter 2 for a detailed account.

4.2.3 Analysis of Plant Organs for Water and Resources

See Chapter 3 for a detailed account of the methods employed.

4.2.4 Resource Concentrations and Allocation

See Chapter 3 for the methods employed.

4.3 RESULTS AND DISCUSSION

4.3.1 Resource Concentrations

Concentration patterns with levels of significance for the constituent plant parts are given in Table 4.1. The calender year was divided into four phenophases and the results are

Table 4.1 Concentration patterns in the constituent plant parts of **S. grandiflora** subsp. **fimbriata** during the different phenological phases of the year.

PHENOPHASES	CONCENTRATION PATTERNS	RESOURCES
Dormant Period (Jan - March)	Corm Only	All Elements
Vegetative Period (March - August)	L >** R >** C L >** C ≥NS R R >** L ≥NS C C >** L >** R	K P, N, Ca, Mg Na, Mn, Zn, Fe Starch;Sol.CHO;Cu
Reproductive Period (Aug - Oct)	L >** RS >** R >** C RS >* C ≥NS L >** R R >** L >** C ≥NS RS C >** RS >** L >** R	P, Ca, Mg, K N Zn,Fe,Mn,Cu,Na Starch, CHO
Senescent Period (Oct - Dec)	L >** RS >** C RS ≥NS L >** C RS >* C >** L L >** C ≥NS RS C >** RS ≥NS L	Ca, K Mg, P N, Fe Mn, Zn, Na Cu,Starch,CHO

Symbols:
** = $p \leq 0.01$ (Highly Significant)
* = $p \leq 0.05$ (Significant)
NS = Not Significant

L = Leaves; C = Corm; R = Roots; RS = Reproductive Structures.

discussed in relation to these.

4.3.1.1 Dormant Period (Jan - March)

For this period the corm is the only aestivating vegetative plant part.

4.3.1.2 Vegetative Period (March - August)

Most of the macronutrient concentrations were significantly higher in the leaves, micronutrients and Na in the roots and starch, CHO and Cu in the corms. The leaves were particularly important during this phase.

4.3.1.3 Reproductive Period (August - October)

The pattern of the vegetative period was largely maintained during the reproductive period, with the reproductive structures also having considerable concentrations except for the micronutrients and Na which were significantly higher in the roots. The corm, as always contained significantly higher levels of starch, but the concentrations of soluble carbohydrates in the corm were not significantly {$t(40) = 1.035$, $p = 0.3067$} higher than those in the reproductive structures although they were significantly higher than in the other vegetative parts.

4.3.1.4 Senescent Period (October - December)

Concentrations of the soluble carbohydrates, starch and Cu were significantly higher in the corm. The leaves still had

significantly higher concentrations of the macronutrients K and Ca, and Na and the micronutrients Mn and Zn, than occurred elsewhere. The nutrients (resources) N, Fe, Mg and P were generally higher in the reproductive structures than elsewhere, but this was not significant for Mg and P {eg. Mg: $t(41) = 1.027$, $p = 0.3268$}.

4.3.1.5 General Discussion

The leaves constituted the major plant part for the macro- and micronutrients throughout the assimilatory phase. The concentrations in the leaves were significantly higher for all nutrients than in the other plant parts. The micro-elements, involved in photosynthetic activity, viz. Zn, Mn and Fe (Evans & Sorger 1966; Whigham 1984), had concentrations that varied from 0.011 to 0.262 $mg.kg^{-1}$ (see Appendix 4.6.1). In the case of reproductive concentration, flowers were relatively low in the majority of the elements, except for N, P and K which were particularly enriched (see Appendix 4.6.1). The fruits contained a significantly higher concentration of all the nutrients than the flowers, except for Ca and Na.

During the first two months of vegetative growth the roots accumulated considerable levels of nutrients. Thereafter they showed a substantial decline for N, K and P. The pattern of the three remaining macro-nutrients were consistent with a few minor fluctuations. A possibility was that nutrients were translocated to the roots from the parent corm during the initial growth

phase. At the end of the growth season they may be translocated to the above ground parts as it senesced, or the nutrients may simply be lost to the soil and later reabsorbed by the plant, with or without an intervening cycle of litter decomposition (Bowen 1981).

4.3.2 Resource allocation

Chmielewski & Ringuis (1987) stated that dry weight can be used as a measurement for biomass (see Fig. 2.6) allocation patterns for the following reasons:

(i) it reflects the integration of all physiological processes throughout the season (Abrahamson & Caswell 1982);

(ii) it is simple and fast to use;

(iii) biomass reflects the functional aspects of all assimilations;

(iv) it is the best available measure of resource allocation for comparing species growing in different environments when the availability of and species requirements for, particular nutrients are unknown (Gross et al. 1983); and

(v) energy content and dry weight equally reflect energy allocation patterns in plants (Hickman & Pitelka 1975).

They stressed that differences in allocation of resources to various tissues may indicate differences in adaptation or life history strategies.

Although the corm was found to be the major storage plant organ, six general patterns were identified and are as follows:

1. Relatively large amounts of the macronutrient K are allocated to the leaves than to the storage organ during both the vegetative and reproductive periods (Fig. 4.1). The trend is the same for P, Mg and Ca and the leaves while present are major sinks for thes elements.
2. Relatively similar amounts of Na (Fig. 4.2) are allocated to the roots and leaves at the beginning of the vegetative period. Equal amounts are allocated to the leaves and daughter corm during the reproductive period with an abrupt decline at the beginning of the senescent period (Oct - Nov). The same is true for the leaves. Relatively constant amounts of Na were present in the parent corm throughout its life-span. During the latter part of the senescent period there was an increase in the amounts of Na in the inflorescence stem and leaves.
3. Relatively large amounts of the micronutrients Zn, Mn and Fe are allocated to the roots and leaves during the vegetative and reproductive stages of the species. This pattern is indicated for Zn in Fig. 4.3 and is similar for the other two micronutrients.
4. Starch (Fig. 4.4) was unique in that the parent- and daughter corms were the only major sites for allocation. Negligible amounts of the resource were allocated to the other plant parts throughout active growth.

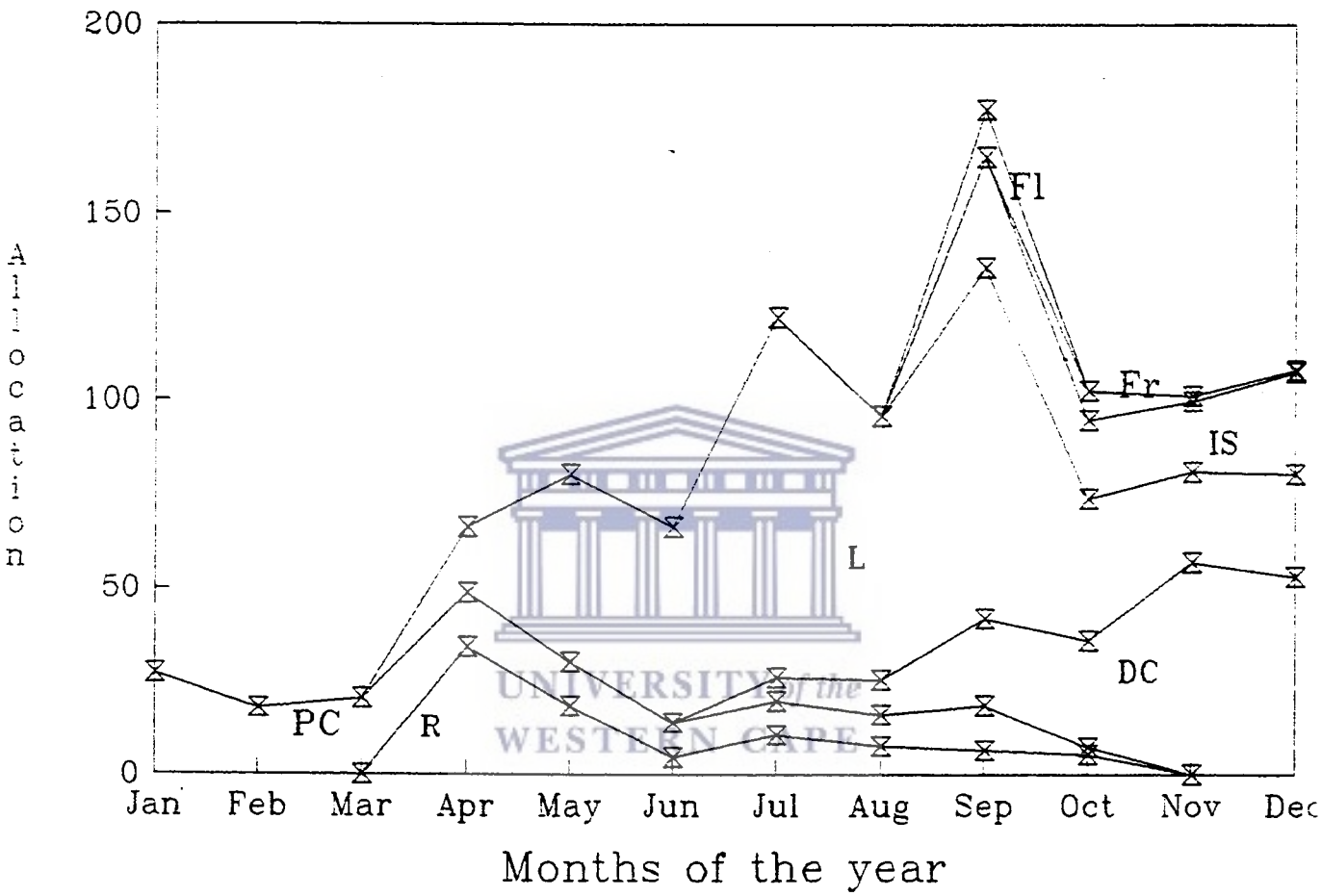

Figure 4.1: Seasonal changes in potassium (mg) allocation patterns in **S. grandiflora** subsp. **fimbriata** plant structures.

See Fig. 2.6 (Chapter 2) for the symbols.

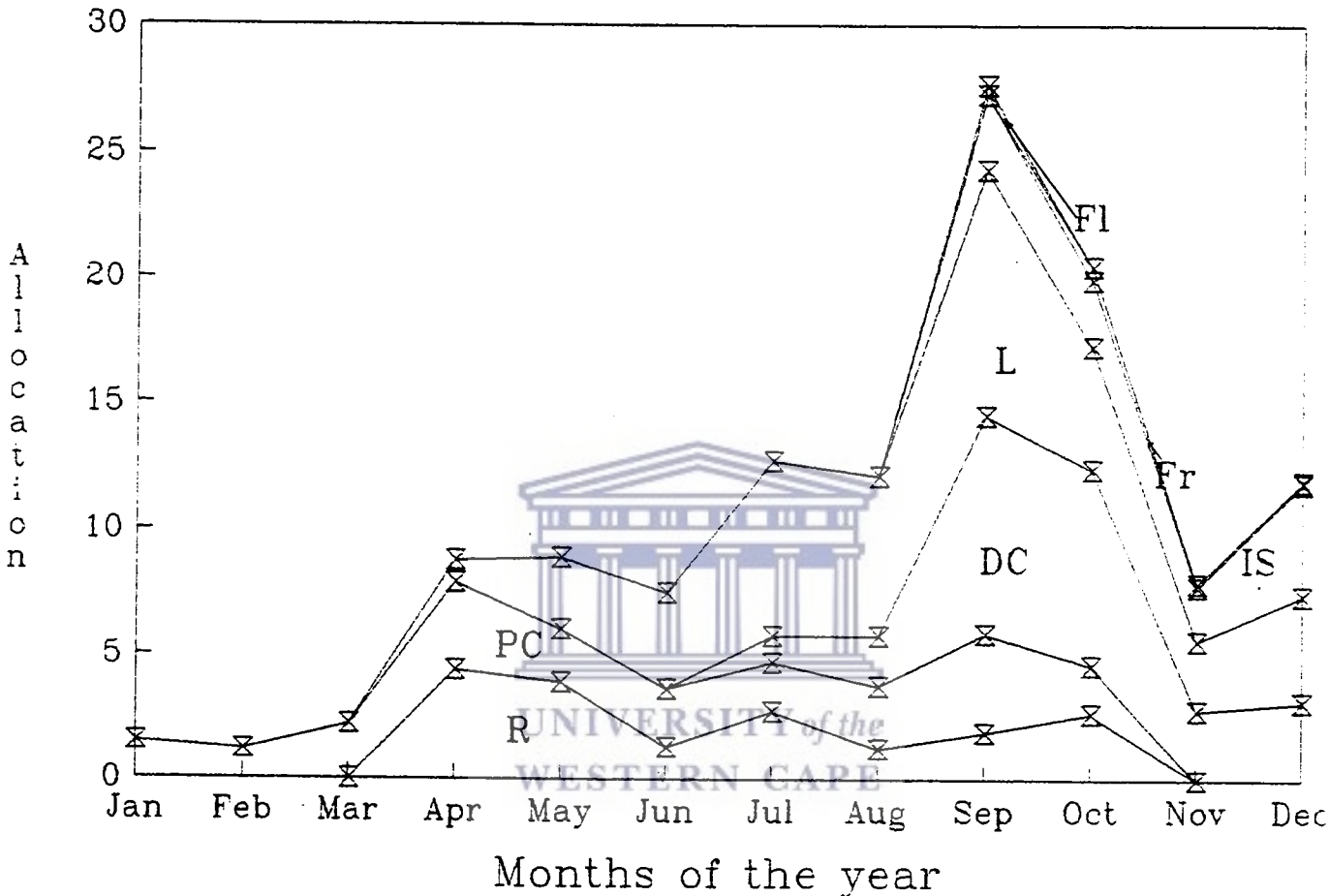

Figure 4.2: Seasonal changes in sodium allocation (mg) patterns in **S. grandiflora** subsp. **fimbriata** plant structures.

