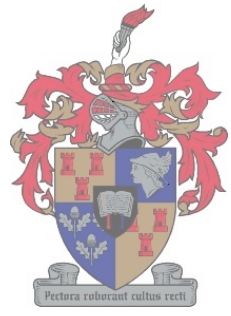
GROWTH AND NUTRITION
OF
BRUNIACEAE

by

Caroline Jacqueline Poole



Thesis presented in partial fulfillment for the degree
of
Master of Agricultural Science
at the
University of Stellenbosch.
December 1999

Supervisors:
Professor G. Jacobs (Supervisor) and D. Saayman (Co-supervisor)

DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

23/11/99
Date

SUMMARY

Growth and nutrition of Bruniaceae

Bruniaceae are increasingly being harvested commercially as cut flowers in South Africa for the European cut flower markets. The need to cultivate certain species requires research to develop economically viable cultivation methods and the selection of productive cultivars. This study deals with horticultural and nutritional aspects of Bruniaceae, particularly *Brunia albiflora* (Pillans). Flower initiation and development of two species of Bruniaceae, *Brunia albiflora* and *Berzelia galpinii* (Pillans) were investigated to determine when floral initiation occurred and to qualify progression of flower differentiation and development. It was observed that development was six months apart with *Brunia albiflora* initiating florets in October and *Berzelia galpinii* in May. Carbohydrate studies were also carried out over a one year period, to determine seasonal changes of carbohydrates which would enable manipulation of cultural practices for increased yield. It was observed that new shoots had lower carbohydrate contents compared to flowering shoots. Side shoots of flowering shoots had higher starch and sugar content than main shoots after winter. The starch content decreased in side shoots following flower initiation in October, with the total sugar content of side shoots showing the same pattern. It appeared that side shoots were net carbohydrate sources and exported assimilates to the developing inflorescence. The increase in carbohydrates of the inflorescence was higher than the loss in the side shoots and it seems that *Brunia albiflora* is mainly reliant on current photosynthates for their growth.

Soil and plant nutrient requirements of *Brunia albiflora* were investigated by selecting three localities in the Western Cape. Variation in terms of growth performance was large at each locality, presumably because of different soil types. Calcium in topsoils showed a significant negative correlation with plant performance, whereas higher exchangeable Na correlated with good plant performance. Soils with high clay content seem to be unsuitable for *Brunia albiflora* possibly due to poor aeration. Positive correlations with plant performance were also found for organic carbon, N, P and K, as well as exchangeable acidity and exchange capacity of the B horizon. Leaf and stems were sampled at two dates to determine which component and time of sampling best reflected the nutrient status of the plant. Leaves were decided on as index tissues and sampling at anthesis (February) was appropriate. Leaf nutrient concentrations of *Brunia albiflora* were found to be low in N, P, K, Mg and Zn compared to other woody plant, whereas Ca, Cu and Mn appeared to have

similar concentrations. The removal of macro-elements by cropping a plantation in full production was calculated as 38 kg N, 1.5 kg P, 35 kg K, 40 kg Ca and 5 kg Mg per hectare based on 25 flowering stems per plant and 5 000 plants per hectare. These results can be used as a basis for fertiliser recommendations, pending the results of fertiliser trials. As the demand for these flowers increases, there will be a greater demand for better quality. Improved production and flower quality should compensate for the extra costs of fertilisers.