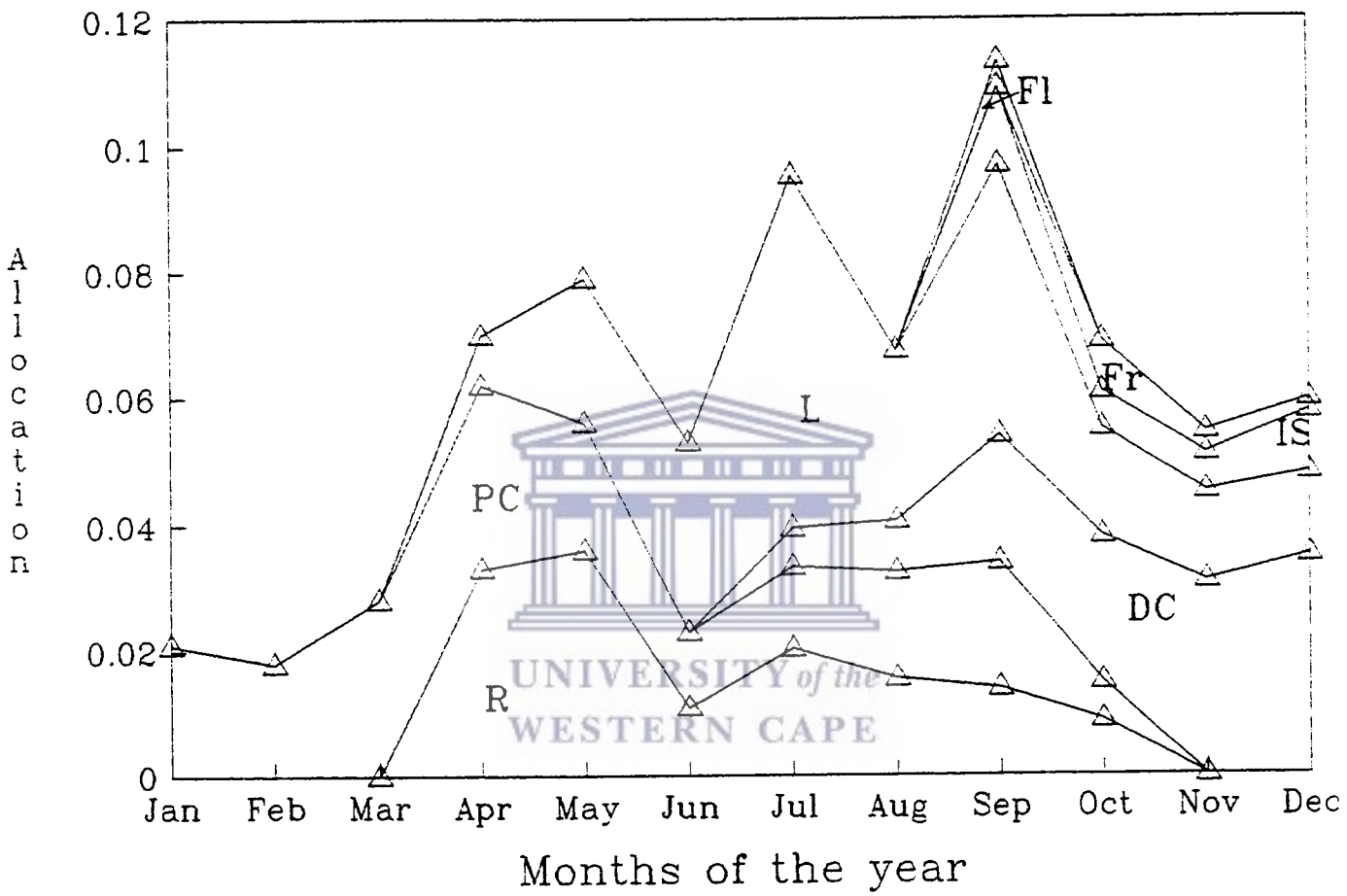

Figure 4.3: Seasonal changes in zinc allocation (ug) patterns in **S. grandiflora** subsp. **fimbriata** plant structures.

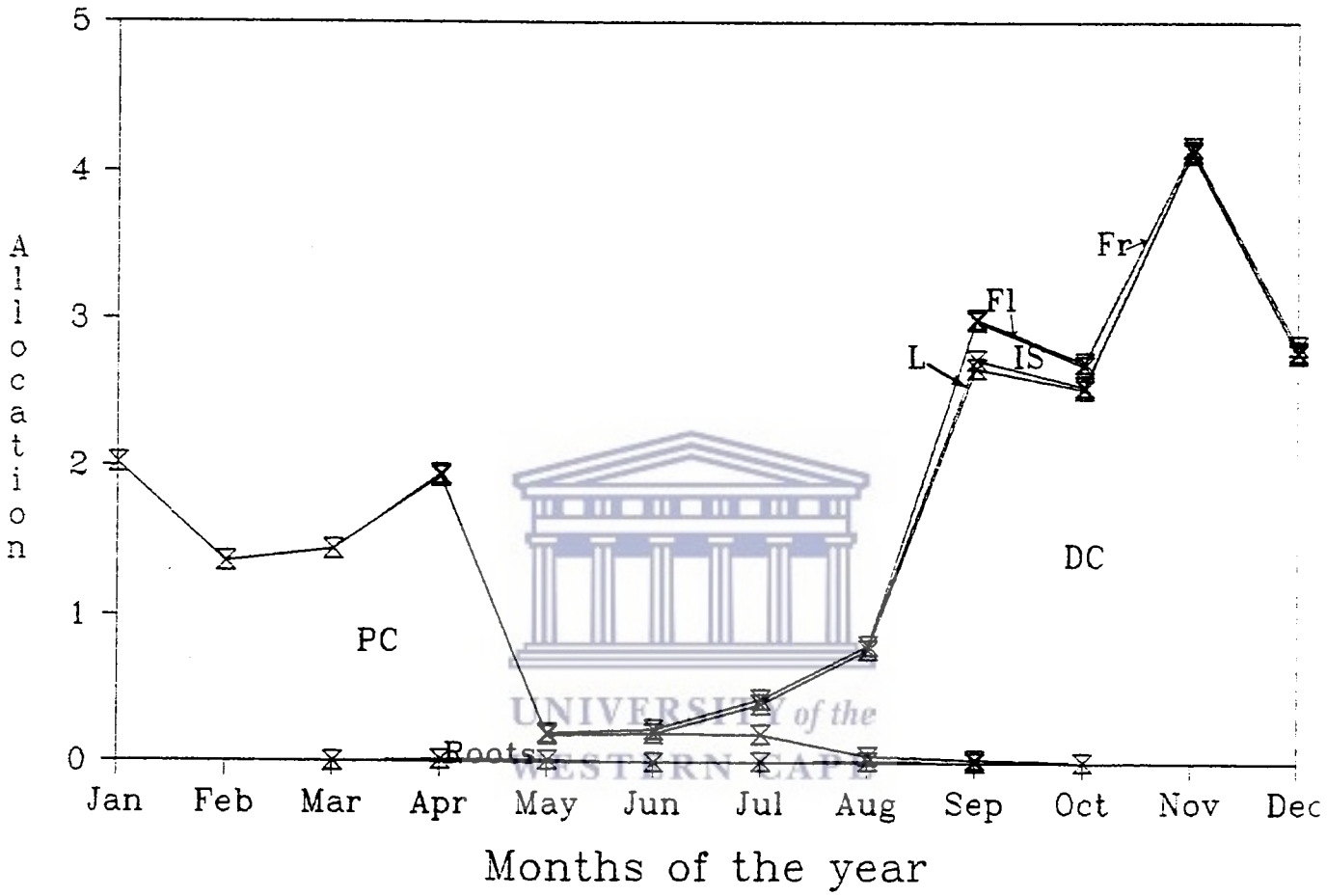

Figure 4.4: Seasonal changes in starch allocation (mg in thousands) patterns in **S. grandiflora** subsp. **fimbriata** plant structures.

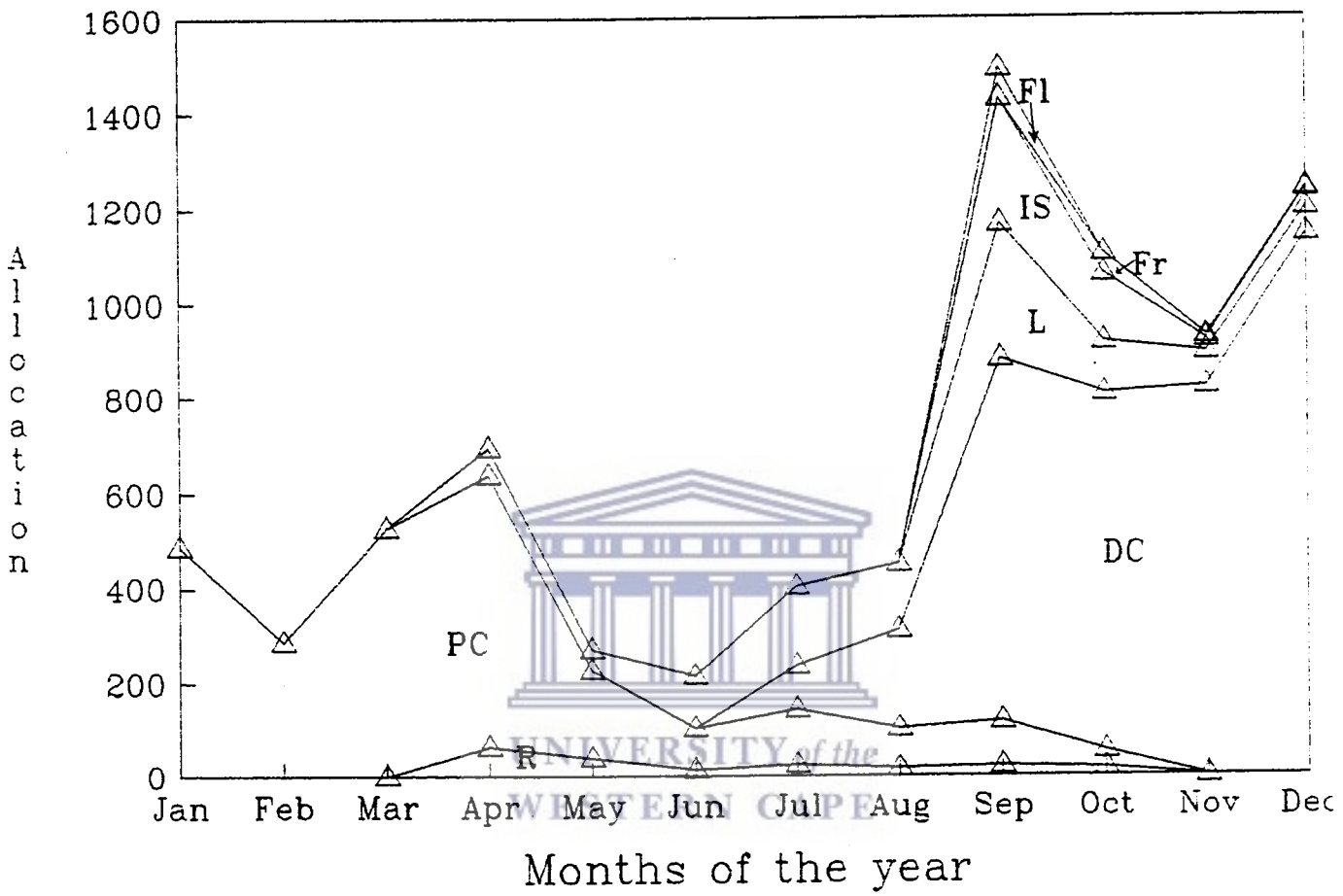

Figure 4.5: Seasonal changes in soluble carbohydrates (mg in thousands) allocation patterns in **S. grandiflora** subsp. **fimbriata** plant structures.

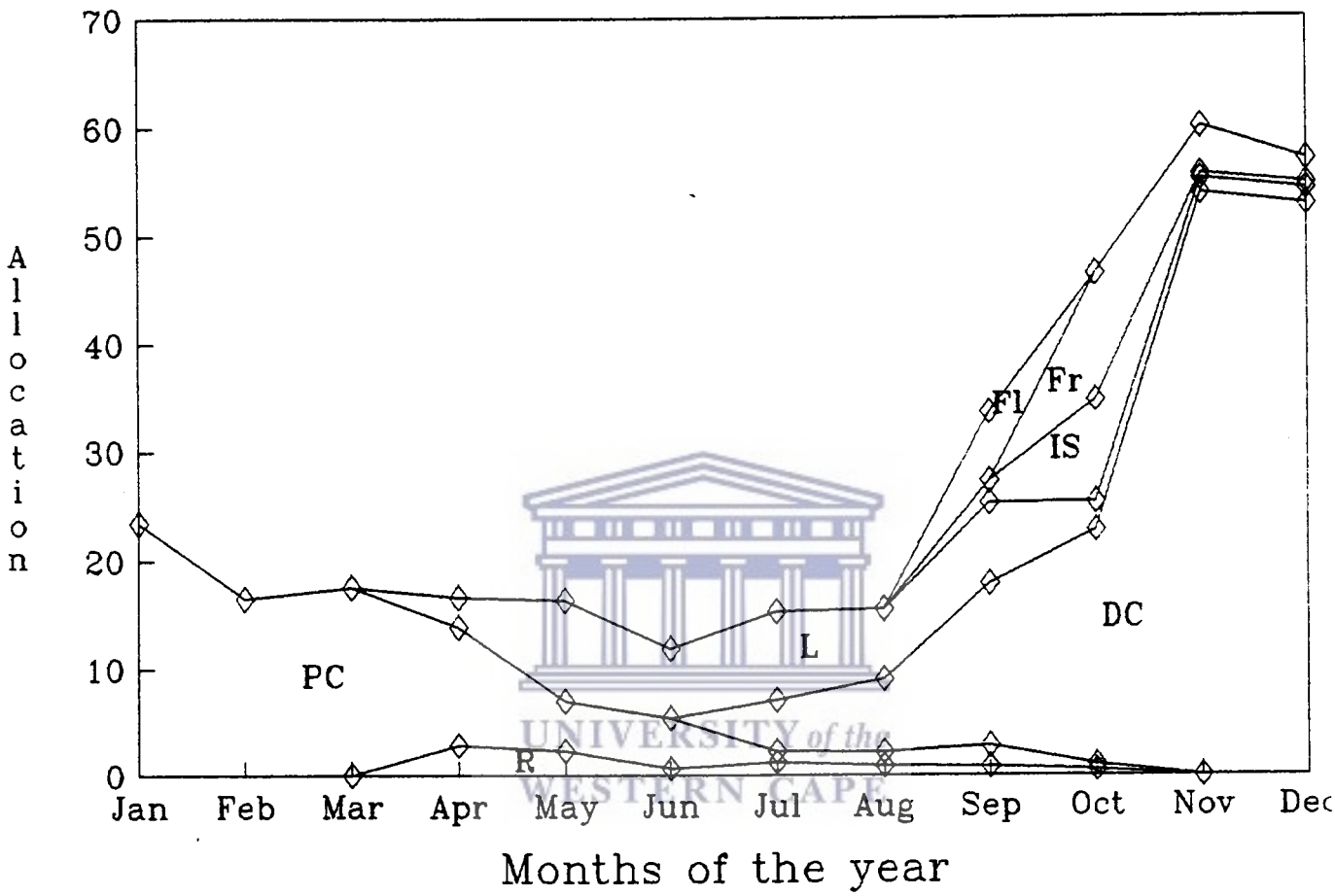

Figure 4.6: Seasonal changes in nitrogen allocation (mg) in **S. grandiflora** subsp. **fimbriata** plant structures.

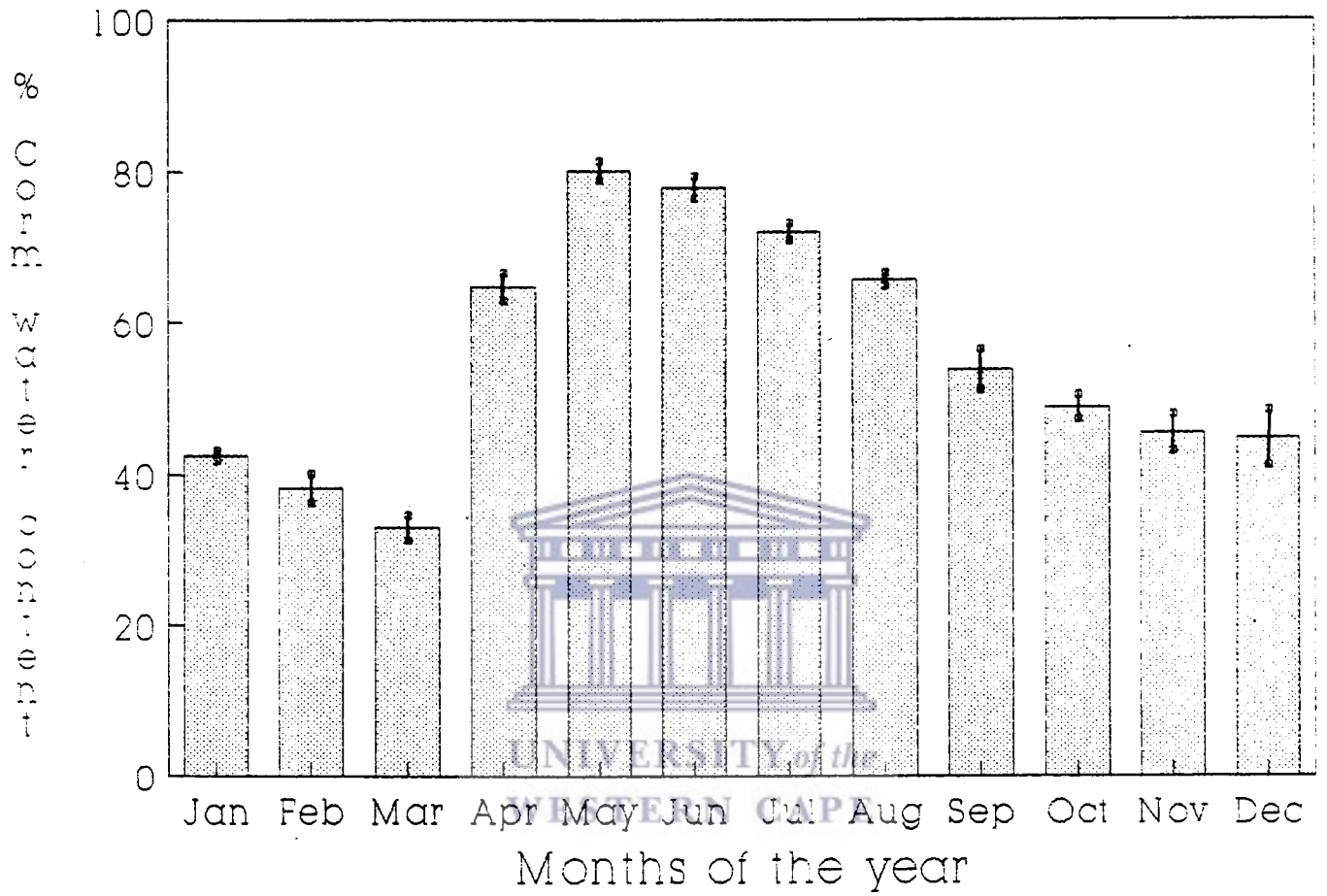

Figure 4.7: Mean monthly corm water content (%) (±SE) of a **S. grandiflora** subsp. **fimbriata** population.

5. For the soluble carbohydrates (Fig. 4.5) the parent and daughter corms served as major allocation sites, but moderate amounts were also allocated to the reproductive parts and to the leaves throughout their life-span.
6. For N and Cu the leaves become less important in terms of allocation after the inception of the reproductive organs. This pattern is indicated for N in Fig. 4.6 and is similar for Cu.

Water is an essential reserve for the species throughout the year. The corms showed a variable water content of 32.9 - 80.2% (Fig. 4.7). The storage organs of this species are often within 1.5 - 2.5 cm of the soil surface, where they are exposed to severe heat and dessication in summer and to frequent waterlogging during winter which explains the fluctuation in the percent water content of the storage organ. This correlation between water content of the corms and soil moisture content (Fig. 2.8) was highly significant ($n = 12$, $r = 0.7663$, $p = 0.0037$, $y = 1.655x + 34.916$).

The allocation patterns for the resources during the phenophases are summarized in Table 4.2 and are discussed in relation to the phenophases.

4.3.2.1 Dormant Period (January - March)

The corm accounted for the entire nutrient bulk during this period (Fig. 4.1 - 4.5; see Appendix 4.6.1)

Table 4.2: Allocation patterns in the constituent plant parts of S. **grandiflora** subsp. **grandiflora** during different phenological phases of the year.

Phenophases	Allocation Patterns	Resource
Dormant Period	Corm only	All Elements
Vegetative Period (March - August)	$L \geq^{NS} C >^{**} R$ $L >^{**} R \geq^{NS} C$ $L >^{**} C \geq^{NS} R$ $C >^{**} L >^{**} R$	N; P K; Mg; Ca; Mn; Zn; Fe; Cu Na Starch; CHO
Reproductive Period (Aug - Oct)	$L >^{**} C >^{**} RS >^{*} R$ $L >^{**} C \geq^{NS} R >^{**} RS$ $C >^{**} RS \geq^{NS} L >^{**} R$	Mg; Ca; Cu; Na; Mn; K; P Zn; Fe Starch; CHO
Senescent Period (Oct - Dec)	$C >^{NS} L >^{**} RS$ $C \geq^{**} L >^{*} RS$ $C >^{**} RS >^{**} L$	Mg; Ca; K; Na P; Mn; Zn; Fe CHO N; Cu; Starch

See Table 4.1 for symbols

4.3.2.2 Vegetative Period (March - August)

Transfer of resources from the parent to the daughter corm is initiated during this period. The leaves serve as a major sink to which the majority of the macronutrients, eg. N (up to 57.07%), K (up to 78.59%), Ca (up to 69.94%), Na (up to 54.50%), Mg (up to 71.65%) and P (up to 64.20%) were allocated (see Table 4.2; Fig. 4.1, 4.2 & 4.6). The micronutrient allocation to the leaves, {eg. Cu (up to 70.9%), Zn (up to 58.70%), Fe (up to 70.95%) and Mn (up to 59.50%)} follows the same pattern as the majority of macronutrients.

Allocation of resources to the leaves are important since already in April leaf initiation accounted for up to 28. 63% of the total macronutrients, up to 16.99% of the total micronutrients and up to 8.25% of the TNC standing nutrient stock which demonstrate the metabolic demands of leaf initiation although they have represented only 11.63% of the total biomass (see Fig. 2.6; Fig. 4.1 - 4.6). Root initiation also demonstrated high metabolic demands for macronutrients (up to 51,68%), micronutrients (up to 53.67%) and TNC (up to 9.06%) during April although the roots only account for 22.21% of the total biomass (see Fig. 2.6; Fig. 4.1 - 4.6). As the **in situ** replacement of the parent corm by a daughter corm takes place (see Chapter 2) the amount of resources allocated to the parent corm are reduced or diminished with the daughter corm becoming the major site for allocation during the latter part of the vegetative period. The only exception is Na

for which the allocation pattern remained relatively constant in the parent corm and roots throughout the growing season. TNC in the parent corm provided for rapid growth of the leaves and roots during winter. Amount of carbohydrates translocated to the roots, which also determine root growth (Davidson 1968), was exceptionally low throughout the growth season. As the leaves become estasblished above-ground the newly produced matter is translocated to the daughter corm, which guaranteed higher net productivity. The leaves contained considerable amounts of soluble carbohydrates (8.25 to 51.61%) of the total standing nutrient stock which can be ascribed to active photosynthesis during this period.

4.3.2.3 Reproductive Period (August - October)

Maximum allocation to the reproductive organs (Table 4.2; Fig. 4.1 - 4.6) occurred for all the resources during this period. Reproductive organs (inflorescence stem, flowers and fruit) accounted for up to 25.31% of the total macronutrients, up to 12.40% of the total micronutrients and up to 17.61% of the TNC standing stock which demonstrated the metabolic demands of them. It is commonly supposed that flowering and fruiting make a serious drain upon the food resources of a plant (Grainger 1941). The reproductive organs were particularly enriched in P, N, K, soluble carbohydrates and to a lesser extent Mg. According to Kraus & Kraybill (1918) plants usually tend to flower when the ratio of carbohydrate to nitrogen is high as depicted in Figures

4.4 - 4.6. The daughter corm became the major plant part to which the majority of the resources were allocated, except for K and P for which the leaves served as a major storage sink, as the parent corm became depauperate towards the end of this period. Changes in the amounts of soluble carbohydrates in the inflorescence stem and fruit were striking (Fig. 4.6), since these organs are initially green and could manufacture carbohydrates to some degree (Grainger 1941). The relative amount of soluble carbohydrates increased in the daughter corm (46.17 to 68.40%) whilst that of the leaves, reproductive structures and parent corm diminished by a similar amount, indicating the transfer from the plant parts to the daughter corm towards the end of this period. Negligitable amounts of starch were present in the leaves (0.71 to 4.1%), roots (0.134 to 1.07%) and reproductive parts(0.43 to 8.74%).

4.3.2.4 Senescent Period (October - December)

There was maximum allocation to the daughter corm during this period (Table 4.2; Fig. 4.1, 4.3 - 4.6), except for Na which showed a decrease (31.23 to 26.57%) for the amount present in the daughter corm during the reproductive period (Fig. 4.2). The parent corm becomes totally depauperate by the end of October, those reserves and the photosynthate from the leaves, roots and reproductive organs are translocated to the daughter corm although it has constituted only 54 to 75.59% of the total biomass. It served as a particularly strong sink for the

occurred in September, except for nitrogen, copper and starch which reached maximum allocation during November. Mineral nutrients and organic substances were mobilized from the vegetative and reproductive organs to the developing daughter corm during the assimilatory phase (Fig. 4.1 - 4.6; see Fig. 2.6). At the end of the senescent-phase variable net losses were recorded in the plant parts for all the resources.

P and K are very phloem-mobile and are generally withdrawn from senescing organs with high efficiency (Loneragan **et al.** 1976), thus it is surprising that the senesced leaves and reproductive organs retained large amounts of these elements at the end of the senescent period (Fig. 4.1). K is also associated with the movement of sugars into and out of the phloem (Baker 1978; Saftner & Wyse 1980), which is the generally accepted pathway for redistribution of carbohydrates and minerals (Loneragan **et al.** 1976). Zn, Mn anf Fe are nutrients with limited mobility which are generally transferred from the xylem to the phloem and transported to the various plant parts (Loneragan **et al.** 1976; Hill **et al.** 1979) (Fig. 4.2). Ca, Mg and Na are generally described as immobile elements in the phloem (Canny 1973; Van Die 1974; Loneragan **et al.** 1976; Ziegler 1975) and the very high amounts in the senesced vegetative and reproductive plant parts is therefore not surprising (Fig. 4.1 & 4.3). Loneragan **et al.** (1976) emphasized that the mobility of the trace-element Cu is conditioned by a number of factors including the current environmental conditions, the level of external supply, the nutritional status of the plant and its stage of development at the

Table 4.3: Loss of reserves (%) from vegetative and reproductive plant parts during the senescent period (October to December).

Reserves	Plant Part				
	Parent corm	Leaves	Infl.stem	Roots	Fruit
Phosphorus	97	73	76	90	94
Nitrogen	98	84	96	83	82
Potassium	93	75	36	86	95
Sodium	15	57	31*	39	87
Magnesium	94	78	17	81	93
Calcium	85	60	23*	64	93
Copper	98	82	1*	68	80
Manganese	97	78	47*	83	85
Iron	82	89	20	57	57
Zinc	79	77	20	75	75
Soluble CHO	94	81	90	74	94
Starch	99.8	65	85	90	96

* Denotes an increase.

Table 4.4: Mobilization of reserves (%) from parent corm during establishment of new season's growth (March to August).

CHO	P	N	K	Na	Ca	Mg	Zn	Cu	Mn	Fe	Starch
94	91	95	85	45	86	95	79	97	97	59	99.8

Table 4.5: Seasonal productivity factor in terms of increase in dry matter and reserve capital.

D.M.	CHO	P	N	K	Na	Ca	Mg	Zn	Mn	Cu	Fe	Starch
2.7	2.2	3.4	3.1	2.8	1.4	1.8	1.7	1.3	1.9	3.5	2	2.9

Table 4.6: Factor indicating dry matter and reserve partitioning for reproduction.

D.M	CHO	P	N	K	Na	Ca	Mg	Zn	Mn	Cu	Fe	Starch
71	298	49	25	83	45	118	37	18	119	214	14	3293

in relation to dry matter, mineral nutrition and organic substances came from assesment of the ability of the plant to increase its capital in the daughter corm (Table 4.5). This was expressed as a "productivity rating" (Pate & Dell 1984), in which the amount of dry matter, mineral nutrients and organic substances in the species at the end of the growing season (in daughter corm and seed) was divided by the amount of those resources present at the beginning of the growth season in the parent corm (Pate & Dixon 1981). According to Pate & Dixon (1981) a productivity value of less than unity would denote loss of that resource from the plant during the growth season, whilst a value greater than unity would denote a gain of capital by the plant and its reproductive parts (Table 4.3 & 4.5). Dry matter and reserve partitioning for vegetative and sexual reproduction was employed as a comparison of the relative costs in terms of photosynthate in filling the corm versus forming seeds (Table 4.6).

Table 4.5 shows how effectively this geophytic species added to the capital which it had carried over from the previous year. Table 4.4 shows that the economy of P, N, and K to have been extremely efficient (85-95%) in the utilization of the starting reserves of the parent corm for growth early in the season. An almost equally efficient withdrawal of these same nutrients from senesced vegetative and reproductive parts at the end of the growing season is evident (Table 4.3). The results described for this species compare favourably with existing data for geophytes (Pate & Dixon 1982; Pate & Beard 1984).

The corm of this species increased in dry weight from its inception till the end of the growth season and during this time became a progressively more important sink for photosynthates. The demand for assimilates by the corm could be an important factor in the regulation of the photosynthetic activity of leaves and flowering stem since it has been stressed that the presence of an active sink for removing photosynthate from the leaves is important to maintain high rates of leaf photosynthesis (Ginzo & Lovell 1973). Typically annual increases for the biomass and the resources associated with developing corms for **Tipularia** (Whigham 1984), **Stylidium petiolare** (Dixon **et al.** 1983) and for the newest portions of rhizomes in **Aster acuminatus** (Ashnum **et al.** 1982) have been found.

In the case of the other elements (Mg, Ca, Na, Fe, Cu, Zn and Mn) the mobilization from the vegetative and reproductive biomass were lower, especially in the case of Ca, Na, and Fe where senescence losses may represent from 15 to 87% of an initial resource. The increased values denoted for the immobile elements Na, Ca, Cu & Fe (Table 4.3)can be ascribed to the fact that these elements become tied up in the cell walls (Guha & Mitchell 1966). Pate & Dell (1984) stated that seasonal loss from vegetative and reproductive parts (except seed) of the plant may be viewed as a mechanism of ridding the plant of excess amounts of these and other elements such as Cl. The values given in Table 4.5 showed variation in "productivity ratings." Specific elements (P, N and K) and the organic substances showed values of between 2.8 and 3.4. The micro-elements and the remaining

macro-nutrients showed relatively low values of between 1.3 and 2. A high value of 3.5 was recorded for Cu. Soluble carbohydrates and starch showed values of 2.2 and 2.9.

The mobility of K, N and P, and soluble carbohydrates and the immobility of Ca, Na, Mg, Zn, Cu, Fe and Mn are well documented (Fonda & Bliss 1966; Risser & Cottam 1968; Epstein 1972; Ginzo & Lovell 1973; Loneragan 1976; van Andel & Vera 1977; Bayly & Shibley 1978; Pate & Dixon 1978, 1981 & 1982; Abrahamson & Caswell 1982; Whigham 1984; Nault & Gagnon 1988). Thus, it seems logical that the variability in resource allocation found was real and was to be expected. What was impressive were the clear trends in resource allocation even without accounting for all the possible sources of variability.