OPSOMMING

Groei en voeding van Bruniaceae

Bruniaceae word toenemend kommersieël as snyblom in Suid-Afrika geoes vir die Europese snyblommark. Die behoefte om sekere spesies kommersieël te kweek vereis navorsing om ekonomies vatbare verbouingsmetodes daar te stel en produktiewe kultivars uit te kies. Die studie handel oor hortologiese en voedingsaspekte van Bruniaceae, veral *Brunia albiflora* (Pillans). Blominisiasie en -ontwikkeling van twee spesie Bruniaceae, *Brunia albiflora* en *Berzelia galpinii* (Pillans) is gebruik om die tydstip van blominisiasie te bepaal en die verloop van blomdifferensiasie en -ontwikkeling te kwalifiseer. Die ontwikkeling van die twee spesies is ses maande uitmekaar, *Brunia albiflora* se blominisiasie is in Oktober, terwyl dit by *Berzelia galpinii* in Mei plaasvind. Koolhidraatveranderinge is oor een jaar bestudeer om die seisoenale veranderinge te bepaal om manipulasie van verbouingsmetodes vir verhoogde opbrengs daar te stel. Nuwe lote het 'n laer koolhidraatinhoud in vergelyking met blomdraende lote. Sylote van blomdraende lote het 'n hoër stysel- en suikerinhoud as hooflote. Die styselinhoud van sylote het verminder na die Oktober blominisiasie. Die totale suikerinhoud van sylote het dieselfde patroon gevolg. Daar is gevind dat sylote 'n bron van koolhidrate was, en ook assimilate na die ontwikkelende bloeiwyse uitgevoer het. Die styging in koolhidrate van die bloeiwyse was meer as die verlies in die sylote en dit blyk dat *Brunia albiflora* hoofsaaklik op huidige fotosintate staatmaak.

Grond- en plantvoedingstofvereistes van *Brunia albiflora* is in drie lokaliteite in die Wes-Kaap ondersoek. Daar was groot variasie in plantprestasie by elke gebied, vermoedelik as gevolg van verskille in grondtipes. Kalsium in grond het 'n opvallende negatiewe korrelasie met plantprestasie getoon, terwyl hoër uitruilbare Na goeie plantprestasie getoon het. Grond met 'n hoë klei-inhoud blyk ongeskik vir *Brunia albiflora* te wees, moontlik as gevolg van swak deurlugting. Positiewe korrelasies is ook vir organiese koolstof, N, P en K, sowel as uitruilbare suurheid en die uitruil kapasiteit van die B horison gevind. Blare en stingels is op twee datums gemonster om vas te stel watter komponent en tyd van monsterneming die voedingstatus van die plant die beste weerspieël het. Daar is besluit om blare as indeksweefsel te gebruik en dat monsterneming by antese (Februarie) geskik is. Konsentrasies van N, P, K, Mg en Zn in die blare van *Brunia albiflora* was laag in vergelyking met ander houtagtige plante, terwyl, Ca, Cu en Mn soortgelyke konsentrasies getoon het. Die verwydering van makro-elemente ten tye van volle produksie is vasgestel as 38 kg N, 1.5 kg P, 35 kg K, 40 kg Ca en 5 kg Mg per hektaar, gebaseer op 25 blomdraende lote per plant

en 5 000 plante per hektaar. Hierdie resultate kan gebruik word vir bemestingsaanbevelings in afwagting van die resultate van bemestingsproewe. Soos die aanvraag vir hierdie produk groter word, sal beter kwaliteit blomme verlang word. Verbeterde kwaliteit en produksie behoort te vergoed vir die bykomstige kostes van bemestingstowwe.

Dedicated to my parents, Grace and Roy Poole, for their support and encouragement throughout my studies and for providing me with everything I could ever wish for.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would like to gratefully acknowledge

The FRD for their financial support throughout my tertiary education, SAPPEX for funding for the project and Molteno Brothers for access to and use of their plant material.

And say a very sincere thank you to

Professor G. Jacobs, my supervisor for his guidance and interest throughout this study and his help in the preparation of this thesis. Mr D. Saayman also for his help in the preparation of this thesis.

Karen Theron for her advice on statistical procedures, Rassie van Zyl from Infruitec for help preparing the SEM material, Marlene Lambrechts and Susan Agenbag for help analysing carbohydrates.

The staff at the Soil Science and Horticultural Science Departments, especially Matt for his patience and assistance with elemental analysis, Kenneth for always lending a hand and Nathmie, Camilla and Des for their help in the field and the grinding of samples.