Bowen (1981) stated that the ability of a plant to store appreciable quantities of resources when not required and to mobilize and re-use restricted resources is an important property when coping with low nutrients. It therefore secures an adequate supply of one or more limiting nutrient(s). An example of efficient re-usage was the withdrawal of large proportions of nutrients such as potassium, nitrogen, phosphorus, soluble carbohydrates and starch from the vegetative and reproductive plant parts before and during senescence (Fig. 4.1 - 4.6; Table 4.3). Karlson (1986) stated that efficient internal reutilization of nutrients could be another feature enabling a species to combine a small root system with a large investment in reproduction. Although elements present in senesced leaves represent

a net loss to the plant at that point in time, without some phosphate, potassium and nitrogen and other elements in the litter, little decomposition and release of immobilized ions such as calcium, copper and zinc would occur (Bowen 1981). The ability of this species to store nutrients during periods of increased active growth, which are used during periods of reduced availability is regarded as luxury consumption (Stock **et al.** 1987; Witkowski 1989). These plants thus possess some competitive advantages over sclerophyllous species which permit geophytes to survive unfavourable conditions, and to carry resources from one growing season to the next.

Westman & Rogers (1977) suggested that the large underground biomass is partly a response to poor nutrition, and partly a strategy for protecting dry matter, mineral and organic resources from fire and unfavourable conditions, thus ensuring rapid resumption of shoot and leaf regeneration after burning and during the onset of favourable climatic conditions.

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4.6 APPENDIX

APPENDIX 4.6.1: Concentrations of macro- ($g.kg^{-1}$ d.m.), micronutrients ($mg.kg^{-1}$ d.m.) and carbohydrates ($g.kg^{-1}$ d.m.) in the constituent plant parts of **S. grandiflora** subsp. **fimbriata**. All values are means (± standard error) of five samples.

Parent Corm

MONTHS	STARCH		Zn		Cu		P		Mg		Na		Ca		Mn		Fe		Sol. CHO		K		N	
	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx
Jan	500.89	46.30	0.005	0.001	0.276	0.003	1.15	0.10	0.92	0.05	0.37	0.11	4.50	0.39	0.051	0.001	0.042	0.005	120.940	6.850	6.79	0.55	5.91	0.68
Feb	583.10	49.60	0.008	0.001	0.154	0.003	1.19	0.08	2.31	1.22	0.51	0.05	5.02	0.35	0.059	0.002	0.044	0.005	123.340	6.750	7.76	0.43	7.11	0.65
March	449.00	15.23	0.009	0.001	0.161	0.002	0.68	0.11	1.13	0.02	0.70	0.08	4.28	1.26	0.056	0.001	0.054	0.005	163.540	7.350	5.45	0.17	6.47	0.97
April	528.20	33.25	0.008	0.001	0.193	0.004	0.47	0.13	1.68	0.20	0.95	0.20	5.14	1.32	0.064	0.001	0.021	0.006	157.580	6.070	3.97	0.23	7.01	0.56
May	141.46	3.39	0.016	0.002	0.217	0.009	0.98	0.12	1.71	0.12	1.65	0.09	5.35	1.40	0.039	0.007	0.129	0.057	147.380	16.590	9.15	0.91	7.56	1.57
June	209.70	2.89	0.013	0.001	0.112	0.007	1.20	0.22	1.20	0.04	2.45	0.22	4.71	0.54	0.039	0.002	0.215	0.021	95.400	5.950	9.50	0.35	6.03	0.75
July	239.59	9.07	0.016	0.001	0.030	0.002	1.46	0.13	1.56	0.14	2.37	0.18	5.60	0.38	0.039	0.002	0.024	0.007	146.300	2.750	11.48	0.21	11.01	0.43
Aug	49.27	10.73	0.021	0.006	0.035	0.001	1.26	0.09	1.53	0.17	3.02	0.27	9.85	1.70	0.039	0.005	0.015	0.003	102.150	11.770	10.47	0.56	11.03	0.70
Sept	12.84	2.16	0.015	0.001	0.044	0.003	0.90	0.13	1.64	0.11	3.05	0.19	7.47	1.21	0.150	0.030	0.067	0.014	74.300	16.530	9.47	0.57	11.58	0.70
Oct	7.50	1.75	0.014	0.001	0.045	0.003	0.38	0.24	0.76	0.04	4.65	0.32	6.55	0.59	0.066	0.021	0.075	0.009	88.900	7.510	5.32	0.35	1.49	0.21

Replacement (Daughter) Corm

MONTHS	STARCH		Zn		Cu		P		Mg		Na		Ca		Mn		Fe		Sol. CHO		K		N	
	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx
July	27.30	12.60	0.008	0.000	0.140	0.004	1.13	0.10	1.37	0.10	1.43	0.11	5.10	0.38	0.019	0.001	0.170	0.014	125.65	10.66	8.47	0.92	6.49	0.41
Aug	439.70	28.70	0.005	0.000	0.158	0.004	0.49	0.12	0.94	0.11	1.20	0.09	3.08	0.74	0.015	0.002	0.063	0.013	126.60	6.78	5.72	0.15	4.15	0.29
Sept	460.50	25.70	0.004	0.000	0.178	0.004	0.26	0.02	0.52	0.02	1.15	0.04	2.06	0.41	0.020	0.001	0.051	0.006	132.86	2.60	4.03	0.14	2.59	0.14
Oct	458.30	74.60	0.004	0.001	0.210	0.002	0.45	0.04	0.76	0.04	1.41	0.09	2.96	0.46	0.028	0.001	0.044	0.019	137.24	3.37	5.22	0.21	3.93	0.61
Nov	474.30	79.10	0.004	0.000	0.232	0.004	0.72	0.09	0.84	0.05	0.32	0.06	3.71	0.18	0.037	0.002	0.023	0.004	94.58	3.99	6.56	0.36	6.20	0.47
Dec	392.00	16.30	0.005	0.001	0.258	0.002	1.06	0.09	0.89	0.06	0.45	0.14	3.50	0.58	0.049	0.005	0.046	0.014	161.83	6.39	7.52	0.59	7.47	0.95

LEAVES

MONTHS	STARCH		Zn		Cu		P		Mg		Ca		Na		Mn		Fe		Sol. CHO		K		N	
	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx
April	22.49	4.17	0.013	0.001	0.106	0.003	2.22	0.22	2.21	0.27	8.17	0.23	1.39	0.22	0.034	0.003	0.069	0.011	89.40	7.26	27.50	1.35	4.24	0.15
May	9.85	1.15	0.017	0.002	0.112	0.003	2.73	0.12	2.76	0.20	9.23	1.51	2.08	0.14	0.039	0.003	0.055	0.003	31.08	7.39	36.26	2.71	6.75	0.37
June	15.57	2.62	0.015	0.001	0.197	0.003	1.26	0.19	2.44	0.41	6.86	1.29	1.92	0.09	0.075	0.003	0.236	0.084	55.36	10.26	26.23	1.43	3.22	0.31
July	10.36	0.53	0.018	0.003	0.081	0.002	1.52	0.39	2.30	0.21	10.69	0.25	2.22	0.18	0.059	0.004	0.263	0.052	53.68	5.66	30.86	2.20	2.62	0.29
Aug	14.50	0.67	0.012	0.001	0.086	0.002	1.72	0.08	2.18	0.50	12.81	1.37	2.79	0.42	0.053	0.003	0.143	0.007	61.70	5.67	30.83	0.81	2.82	0.27
Sept	15.75	0.36	0.012	0.001	0.091	0.001	1.18	0.08	2.11	0.37	9.51	1.05	2.75	0.20	0.065	0.003	0.138	0.020	79.50	4.57	26.10	1.27	2.97	0.36
Oct	12.48	0.56	0.011	0.001	0.093	0.001	1.06	0.20	1.64	0.07	7.86	1.00	3.18	0.46	0.044	0.002	0.054	0.006	71.12	3.83	24.55	3.49	1.88	0.09
Nov	13.62	1.94	0.012	0.000	0.092	0.004	0.79	0.06	1.47	0.10	10.46	1.88	2.33	0.10	0.043	0.003	0.127	0.021	60.54	8.23	20.96	1.79	1.10	0.29
Dec	16.37	1.15	0.013	0.000	0.094	0.002	1.08	0.12	1.41	0.14	12.40	2.20	3.54	0.24	0.043	0.004	0.072	0.004	45.58	6.01	22.91	1.54	1.22	0.24

APPENDIX 4.6.2: Monthly biomass weights (g. dry mass) for component parts of **S. grandiflora** subsp. **fimbriata**. All values are means (± standard error) for five samples.

PARENT CORM

	X	SE
JAN	4.31	0.80
FEB	2.33	0.63
MARCH	3.21	0.81
APRIL	3.64	0.71
MAY	1.27	0.12
JUNE	0.95	0.05
JULY	0.81	0.15
AUGUST	0.83	0.13
SEPTEMBER	1.29	0.47
OCTOBER	0.41	0.11
NOVEMBER	-	-
DECEMBER	-	-

DAUGHTER CORM

	X	SE
JULY	0.74	0.17
AUGUST	1.64	0.36
SEPTEMBER	5.75	0.48
OCTOBER	5.50	1.19
NOVEMBER	8.68	1.91
DECEMBER	7.06	1.84

LEAVES

	X	SE
APRIL	0.64	0.14
MAY	1.38	0.18
JUNE	1.99	0.07
JULY	3.11	0.92
AUGUST	2.28	0.62
SEPTEMBER	3.58	0.81
OCTOBER	1.54	0.57
NOVEMBER	1.19	0.10
DECEMBER	1.19	0.15

ROOTS

	X	SE
APRIL	1.22	0.14
MAY	1.32	0.13
JUNE	0.52	0.07
JULY	0.85	0.21
AUGUST	0.75	0.03
SEPTEMBER	0.67	0.07
OCTOBER	0.44	0.16
NOVEMBER	0.18	0.04
DECEMBER	0.10	0.02

FLOWERS

	X	SE
SEPTEMBER	0.46	0.04

FRUIT

	X	SE
OCTOBER	0.70	0.18
NOVEMBER	0.26	0.06
DECEMBER	0.10	0.09

INFLORESCENCE STEM

	X	SE
SEPTEMBER	1.96	0.27
OCTOBER	1.42	0.39
NOVEMBER	1.18	0.23
DECEMBER	1.75	0.34

CHAPTER 5

RESOURCE ALLOCATION PATTERNS IN THE BULBS OF *HAEMANTHUS PUBESCENS* L.f. SUBSPECIES *PUBESCENS*

CONTENTS

5.1 INTRODUCTION

H. pubescens L.f. subsp. **pubescens** is an endemic geophytic species of the South-western Cape, which survives the unfavourable season in the form of a dormant bulb (Snijman 1984). It stores resources in laterally compressed scale-like leaf-bases which are packed together in two ranks on a vertically-compacted stem (Raunkiaer 1934; Pate & Dixon 1982; Snijman 1984).

Geophytic monocots account for 16% of the Cape Flora, and for two-thirds of the monocots of this flora (Goldblatt 1978). Studies of resource allocation in geophytes for the South-western Cape have been neglected although conceptual frameworks exist to describe allocation patterns (Harper & Ogden 1970; Hickman & Patelka 1975; Muller 1979; Abrahamson & Caswell 1982; Gross **et al.** 1983; Hume & Cavers 1983; Whigham 1984).

The concept of resource allocation is generally described as the connection between fitness and the allocation of some crucial substances in a species. Allocation implies the movement of materials differentially to and from various organs (Fitter & Setters 1988). Resource allocation patterns of plants are considered

a fundamental aspect of their life-history strategies which include important functions such as growth, reproduction and the maintenance of vegetative structures (Kawano & Nagai 1975; Abrahamson 1979).

The use of biomass allocation (the proportion of total biomass stored in each organ) was originally introduced as a means to study resource allocation by Harper & Ogden (1970). Thompson & Stewart (1981) questioned the use of carbon as the primary limiting resource in plants and suggested that nutrient content also be investigated in resource allocation studies because in certain geophytic species, as for this species, the biomass of the below-ground storage organ represents the summation of several years of growth (Gross **et al.** 1983).

The plants have a hysteranthous flowering pattern which allows the avoidance of pollination competition (Dafni **et al.** 1981) and the leaf-period spans the favourable winter season. It would thus be expected that populations of this species would also be adapted to their environment in a predictable manner with respect to resource allocation. Work has shown that resource allocation in plants is the result of both their genotype and their environment and intra- and interspecific variation have been illustrated for both biomass and nutrient allocation (Harper & Ogden 1970; Harper 1977; Abrahamson & Caswell 1982).

With these considerations in mind a study of the resource allocation of **H. pubescens** subsp. **pubescens** bulbs was undertaken in order

to gain a better understanding of its life-history strategy. The objectives of the study were:

1. to describe the biomass allocation in the leaf-bases of bulbs of reproductive age,
2. to determine the concentrations of the various nutrient elements and carbohydrates and see if there is any pattern within the leaf-bases,
3. to compare the allocation of various nutrients in the leaf-scales and stem of the bulbs.
4. to investigate what nutrients exhibit allocation patterns similar to biomass, and
5. to find out how the storage capacity of the stem compares with that of the leaf-bases.

5.2 SITE DESCRIPTION

See Chapter 1 for detail site description.

5.3 METHODS

5.3.1 COLLECTION OF SPECIMENS

A single, large, well protected population was selected for this study. The population was sacrificed by destructive removal of the plants for ageing and chemical analyses. Sampling was done in September 1988 after the seasonal die-back period of the above-ground portion of the foliage leaves. All the specimens were brought to the laboratory where they were cleaned and dissected. They were cut through their longitudinal median

section and aged as illustrated in Figure 5.1 and described in Chapter 1.

Twenty-three year old plants were used for the resource allocation pattern studies. The plants were pooled into three batches of three each. The leaf-bases were dissected from the stem and grouped according to their ages and dried at 60°C until the weights stabilized. The stems were dried separately.

5.3.2 Analysis of Dormant storage organ for water, dry matter, mineral content and carbohydrates

Water content was expressed as a percentage of both the fresh and the dry mass. The pooled dry material was ground with a Wiley mill to pass through a forty mesh prior to chemical analyses.

See Chapter 3 for a detailed account of the methods employed for concentration and allocation determinations of the resources.

5.4 RESULTS AND DISCUSSION

Chmielewski & Ringius (1987) stated that dry mass can be used as a measurement of biomass allocation patterns for the following reasons:

1. it reflects the integration of all physiological processes

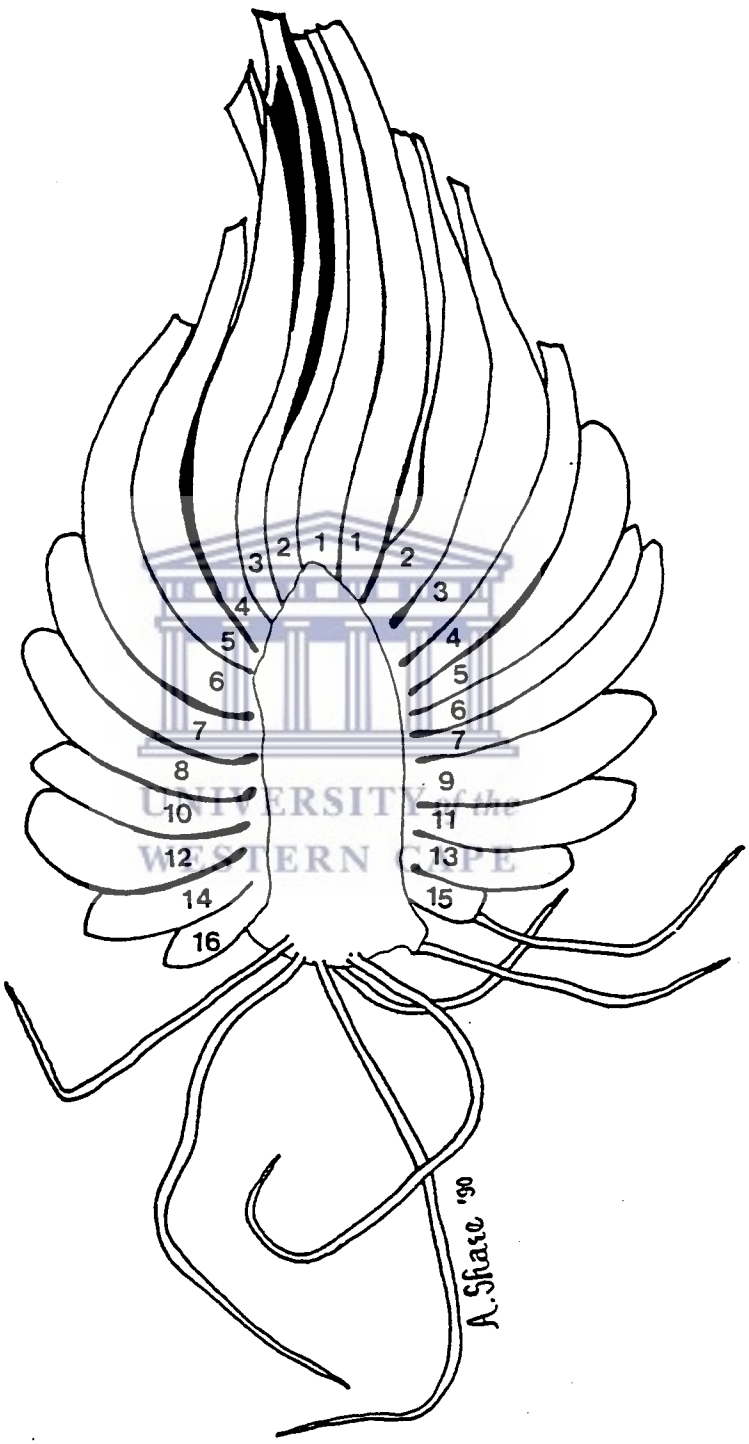

Figure 5.1: Longitudinal section of a SiXteen year old **H. pubescens** subsp. **pubescens** Bulb (Numbers indicate how the chronological age of the leaf-bases was determined).

throughout the season (Abrahamson & Caswell 1982);

2. it is simple and fast to use;
3. biomass reflects the functional aspects of all assimilates;
4. it is the best available measure of resource allocation for comparing species growing in different environments when the availability of and species requirements for, particular nutrients are unknown (Gross **et al.** 1983); and
5. energy content and dry weight equally reflect energy allocation patterns in plants (Hickman & Pitelka 1975).

5.4.1 Concentration of Nutrients in Bulb Parts

Data obtained for contrations of the elements K, Zn and for the organic substance starch are shown in Figures 5.2 - 5.4. Linear regression analyses were applied to these prominent concentration trends. The important observations are listed below.

1. Five of the important macro-elements (P, Na, Mg, K, Ca), soluble carbohydrates and two of the micro-elements (Fe and Cu) showed a more or less constant concentration. (eg. potassium; Fig. 5.2). The actual concentrations of the individual substances differed considerably with both substance and organ.
2. Nitrogen showed a declining concentration from the young- to the old leaf-bases {$n = 69$, $r(67) = -0.3262$, $p < 0.0062$, $y = 1.356 - 0.190x$}. The same pattern was exemplified by starch {$n = 69$, $r(67) = -0.4058$, $p < 0.0005$, $y = 29.96 - 0.326x$} (eg. nitrogen; Fig. 5.3).

3. In the case of the two remaining micro-elements (Zn and Mn) concentration increased with leaf-base age {Zn: n = 69, r(67) = 0.5137, $p < 0.00005$, $y = 0.0614 + 0.0033x$ and Mn: n = 69, r(67) = 0.4097, $p < 0.0005$, $y = 0.036 + 0.0015x$} (eg. zinc; Fig. 5.4).

The absence of marked concentration trends for P and K is not surprising since these elements are very phloem-mobile and are generally withdrawn from senescing organs with high efficiency (Loneragan **et al.** 1976). Potassium is associated closely with the movement of sugars into and out of the phloem (Baker 1978; Saftner & Wyse 1980), which is the generally accepted pathway for redistribution of carbohydrates and minerals (Loneragan **et al.** 1976). Thus the starch and carbohydate concentration trends for this particular study do not depict a situation of high concentrations in the young and central/middle located leaf-bases. Zn, Mn and Fe are nutrients with limited mobility which are normally transferred from the xylem to the phloem and transported to the various vegetative parts of plants efficiently (Loneragan **et al.** 1976; Hill **et al.** 1979). Fig. 5.4 depicts that the Zn (and Mn) which were taken up by the roots or transported from the leaves during previous years are retained (tied-up) in the older leaf-bases as a result of their limited mobility. Ca, Mg and Na are generally described as immobile elements in the phloem (Canny 1973; Van Die 1974; Loneragan **et al.** 1976; Ziegler 1975) and the very even concentration distribution is thus surprising. Loneragan **et al.** (1976) emphasized that the mobility of trace-elements such as Cu is

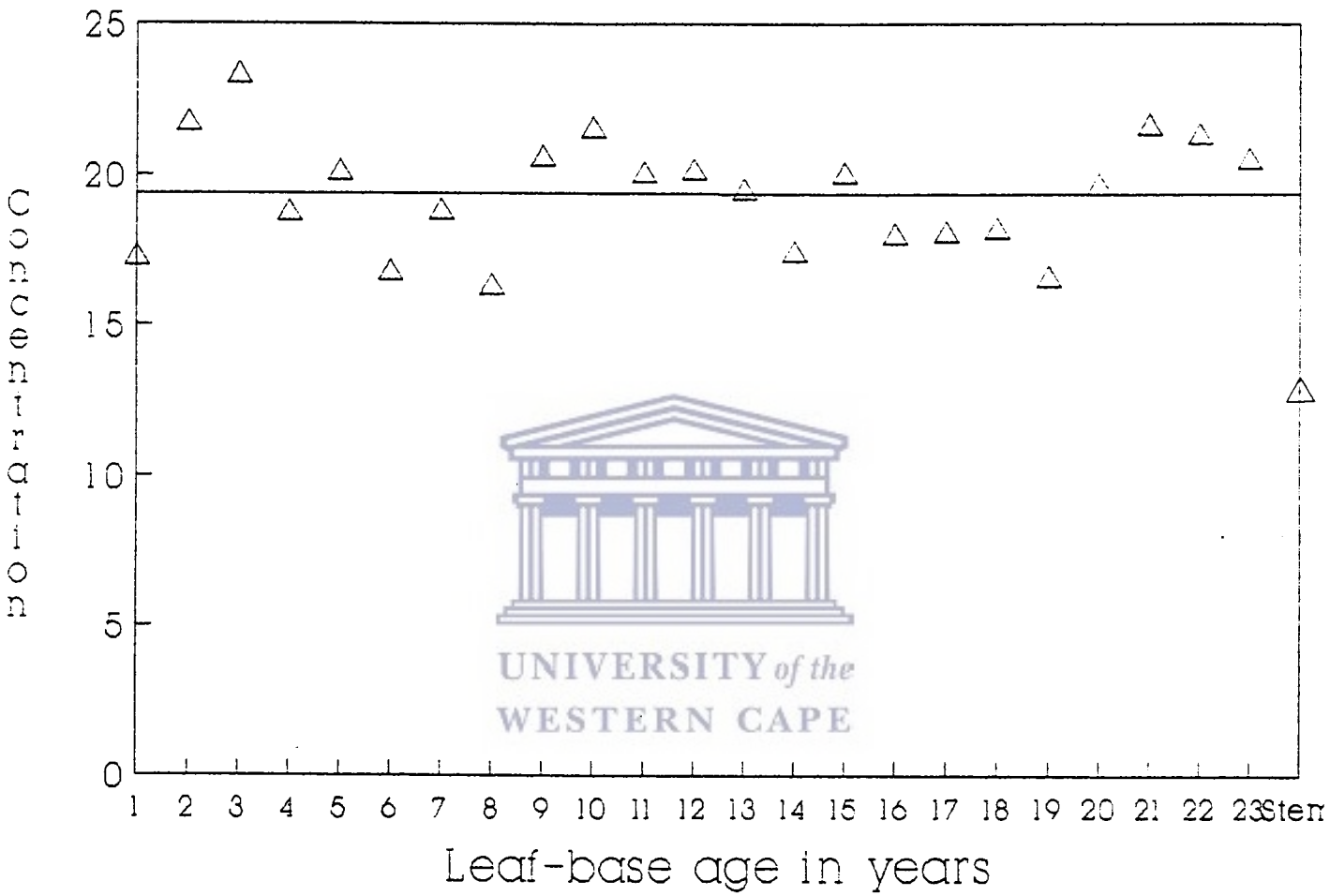

Figure 5.2: Concentration ($g.kg^{-1}$ d.m.) trend for potassium in the leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

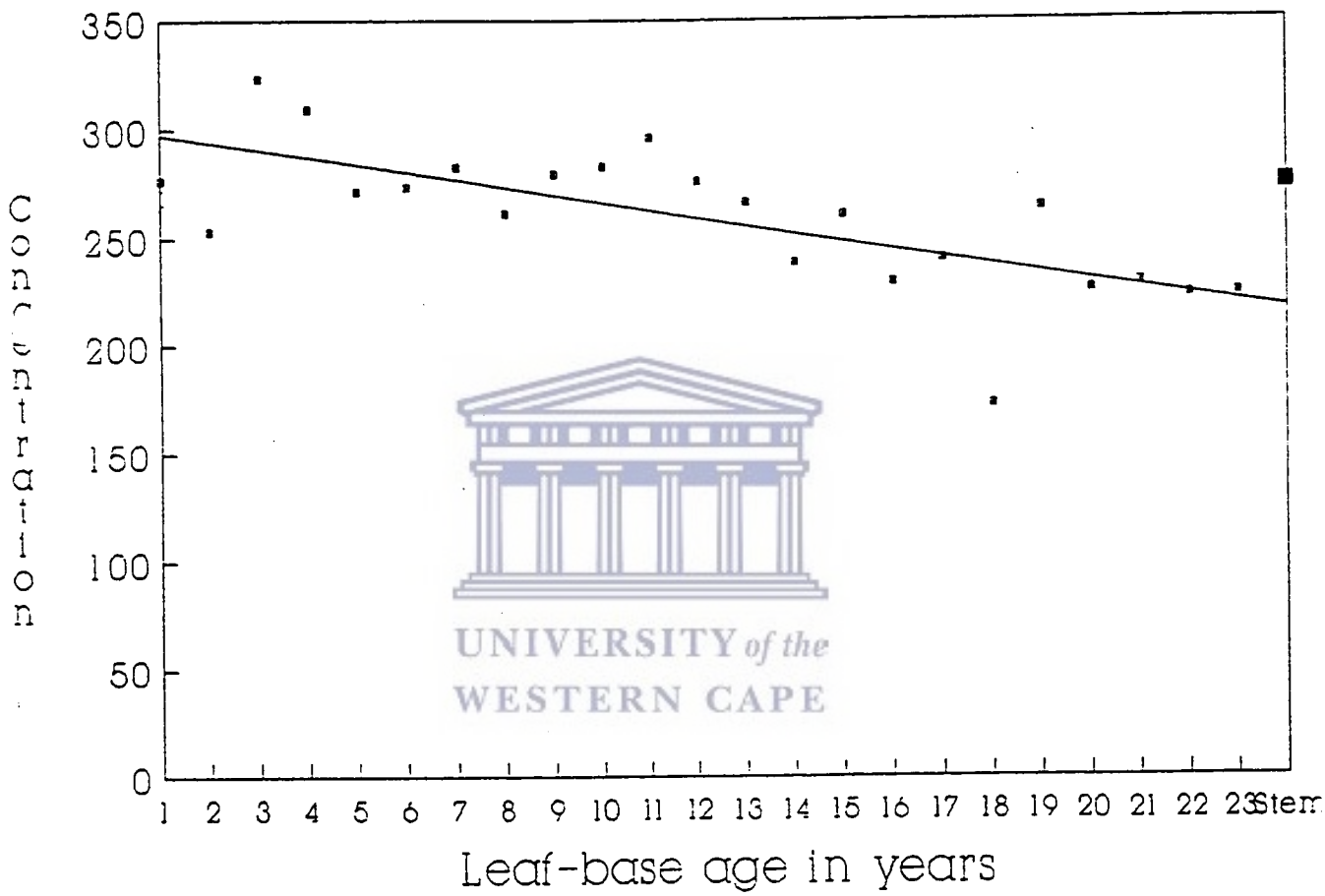

Figure 5.3: Concentration ($g.kg^{-1}$ d.m.) trend for starch in the leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

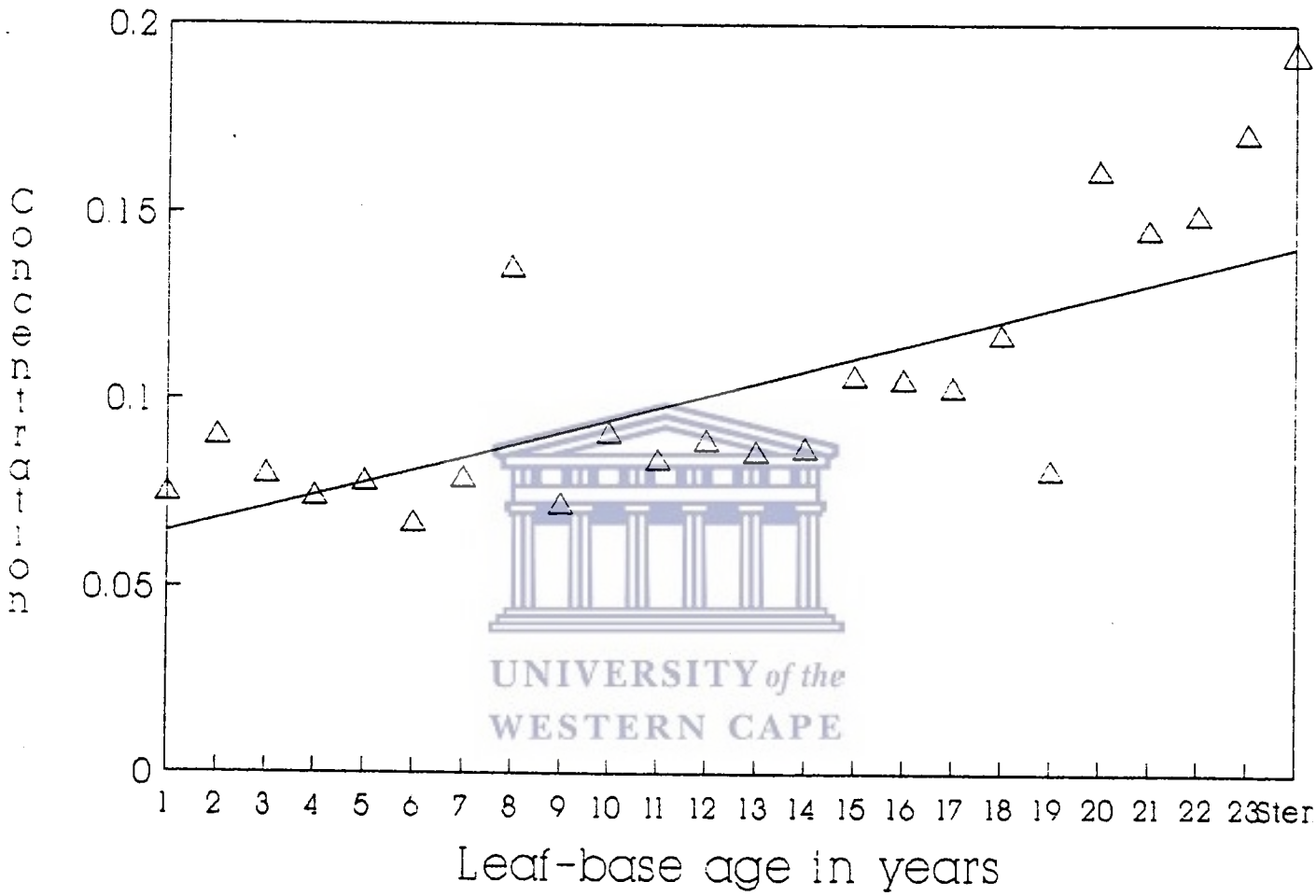

Figure 5.4: Concentration (g.kg^{-1} d.m.) trend for zinc in the leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

conditioned by a number of factors including the current environmental conditions, the level of external supply, the nutritional status of the plant and its stage of development at the time of study. Guha & Mitchell (1966) stated that concentrations of immobile elements, eg. Ca increases in senescing structures primarily because they are tied-up in the cell walls. Thus one would expect high concentrations of the immobile macro- and micronutrients in the oldest leaf-bases with concentration curves similar to Zn and Mn which did not occur.