To all my friends who lent a hand and offered encouragement, especially Ian who helped with the editing and printing and was a tremendous support, Audrey for her advice and support, Loren for her support and friendship as well as Iain, Tina, Judith, Max, Rinky and Libby, I value you all.

Richard for his love, interest and sound advice and my parents for their love, encouragement and continual support throughout my University education.

INTRODUCTION

The South and South-West Cape have a large variety of unique flora. The Cape Floral Kingdom consists of only 0.04% of the earth's surface yet more than 8500 floral species are found. The main family cultivated is that of the Proteaceae with the genera *Protea, Leucadendron* and *Leucospermum.* Although cultivation of Bruniaceae has not reached the same level as that of the Proteaceae, the long term aim is to produce better quality products by selecting for commercially viable characteristics.

There is a need to commercially cultivate certain products of Bruniaceae. Bruniaceae are mostly endemic to the Cape and are becoming an important cut flower product. Investigation of certain aspects which will provide information beneficial to developing strategies for plantation management are required, these are particularly pruning and yield prediction, selection of superior plants for future clonal propagation and nutritional requirements. Commercial cultivation can only be successful if preceded and supported by research to develop economically viable cultivation methods and by the selection of productive cultivars.

This study was divided into two parts, the first dealing with horticultural aspects and the second with nutritional aspects of Bruniaceae, particularly *Brunia albiflora.* Flower initiation and development of two species of Bruniaceae were investigated, with the aim of determining when flower initiation took place to provide a description of floral initiation, differentiation and growth. Studies were also carried out to determine the seasonal changes of carbohydrates which, could enable manipulation of cultural practices for an increased yield. Soil and plant analyses were taken at three localities to determine the nutrient requirements of *Brunia albiflora.* Nutritional data of leaves of *Brunia albiflora* are given which can be used as a reference in future and nutrient removal data for three different localities are also reported to give an idea of the nutrients removed by harvesting.

The Bruniaceae family has 12 genera and 74 species endemic to South Africa (Pillans, 1947) and nearly all of them endemic to the fynbos region, except *Raspalia trigyna* found in Southern Natal (Bond & Goldblatt, 1984; Hall, 1987). They are woody schlerophyllous shrubs or undershrubs of medium size (Hall, 1987). The family shows similarities with the oldest angiosperm fossil described by E.M. Friis as *Actinocalyx bohrii* from the Upper Cretaceous time period in south Sweden. It is assumed that the Bruniaceae originate from the same forefathers as Actinocalyx (Friis, 1985). It is not unusual, therefore, that the family is thought to be an old one.

Many factors play a role in the absence of Bruniaceae and related families on the other southern hemisphere fragments of Gondwana. The family could have reached South Africa at the time when continental fragments were already removed from each other. Another possibility, from the view that the Bruniaceae are in a senescent state in the Cape, is that this family is already extinct in the rest of the southern hemisphere (Hall, 1987).

Of the 74 species of Bruniaceae, 18 are threatened with extinction and 3 species are already extinct (Hall & Veldhuis, 1985). Three quarters of Bruniaceae are in a retrogressive senescent state. The weakness of reproductive vigour, and the fact that a quarter of them have more than 20% of their pollen inviable, is possibly the reason for the paleo-endemic condition of Bruniaceae.

The wood and leaf anatomy of the Bruniaceae show similarities with that of Grubbiaceae, an endemic fynbos family (Carlquist, 1978). In broad context the Bruniaceae are related to the Rosales and Hamamelidales families (Carlquist, 1991). Dahlgren & Van Wyk (1988) proposed that the relation with Grubbiaceae should be recognised by placing them both in the same order, Bruniales, near the Ericales.

The Bruniaceae tend to occur in mesic-microhabitats such as south directed slopes, rock crevices, marshes and next to streams where they generally grow in patches of isolated individuals (Hall, 1987). The majority of species grow on rocky mountain slopes, favouring south and south-east aspects. Some species are confined to them while some occur on all aspects (Dummer, 1912; Hall, 1987). They are variable species considerably influenced by the conditions of soil, moisture, light and temperature. Sufficient soil moisture is thought to be essential for the growth of the larger species and all species appear to require full sunlight (Pillans, 1947). As with other fynbos, Bruniaceae are mainly present on shallow, acidic, nutrient poor soils derived from geologically porous sandstone rock formation of the Table mountain series (Bond & Goldblatt, 1984).

The Bruniaceae family have large morphological variations within the family, a result of evoluting to different habitats (Carlquist, 1978). The flowers vary from being solitary and terminal or in weakly to highly condensed, round to flattened capitula of varying colours (Hall, 1987). There is great variation in the size, shape and surface characteristics of the leaves of the Bruniaceae. Leaves are usually small, alternate and of a variety of shapes (Pillans, 1947). Leaves fall into the most advanced spatalla type which offers the smallest possible transpirational surface. They have not developed mechanisms to reduce the rate of transpiration, but have developed mechanisms to produce maximum photosynthesis with

minimum water loss (Van der Merwe, 1992). Fifteen species possess a lignotuber which is a woody rootstock, developed for rapid resprouting after fires. Resprouters take longer to come into production possibly because all their reserves are put into the formation of the lignotuber. An advantage is that the lifespan of these plants is longer, due to their regenerative ability. From a preliminary investigation it appears that roots of *Brunia albiflora* have a symbiosis with an endotrophic mycorrhiza (Poole, 1998, unpublished data).

The two genera focused on in this thesis are *Brunia* and *Berzelia*. The *Brunia* have seven species in the Cape, concentrated in the south-western districts and extending eastwards to the Uitenhage district. *Berzelia* have 12 species concentrated in the same areas but also occur in Albany near Grahamstown (Dyer, 1975). The *Brunia* are distinguished from *Berzelia* in that they have a bilocular ovary and filaments of equal length which are not longer than the petals. *Berzelia* have a unilocular ovary and stamens which are longer than the petals and which curve outwards. The filaments are free (Pillans, 1947).

The trend in the genetic development appears to have been from a trilocular to a unilocular ovary and towards a reduction in the number of ovules. The progress in development has often been uneven. In several genera the inflorescence shows greater advancement than the ovary. In *Brunia* the transition from two to one ovary is evident in the imperfectly formed partition between the two chambers. In *Brunia albiflora* the chambers are normally two but they may by abortion, be reduced to one. In *Berzelia* all traces of a second chamber have disappeared (Pillans, 1947).

The indigenous flower industry has grown gradually and today forms an important part of the Western Cape agricultural sector. Because of the poor quality of wild picked flowers, flowers not cultivated can not be sold on international markets. The demand for South African flowers is greatest during the European winter (November/December). As there is little demand between June and August, only products which can be harvested over the peak period should be focused on.

Literature cited

Bond, P. & Goldblatt, P. 1984. Plants of the Cape Flora. A descriptive catalogue. *J.S.Afr.Bot.*, suppl. **13**:1-455.

Carlquist, S. 1978. Wood anatomy of Bruniaceae: Correlations with ecology, phylogeny and organography. *Aliso* **9:** 323-364.

Carlquist, S. 1991. Leaf anatomy of Bruniaceae: Ecological, systematic and phylogenetic aspects. *Bot.J.Linn.Soc.* **107**: 1-34.

Dahlgren, R. & Van Wyk, A.E. 1988. Structures and relationships of families endemic to or centred in South Africa. *Ann. Missouri Bot. Gard.*

Dummer, R.A. 1912. An enumeration of the Bruniaceae. *J.Bot.Lond.* **50**: suppl. 2: 16.

Friis, E.M. 1985. Actinocalyx Gen. Nov.,sympetalous Angiosperm flowers from the Upper Cretaceous of southern Sweden. *Rev. Palaeobot. Palynol.* **45**: 171-183.