The concentrations of the various macro- and micro-elements and organic substances for the constituent leaf-bases and stem of H. **pubescens** subsp. **pubescens** bulbs are given in appendix 5.7.1.

The mean concentration values for the nutrient elements and carbohydrates of the constituent bulb parts are given in Table 5.1. The following conclusions were made:

1. The macronutrients showed relatively low values when compared with typical ranges (Epstein 1972; Hewitt & Smith 1974; Larcher 1980 see Chapter 3 for the typical concentration ranges in plant parts).
2. The micronutrients exhibit typical high values when compare to the typical ranges (Stiles 1961; Epstein 1972; Hewitt & Smitt 1974; Larcher 1980). This can be ascribed to their limited mobility (Loneragan **et al.** 1974).
3. The soluble carbohydrates values compare favourable with those found in other below-ground storage organs, but the

Table 5.1: Concentrations of the macro- ($g.kg^{-1}$ d.m.), micronutrients ($mg.kg^{-1}$ d.m.) and carbohydrates ($g.kg^{-1}$ d.m.) in the leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

Resource	leaf-bases		Stem	
	X	SE	X	SE
N	11.270	0.45	6.59	1.00
P	1.227	0.022	2.188	0.886
K	19.366	0.394	13.413	2.324
Ca	9.663	0.300	6.288	0.958
Na	8.480	0.409	10.085	2.891
Mg	0.975	0.044	0.872	0.155
Fe	0.316	0.021	0.323	0.054
Zn	0.101	$6.37x10^{-3}$	0.190	0.024
Cu	0.023	$1.34x10^{-3}$	0.024	0.007
Mn	0.054	$2.77x10^{-3}$	0.066	0.012
Starch	258.70	6.930	245.28	16.360
Sol. CHO	244.02	5.280	263.00	2.500

starch values were considerable higher (Grainger 1941; Fonda & Bliss 1966). It thus illustrates their importance as a storage reserve for new growth and metabolic processes.

Shaver (1981) stated that "the essentially opposite behaviour of the mineral elements versus carbon pools suggests an interaction between them." Normally the low nutrient levels lead to accumulation of total nonstructural carbohydrates (Shaver 1981). This statement is based on the interpretation that growth is more sensitive than photosynthesis to variation in mineral nutritional status. Hannon (1956) concluded in her study that in nutrient-deficient plant communities, phosphate levels interact with and have always controlled the economy of other nutrients, including nitrogen.

5.4.2. Biomass, Mineral Nutrient and Organic Substances Allocation Patterns, and Water as a Storage Reserve.

The variations in element concentration between different parts of plants have been known for many years (Smith 1962; Chapin 1980), but few studies have examined the phenomenon of resource allocation in an ecological context or have looked for its ecological correlates. One aspect is that sexual reproductive structures accumulate certain mineral substances more than do vegetative structures. This has been noted for **Verbascum thapsus** and several **Solidago** species (Abrahamson & Caswell 1982) and for **Senescio sylvaticus** and **Chamaenerion**

angustifolium (Van Andel & Vera 1977) in comparative studies.

The leaf-bases and stem accumulated distinctly different amounts of biomass, nutrients and organic substances during development (Fig. 5.5 - 5.8). The nutrient allocation for the leaf-bases and stem was expressed as a percentage of the total amount accumulated in the two vegetative bulb parts. The results were expressed by taking the mean of two consecutive years.

Lowest biomass allocation (%) was to the older leaf-bases formed during the juvenile stage of the bulbs (Fig. 5.5). Highest biomass allocation was found in the central or middle leaf-bases which developed during the mature reproductive stages and a lower allocation was make to the young leaf-bases formed during the old reproductive stages of the bulbs (see Chapter 1).

The resources with constant concentrations (see setion 5.4.1.1: Fig. 5.2) exhibit allocation patterns similar to that of biomass allocation. Nutrient allocation is generally described as a product of dry weight and nutrient concentration. The majority resource allocation patterns mirror the biomass allocation pattern (eg. potassium; Fig. 5.6). Nitrogen and starch, which exhibit declining concentration trends (see section 5.4.1.2; Fig 5.3), have an allocation pattern which deviates slightly from that of biomass in that they reached peak allocation in the leaf-bases that are two years younger (eg. nitrogen; Fig. 5.7).

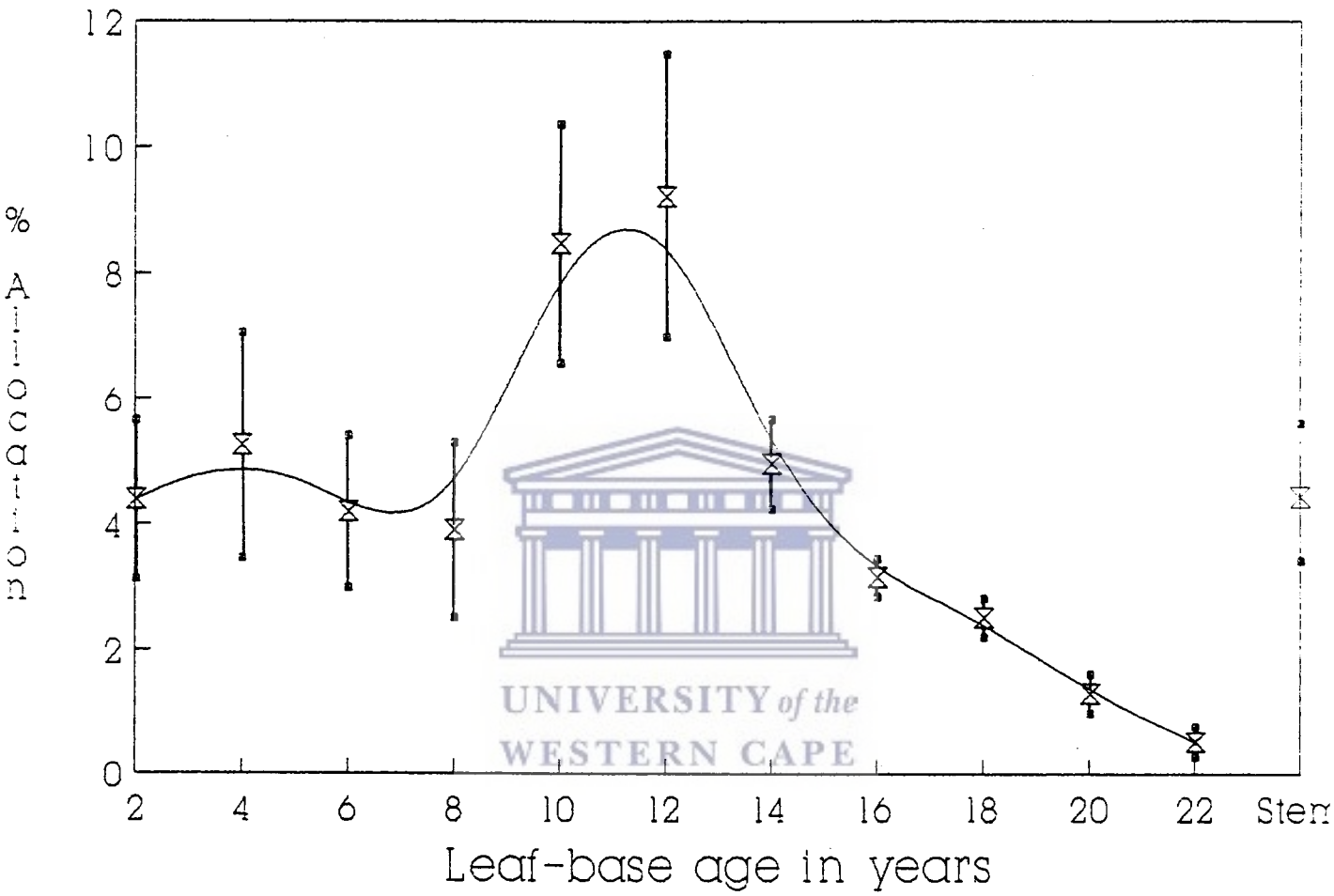

Figure 5.5: Biomass allocation (% dry mass) in the constituent parts of **H. pubescens** subsp. **pubescens** bulbs.

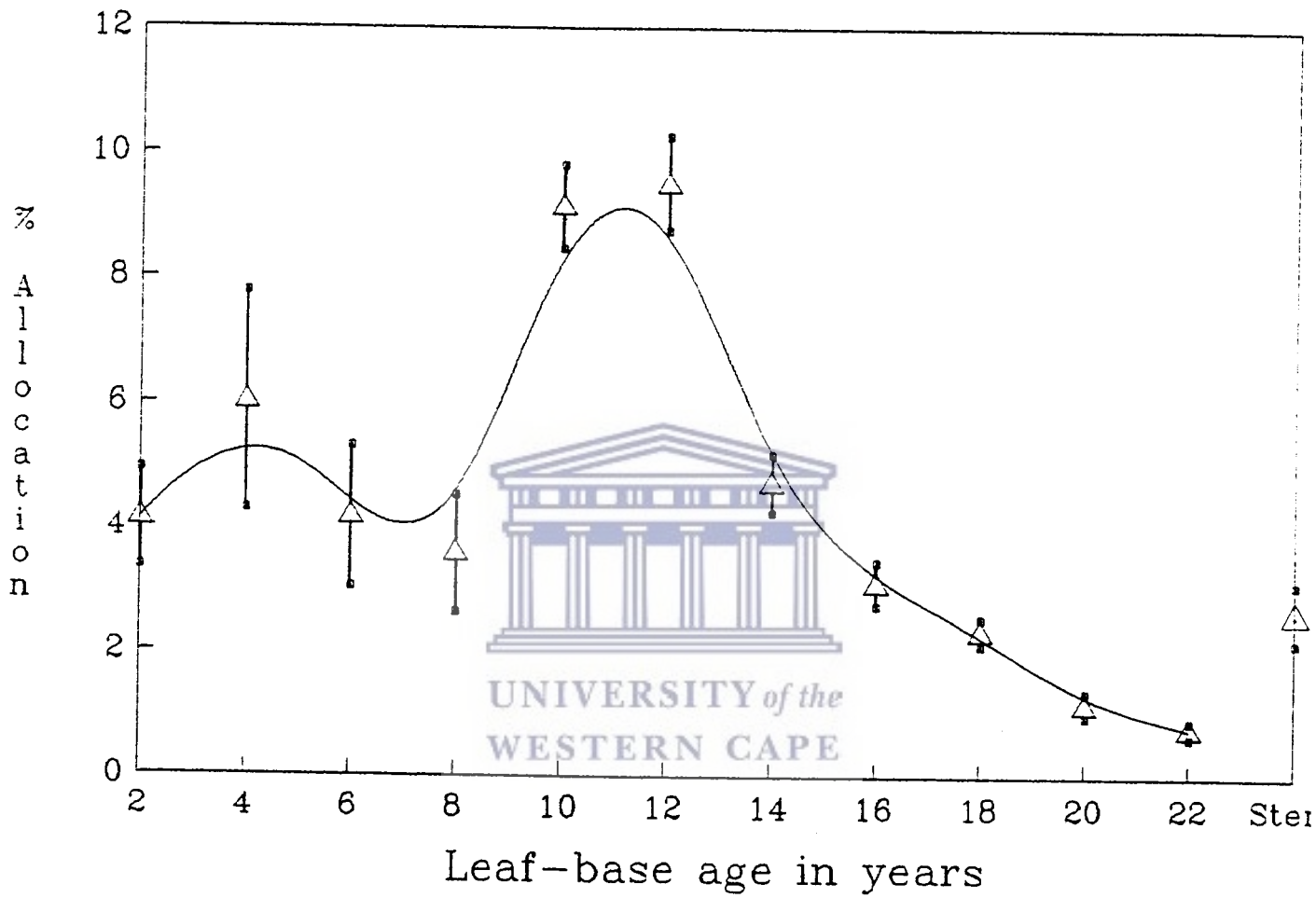

Figure 5.6: Potassium allocation (%) in the constituent parts of **H. pubescens** subsp. **pubescens** bulbs.

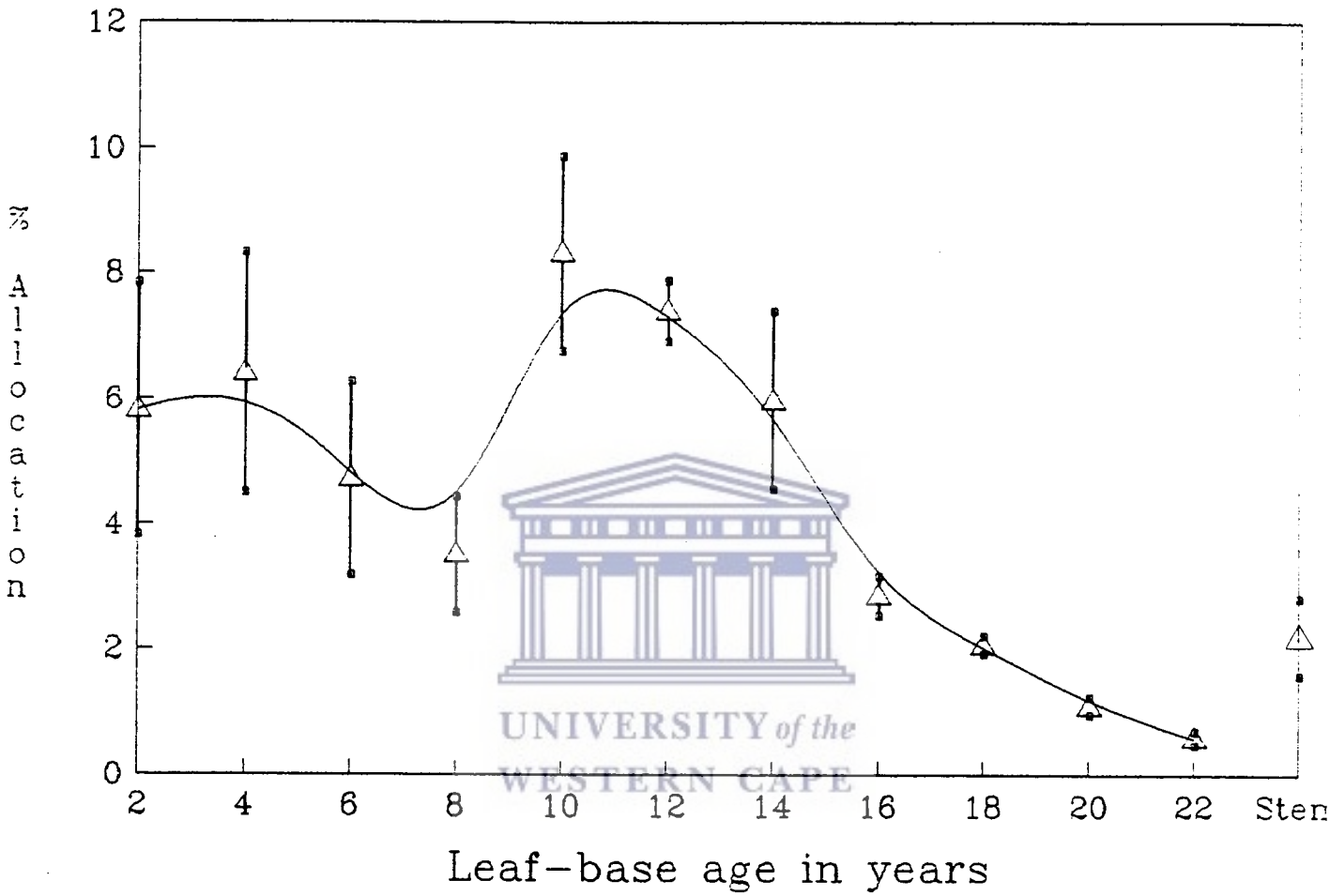

Figure 5.7: Nitrogen allocation (%) in the constituent parts of **H. pubescens** subsp. **pubescens** bulbs.

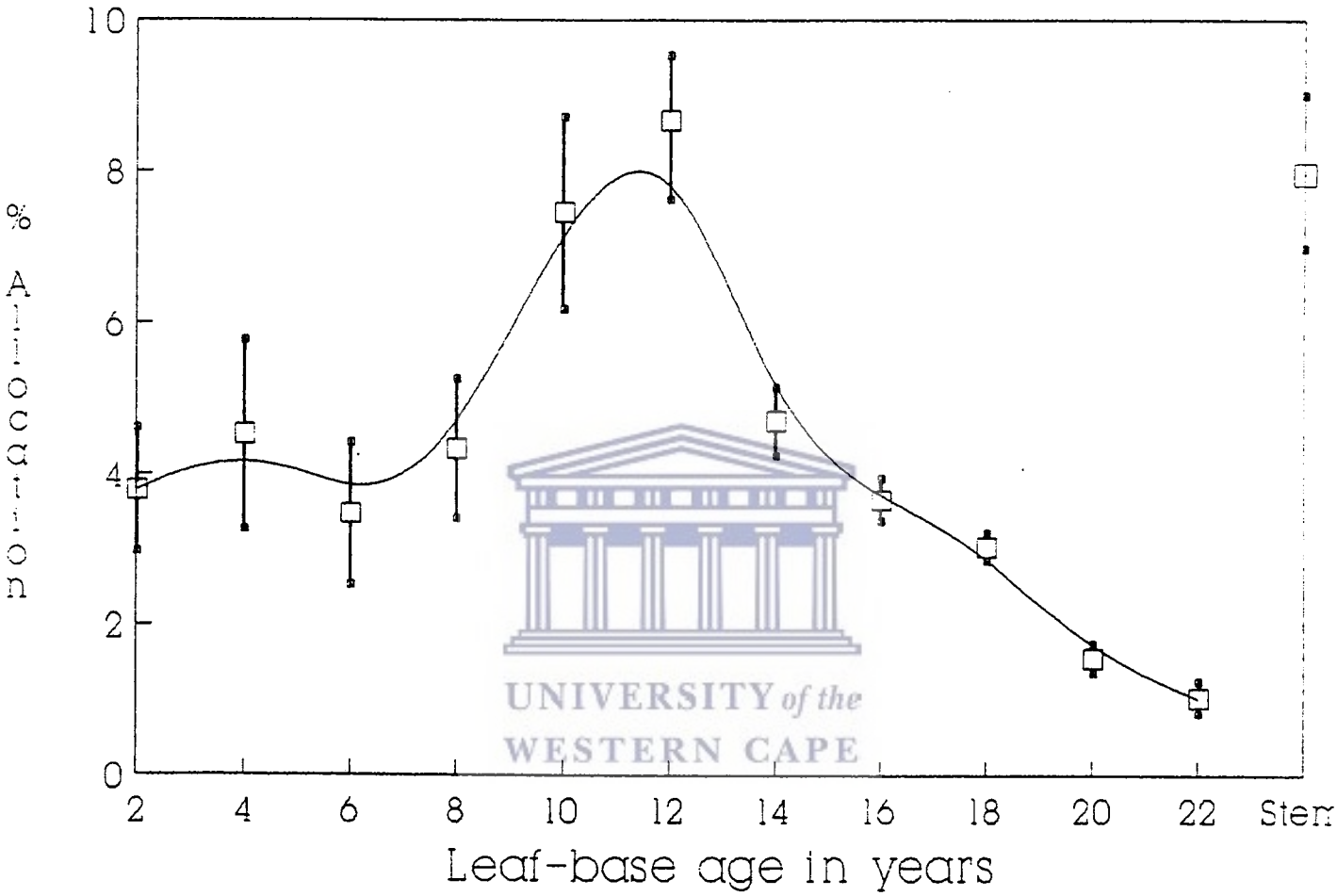

Figure 5.8: Zinc allocation (%) in the constituent parts of H. pubescens subsp. pubescens bulbs.

Thereafter they showed a decline similar to biomass. Zinc and manganese, with increased concentrations with leaf-base age (see section 5.4.1.3; Fig. 5.4) showed a decline in allocation that does not tail off as rapidly as that of biomass (ages 14 -22) (eg. zinc; Fig. 5.8).

The majority (>50% of the total amount) of the biomass, mineral nutrients and organic substances examined were located in the central leaf-bases (9 - 15 years of age) (Appendix 5.2). Considerable lesser amounts occurred in the young leaf-bases (i.e. recently formed leaf-bases; 1 - 8 years old contained 23.5 - 36.5%) and progressively smaller amounts (12.8 - 18.3%) were found in the older leaf-bases (16 - 23 years old). Fe and Ca were the only two mineral elements with <50% allocation in the central leaf-bases, with 46.2 and 49.1% respectively. Cu has had the highest accumulation in the above-mentioned leaf-bases, viz. 58.8%. The majority of the mineral nutrients and organic substances have had allocation percentages between 50 and 55% for the above-mentioned leaf-bases. Only four mineral elements, viz. Fe, N, Ca and Na, have had allocation percentages from 31 to 37% in the young leaf-bases. The marjority of substances had percentages between 23.5 and 29.4%. The portion of mineral and organic substances allocated in the older leaf-bases have constituted 12.8 to 18.3% of the nutrient bulk stored in the bulbs. The fraction accumulated in the stem was only 2.2 to 8.0% of the nutrient bulk for the total bulb.

Figure 5.9: Water content (%) trend in the different aged leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

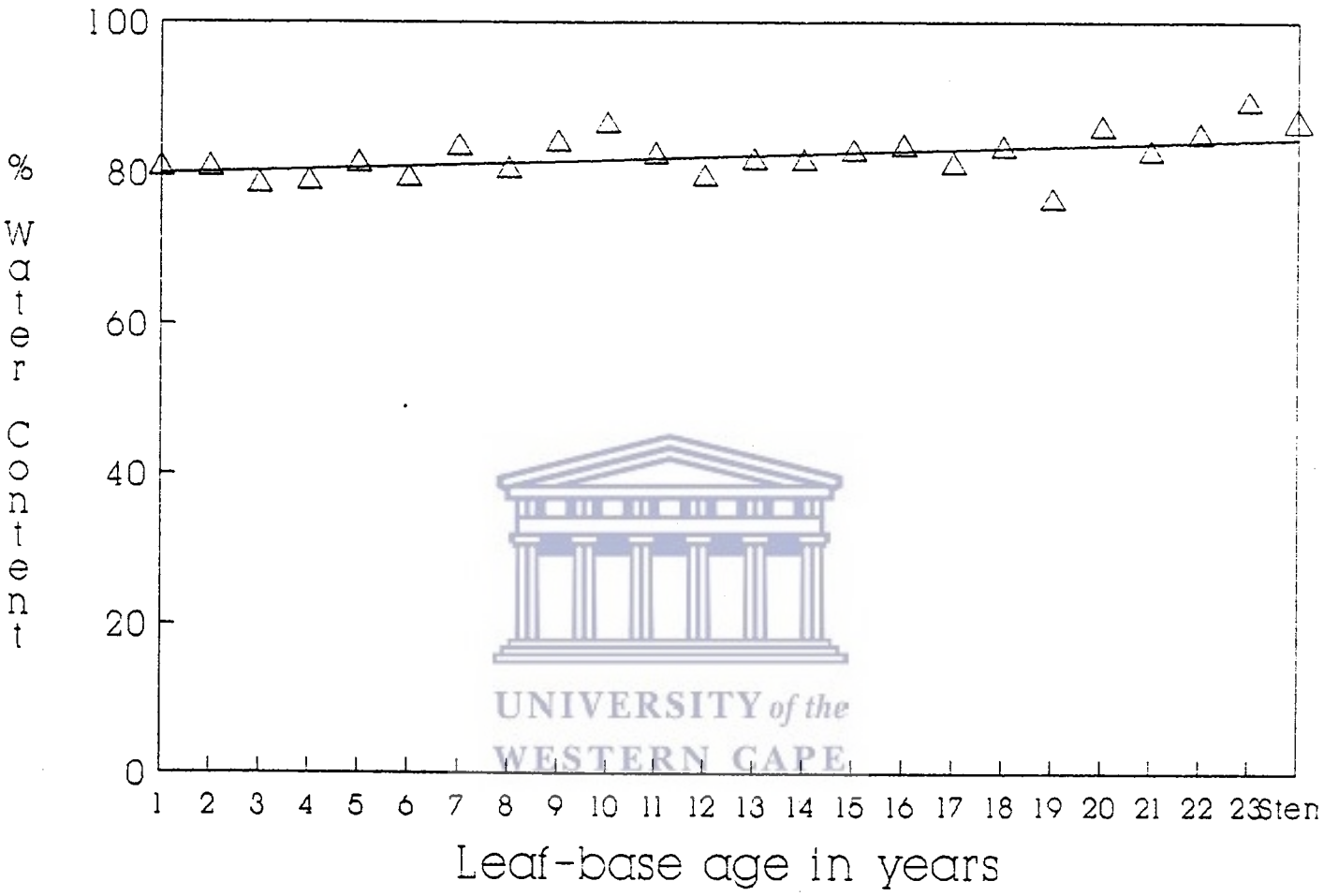

Figure 5.9: Water content (%) trend in the different aged leaf-bases and stem of **H. pubescens** subsp. **pubescens** bulbs.

Some 78% of the leaf-bases showed water contents of >80%. The stem contained 83.64% of its fresh weight as water. A graph showing the range of water contents obtained is shown in Figure 5.9.

5.5 CONCLUSION

The allocation of the majority of the resources does not differ from that of biomass. This is not a novel conclusion: variations in element concentration between different part of plants have been known for many years but few studies have examined this phenomenon in an ecological context.

The leaf-bases do exhibit different storage capacities. From this study it is conspicuous that the older leaf-bases are generally less important in terms of biomass and resource allocation. Most of the relative biomass and resource storage takes place in the middle aged leaf-bases. The young (i.e. most recent leaf-bases) store relatively less resources than the middle aged ones.

In this species the development of a cryptic adaptive strategy can be regarded as an ability to store appreciable quantities of nutrients when not required for growth is undoubtedly a most important attribute in coping with soils of a low nutrient status. The development of large underground biomass is regarded as partly a response to the low availability of nutrients, and partly a strategy for protecting mineral and dry matter resources from fire, a major disturbance factor in fynbos and regarded as the major selective agent for the life histories of seeders and resprouters. This study gives some indication how hysteranthous bulbous geophytes might differentially allocate their resources to the different constituent parts of the bulbs.

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5.7 APPENDIX

APPENDIX 5.7.1: Concentrations of the macro- ($g.kg^{-1}$ d.m), micronutrients ($mg.kg^{-1}$ d.m) and carbohydartes ($g.kg^{-1}$ d.m) and dry mass (g) for the bulb component parts of ***H. pubescens*** subsp. ***pubescens***.