Hall, A.V. & Veldhuis, H.A. 1985. South African Red Data Book: Plants - fynbos and Karoo biomes. *South African National Scientific Programmes Report* **177**: 1-157.

Hall, A.V. 1987. Evidence of a Cretaceous alliance for the Bruniaceae. *S.Afr.J.Sci.* **83**: 58-59.

Pillans, N.S. 1947. A revision of Bruniaceae. *J.S.Afr.Bot.* **13**: 121-206.

Van der Merwe, A.M. 1992. A study to determine anatomical and morphological adaptations in the leaves of selected fynbos species. *MSc-thesis.* University of Stellenbosch.

PART ONE

HORTICULTURE

LITERATURE REVIEW I

Growth and development of selected Proteaceae species

Introduction

South African fynbos species provide important cut flower products for export. In 1988 the trade turnover derived from wildflowers was approximately 30 million Rand (Middelmann, Gibson & Bell, 1989). Proteas and other fynbos products are still partly picked from natural stands. The picking of flowers from the veld has a negative impact on the ecosystem; trampling occurs, seed reserves are depleted and in many cases the eventual product does not fulfil the stringent quality requirements for export flowers. The indigenous flower industry has grown steadily and forms an integral part of the agricultural production of the Western Cape. The growth in the fynbos cut flower industry, as well as a need to protect our natural resources, has led to the need for commercial cultivation of fynbos plants. To cultivate fynbos successfully, an understanding of their seasonal growth pattern is required.

Most research has been done on the Proteaceae family which has made it possible to establish commercial blocks of certain species, thereby producing better quality flowers than those picked from the veld. This has only been achieved in recent years in South Africa . The three genera of most commercial importance are that of *Protea, Leucospermum* and *Leucadendron.*

Protea growth and development

Protea shoot growth occurs in flushes produced from spring to autumn. The inflorescence develops terminally on a shoot with 2-5 growth flushes arising in succession from terminal buds. Apical dominance is usually strong during the active growth of terminal flushes, limiting the formation of sylleptic side shoots (De Swardt, 1989). Proleptic branching occurs after a growth cycle is completed, with the resumption of shoot growth during a second growth cycle. Following harvesting new growth for the following years crop sprouts from axillary buds on bearers. Responses to pruning have been found to vary due to the requirements of flower shoot development, which can be from three to 11 months, and inflorescence development from seven to 11 months. Optimal pruning time would be the shortest time from pruning to anthesis (Malan & Le Roux, 1995). Lateral buds are released from apical dominance by pruning which results in growth of vegetative shoots which elongate by successive flushes. Elongation stops when inflorescence initiation occurs terminally (Gerber, Greenfield, Theron & Jacobs, 1995). Flowering times vary within and between types.

Protea neriifolia flowers from January to July in the summer rainfall area, with the maximum commercial harvest in April/May. Extension growth of both primary shoots that remained vegetative and those that became reproductive showed peak growth in September (Spring). Summer growth rates were only slightly higher than autumn and winter rates. Initial vegetative extension was greater on shoots that became floral, compared to those that remained vegetative. Shoots which became reproductive reached high growth rates one month prior to shoots that remained vegetative. This difference in timing between reproductive and vegetative shoots is apparent in the spring growth flush even though flower buds had not yet visibly set. This implies that the flowering signal is received and acted upon very early in the growing season and that it affects vegetative growth that occurs prior to flower bud initiation (Heinsohn & Pammenter, 1988). Dupee & Goodwin (1990) found flower initiation to occur after the spring flush was complete.

Cool winter temperatures can slow the rate of development of *Protea neriifolia* until September. A phenophase change can therefore be expected if plants are grown under different conditions to their natural ones. If early shoot growth does not have a high water demand, early shoot growth in a summer rainfall area results in a full complement of photosynthesising tissue when air temperatures and soil water conditions become suitable for rapid photosynthesis. Early shoot growth will result in the completion of a disease-vulnerable growth phase before the onset of the wet period with the associated increase in the incidence of pathogens, which is not desirable (Heinsohn & Pammenter, 1988).