CHRONOLOGICAL AGE	F.M. (g)		D.M. (g)		Starch (mg/g d.w.)		Crude Protein		P (mg/g d.w.)		Sol. CHO (mg/g)		Mn (ug/g d.w.)		Fe (ug/g d.w.)	
	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx
1	40.61	11.22	7.73	1.93	276.50	1.20	6.56	4.61	1.04	0.31	233.47	12.10	0.042	0.020	0.353	0.055
2	14.04	5.15	2.57	0.76	332.80	41.10	7.51	1.69	1.19	0.40	236.48	21.51	0.050	0.026	0.515	0.245
3	45.66	11.56	9.68	2.54	382.30	41.00	8.01	1.50	1.31	0.36	239.38	13.40	0.055	0.023	0.427	0.234
4	12.62	5.27	2.64	1.07	308.50	32.70	7.21	1.57	1.19	0.38	176.18	10.28	0.053	0.040	0.265	0.062
5	42.44	11.24	7.62	1.55	271.00	48.20	7.62	1.50	1.21	0.35	288.15	15.18	0.045	0.012	0.583	0.172
6	10.63	3.75	2.21	0.80	272.70	36.70	5.62	0.33	1.21	0.36	240.68	15.58	0.053	0.014	0.332	0.064
7	32.86	17.74	5.53	2.79	281.60	17.50	5.75	0.33	1.29	0.36	289.67	17.89	0.036	0.008	0.235	0.049
8	22.20	15.39	3.64	2.16	260.60	16.70	5.16	0.73	1.44	0.43	204.18	9.48	0.033	0.015	0.209	0.018
9	64.99	15.15	10.81	3.12	278.90	8.70	5.64	2.44	1.06	0.31	273.55	12.10	0.041	0.012	0.337	0.031
10	58.81	18.91	9.04	3.77	286.60	9.60	6.74	1.33	1.04	0.31	285.68	27.63	0.042	0.009	0.243	0.030
11	71.76	27.90	12.46	4.50	295.90	23.30	4.52	0.42	1.23	0.36	225.85	18.49	0.047	0.009	0.369	0.158
12	45.53	14.21	9.18	2.78	275.70	20.90	5.28	0.44	1.42	0.55	245.35	26.46	0.048	0.013	0.232	0.056
13	36.00	8.58	6.45	1.26	265.80	21.40	7.22	3.38	1.25	0.48	247.12	19.53	0.050	0.010	0.394	0.052
14	28.24	6.19	5.17	1.23	287.80	6.90	5.93	0.60	1.27	0.46	243.48	5.57	0.047	0.010	0.220	0.046
15	25.39	5.09	4.16	0.82	286.30	15.60	6.04	0.63	1.35	0.45	276.00	18.92	0.058	0.021	0.214	0.055
16	19.73	3.30	3.21	0.39	229.00	3.90	4.98	0.39	1.36	0.44	205.95	42.82	0.055	0.012	0.280	0.036
17	16.23	2.72	2.97	0.40	239.90	10.10	5.03	0.49	1.19	0.40	251.38	28.48	0.055	0.016	0.213	0.070
18	17.48	3.65	2.94	0.18	172.30	14.00	5.05	0.70	1.27	0.46	230.18	5.30	0.060	0.009	0.341	0.114
19	9.68	3.68	1.98	0.54	263.60	19.10	5.00	0.69	1.27	0.51	239.62	7.67	0.065	0.011	0.298	0.079
20	8.19	3.71	1.06	0.43	225.50	43.80	5.64	0.43	1.23	0.50	230.17	17.12	0.074	0.017	0.379	0.062
21	6.66	3.25	1.08	0.43	228.70	45.00	5.43	1.02	1.19	0.37	252.77	14.19	0.073	0.015	0.346	0.135
22	3.68	2.56	0.46	0.27	23.70	45.10	6.20	0.10	1.21	0.38	240.98	13.13	0.077	0.014	0.282	0.083
23	3.55	1.71	0.19	0.07	223.30	39.30	4.46	0.73	1.19	0.37	236.23	5.37	0.084	0.016	0.368	0.131
STEM	27.54	7.21	4.51	1.19	263.00	2.50	3.20	1.14	2.19	0.81	245.28	16.36	0.066	0.012	0.323	0.054

Appendix 5.7.1: Continues

CHRONOLOGICAL Age	K (mg/g d.w.)		Ca (mg/g d.w.)		Na (mg/g d.w.)		Mg (mg/g d.w.)		N (mg/g d.w.)		Cu (ug/g d.w.)		Zn (ug/g d.w.)	
	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx	x	SEx
1	17.24	1.41	11.17	1.14	13.73	5.70	0.79	0.40	15.62	5.30	0.022	0.002	0.075	0.010
2	21.72	1.32	9.52	0.14	11.14	3.44	0.56	0.72	13.48	2.70	0.019	0.003	0.050	0.019
3	23.30	1.30	11.59	1.81	7.45	2.22	0.86	0.73	14.23	2.40	0.023	0.003	0.080	0.008
4	18.74	1.21	6.71	0.70	10.66	3.38	1.07	0.64	12.59	2.50	0.017	0.002	0.074	0.008
5	20.08	0.98	9.91	2.30	7.84	2.37	0.80	0.64	13.66	3.08	0.026	0.015	0.078	0.006
6	16.72	0.74	8.43	1.27	7.58	1.04	1.04	0.97	10.46	0.50	0.019	0.005	0.067	0.005
7	18.77	1.54	8.52	1.29	8.51	2.59	0.83	0.65	10.67	0.50	0.017	0.002	0.079	0.005
8	16.26	3.65	7.37	1.52	8.48	2.42	0.79	0.64	9.72	1.20	0.016	0.004	0.135	0.060
9	20.56	1.56	7.49	1.10	7.52	1.84	0.80	0.55	10.49	3.90	0.033	0.009	0.072	0.006
10	21.52	2.20	6.81	1.14	7.10	3.15	1.21	1.01	12.24	2.15	0.031	0.004	0.091	0.023
11	20.00	1.48	9.36	0.09	6.88	3.63	1.18	0.95	8.70	0.70	0.028	0.004	0.084	0.005
12	20.11	1.26	9.38	0.02	8.96	2.91	1.03	0.84	9.91	0.70	0.031	0.003	0.087	0.002
13	19.45	1.92	10.44	1.14	9.46	2.80	1.09	0.81	10.22	5.30	0.026	0.001	0.086	0.004
14	17.35	2.07	9.60	0.19	7.69	2.58	0.96	0.77	10.95	0.90	0.023	0.002	0.087	0.002
15	19.99	2.25	10.04	0.11	7.27	2.96	1.21	1.04	11.13	0.90	0.018	0.007	0.106	0.010
16	17.94	2.25	9.61	0.44	7.69	2.15	0.85	0.64	9.43	0.60	0.019	0.005	0.105	0.003
17	18.02	2.53	10.51	0.62	6.29	1.81	1.01	0.78	9.51	0.80	0.021	0.005	0.103	0.008
18	18.13	2.64	9.82	0.18	9.59	4.65	1.09	0.86	9.53	1.15	0.020	0.009	0.117	0.011
19	16.52	3.89	9.49	1.29	4.16	0.16	0.67	0.47	9.47	1.10	0.014	0.007	0.081	0.012
20	19.63	3.34	10.37	0.20	9.24	4.69	0.96	0.74	10.50	0.70	0.040	0.019	0.161	0.035
21	21.60	3.67	10.83	0.97	7.21	2.86	0.88	0.66	10.15	1.60	0.028	0.010	0.145	0.020
22	21.28	3.62	11.53	0.52	9.77	4.04	1.37	1.10	11.39	0.20	0.019	0.008	0.149	0.029
23	20.74	4.81	12.24	2.29	10.77	2.71	1.35	0.95	8.60	1.10	0.029	0.014	0.171	0.053
STEM	13.41	2.32	6.29	0.96	10.09	2.89	0.87	0.66	6.55	1.00	0.024	0.007	0.150	0.024

APPENDIX 5.7.2: **Nutrient allocation in the leaf-bases and stem of H. pubescens subsp. pubescens bulbs.**

AGE	% STARCH	% Cu	%Zn	%Mn	%Fe	%N	%K	%Ca	%Na	%Mg	%P	%Sol. CHO	%F.M.	%D.M.	%WATER
1	6.68	5.844	5.406	5.417	6.079	9.08	5.83	7.98	10.79	5.47	5.49	6.17	6.11	6.59	90.67
2	2.03	1.650	2.153	2.150	3.548	2.57	2.44	2.86	2.91	1.28	2.05	2.07	2.11	2.19	89.71
3	9.77	7.666	7.214	6.817	11.093	10.27	9.89	10.38	7.33	7.45	7.96	7.92	8.97	9.25	89.54
4	2.55	1.543	1.827	2.333	1.879	2.55	2.17	2.15	2.56	2.51	2.14	1.77	1.90	2.25	78.99
5	6.46	6.206	5.546	5.367	11.928	7.74	6.71	6.91	6.07	5.44	6.28	7.51	6.39	6.50	81.32
6	1.68	1.444	1.379	1.950	1.908	1.72	1.66	1.72	1.70	2.25	1.82	1.62	1.53	1.38	79.33
7	4.87	3.300	4.073	3.317	3.503	4.38	4.55	4.35	4.76	4.09	4.66	5.47	4.96	4.71	83.45
8	2.97	2.028	4.576	2.000	2.043	2.63	2.59	2.46	3.14	2.57	3.56	2.54	3.34	3.10	89.53
9	9.43	12.169	7.251	7.383	6.877	8.43	9.74	7.49	8.26	7.74	7.63	10.11	9.78	9.22	83.99
10	7.99	9.487	7.661	6.333	5.894	8.22	8.52	5.19	6.52	9.78	6.41	8.82	8.85	7.70	86.58
11	11.52	11.859	9.749	9.750	12.336	8.05	10.92	10.73	6.78	13.12	10.43	9.61	10.80	10.62	82.43
12	7.91	9.762	7.615	13.616	5.714	6.76	8.06	7.96	8.36	8.40	8.86	7.65	6.85	7.82	79.44
13	5.36	5.775	5.173	5.367	6.820	7.77	5.50	6.23	6.20	5.77	5.49	5.45	5.42	5.50	81.67
14	3.84	4.091	4.155	4.050	3.049	4.20	3.93	4.55	4.04	4.43	4.47	4.30	4.25	4.40	81.57
15	3.40	2.578	4.129	4.033	2.397	3.45	3.66	3.88	3.69	4.51	3.85	3.94	3.82	3.56	86.63
16	2.30	2.131	3.141	2.950	2.416	2.25	2.53	2.92	2.51	2.43	2.97	2.26	2.97	2.74	83.42
17	2.23	2.131	2.852	2.717	1.699	2.10	2.35	2.89	1.90	2.69	2.23	2.53	2.44	2.53	81.11
18	1.58	2.062	2.572	2.933	2.667	2.08	2.33	2.67	2.86	2.85	2.54	2.31	2.63	2.50	83.31
19	1.63	0.942	1.501	1.065	1.586	1.40	1.44	1.74	0.84	1.18	1.72	1.62	1.46	1.69	76.31
20	0.76	1.502	1.622	1.335	1.100	0.94	0.93	1.04	1.05	0.93	0.91	0.85	1.22	0.92	85.90
21	0.77	1.035	1.454	1.308	0.998	0.81	1.02	1.08	0.79	0.85	0.67	0.93	1.00	0.92	82.68
22	0.32	0.296	0.634	0.568	0.346	0.39	0.43	0.49	0.46	0.56	0.38	0.38	0.55	0.39	84.97
23	0.14	0.186	0.309	0.272	0.191	0.12	0.17	0.22	0.21	0.23	0.16	0.16	0.53	0.17	89.23
Stem	3.62	3.712	7.978	4.950	3.908	2.21	2.65	2.62	4.62	3.50	6.72	3.78	4.14	3.84	83.64

CONCLUSION

The results of the present analyses of the expression of the life- cycles, programme of energy expenditure (nutrient utilization), and reproductive efforts indicated that the two geophytic species have strikingly different life history strategies.

a. **S. grandiflora** subsp. **fimbriata** is classified as an annual cormous geophyte with synanthous leaves. Leaves and flowers are simultaneous and the course of events is growth, storage, flowering and dormancy.

b. **H. pubescens** subsp. **pubescens** is classified as a perennial bulbous geophyte with hysteranthous leaves, in which flowers and leaves appear sequentially and the course of events is growth, storage, dormancy and flowering.

The storage organs of both species have the characteristic of retaining and supplying reserves for growth in periods when net production is reduced. The accummulation of a critical minimum level of storage material in the two species is considered as a prerequisite for flowering.

In **H. pubescens** subsp. **pubescens** a relatively long period of ten years of vegetative growth precedes transition to the flowering and fruiting stage. In contrast **S. grandiflora** subsp. **fimbriata** requires a period of only four years of vegetative growth before transition to the flowering and fruiting stage takes place. The change from the vegetative to reproductive phase in both these species appears to be determined by the accummulation of reserved resources in the underground storage organs to acquire a "minimum critical biomass". In the case of **H. pubescens** subsp. **pubescens** the "minimum critical biomass" was determined as 69.1 ± 13.1g fresh mass and for **S. grandiflora** subsp. **fimbriata** a corm diameter of 0.78 cm (0.37 g d.m.). In the case of **H. pubescens** subsp. **pubescens** it was shown that individual plants may revert to the juvenile stage if a "shortage fund" is not sufficient.

S. grandiflora subsp. **fimbriata,** which can be regarded as a colonizing species, allocates a greater proportion of its resources to reproduction than does the perennial longer lived **H. pubescens** subsp. **pubescens** plants. These longer lived plants also require more resources for self-maintenance. Results have generally supported the theory that a high reproductive allocation will be favoured under conditions of density independent mortality (r-strategists) and low reproductive alloction under density dependent mortality (K-strategists). It follows from these results that an annual geophytic plant such as **S. grandiflora** subsp. **fimbriata** has

a higher reproductive allocation (r-strategist) than the perennial geophytic species **H. pubescens** subsp. **pubescens** (K-strategist). The strategy exhibited by **S. grandiflora** subsp. **fimbriata** is essentially one of *in situ* replacement of the corm coupled with extensive seed production. Resource allocation is divided between these two major sinks and under environmental conditions restricting growth the corm becomes relatively more important than seed production.

Marked differences were found in the morphological patterns amongst seedlings of the studied species relating to the burial of the storage organ formed during the first season of growth. In the bulbous species down growth of the cotelydonary sheath and activity of contractile roots were the agencies found responsible for pulling the shoot apex underground, thus ensuring adequate depth of placement of the bulb which subsequently formed around this buried apex. In the cormous species downward placement of the storage organ was exhibited through the agency of contractile roots. The life-histories explained for the species represent a small portion of the variations which can exist in geophytes. It is emphasized that the ontogeny of a storage organ in seedling stages may provide vital clues as to the morphological nature of the storage organs of the mature plant.

Demographic studies of the species, showed how plants could be aged by counting remains of previous season's storage organs,eg.

tunics, or subterranean markers which develop repeatedly, eg. leaf-bases. The demographic data however, have several unique features, suggesting that further exploration of behavioural patterns in the selected and other species might be rewarding.

Contrasting strategies were displayed between the studied species in relation to the monthly content of water, organic substances and mineral elements in their constituent plant parts. This can partly be explained by the differences in their physiological behaviour and probably their adaptations to the specific habitats from which they were collected. Mobilization of resources from the parent corm, reproductive and vegetative parts during a new-season's growth to the daughter corm, occurred with variable efficiency in **S. grandiflora** subsp. **fimbriata**. In **H. pubescens** subsp. **pubescens** mobilization of resources only takes place from the above-ground vegetative and reproductive parts to the bulb components, but the majority of resources were found to be located in the central located leaf-bases. The water content of **Sparaxis grandiflora** subsp. **fimbriata** corms fluctuated with soil water availability, whereas in **H. pubescens** subsp. **pubescens** it remained constant.

As is the case with the geophytic habit, nutrients are a major selecting force for sclerophylly since plants with sclerophyllous leaves occur primarily on nutrient-deficient soils. There is firm evidence in fynbos that the decomposition

of proteoid leaf litter and restioid litter is very slow. Periodic fires are regarded as a more important agent for the release of nutrients from litter layers than decomposition for sclerophyllous species. This mineralization of nutrients is an important mechanism of making it available to plants through leaching during the wet season. In contrast, nutrients in geophytes are retrieved from senescing structures at the end of the growth season which is regarded as a luxury composition.

Their leaves have high decomposition rates and thus the nutrients are released easily and leached into the soil and made available for reabsorption. Thus periodic fires are not prerequisites for the releasing of nutrients from foliage in geophytes.

It is stressed that there is no single strategy for coping with low nutrient soils. The geophytic life-form can be regarded as one such strategy to cope with low nutrient soils. The acquisition of an underground storage organ can be regarded as a competitive advantage for geophytes because it contains large quantities of quickly available food, and allows very rapid growth after natural disturbance, viz. herbivory, fire, etc., and conservation of the limited available nutrients through internal re-utilization.

Future research:

Future research concerning geophytes in the South-western Cape

could include the following. 1. Advantages in the pollination syndromes of synanthy, hysteranthy and protanthy. 2. Influence of the fire-regime on geophyte life-cycles, especially on their flowering-rhythm, and the effect of population density on biomass allocation and flowering. 3. Microscopic and histochemical examination of storage reserves of storage organs and more elaborate physiological studies.

4. Importance of soil types and edaphic factors, eg. rainfall, temperture, latitude, altitude, etc., in the geographical distribution of species. 5. Aspects of herbivory on population structure. 6. Phytochemistry and pharmacological studies.