Protea cv. Carnival (probably a cross between *P. compacta* R.Br. x *P.neriifolia* R.Br.) flowers from February to April (Greenfield, Theron & Jacobs, 1994), with flower initiation on regrowth during November. This cultivar showed variation in the time the flush started depending on the pruning date. Plants pruned on 2 July or later did not flower the following season. The later pruning takes place, the smaller the probability that flowering shoots will develop. Short days in winter caused non-sprouting in other members of the Proteaceae and may also be implicated in 'Carnival'. It was observed that two consecutive flushes of shoot growth were necessary for flower formation, the second flush being a spring flush, as flowering did not occur on the autumn or second summer flush. The reason for no inflorescence forming on the autumn flush may be due to limited leaf area and carbohydrates. Flower initiation coincided with an increase in reducing sugar levels and starch in bark and a decrease of nitrogen in bark and wood (Greenfield *et al.,* 1994).

Protea cv. Ivy (probably a cross between *P. aurea* (Burm.f.) Rourke x *P. punctata* Meisn.) flowered from January to April. This cultivar becomes dormant under short days when no shoot

growth takes place and development of initiated inflorescences continues at a reduced tempo. This is in contrast to *Leucospermum* where short days cause reproductive development. In early spring (middle September to middle November) shoot growth takes place and after completion of the first cycle, the reproductive phase, as manifested by flower development on the shoots, starts from the beginning of December. At this stage shoots segregate on a plant, some reach the reproductive phase after one shoot growth cycle, whereas others reach it after two cycles and others not at all. This shows that a qualitative induction factor with respect to flower initiation, e.g. day length, is not required and the ability to flower is probably linked to a quantitative change, e.g. light intensity, as in other plants, namely *Leucospermum* and rose (De Swardt, 1989).

New shoots which form in the spring originated from terminal or axillary buds on shoots which did not flower the previous year and axillary buds on shoots which flowered the previous year and where the basal part of the shoot remained after the flower was harvested post-summer. Flowers which formed terminally on the first growth flush (spring) gave origin to early flowering, whereas those which flowered on the second shoot growth flush (1st summer) initiated flowers later (De Swardt, 1989).

After flowers were harvested plants entered the winter condition, when no shoot elongation took place. A gradual increase in main stem diameter occurred. During the reproductive phase no secondary thickness was observed. One-year-old shoots had essentially the same gradual increase in thickness growth as the main stem during winter (De Swardt, 1989). Cambium growth goes through a yearly cycle of high activity and dormancy (Little & Savidge, 1987). Young buds and leaves of young shoots are sources of auxin, gibberrellin and cytokinin which are responsible for cambium growth stimulation (Little & Savidge, 1987). Seasonal cambium growth begins at the same time as shoot elongation, but continues sometimes after shoot elongation has stopped (Kramer & Kozlowski, 1979).

It is possible that secondary thickening, which takes place during the winter on one-year-old shoots which did not flower the previous year, may have an influence on the quality of vegetative growth and, therefore, on the ability to flower on the first shoot growth cycle (De Swardt, 1989). According to observations in the field, long, thick shoots flower first and give better quality flowers than thin, short shoots which flower later.

It seems that shoots developing distally on bearers from axillary buds have the highest potential to flower on the first shoot growth cycle. Flowering potential decreases the lower down shoots sprout from axillary buds. Other factors playing a role are age or complexity of the plant, intra

plant factors, such as the position of shoot on plant, if terminal bud shoots relatively early or late, and interactions of these factors with climate and properties such as light management of the shoot relative to its position on the plant. A percentage of 61 was achieved for flowering of axillary buds on thick mother shoots and only 21% for thin mother shoots after the first growth cycle. Further shoots originating from axillary buds on shoots cut back in the winter never flowered on the first cycle. Shoots which grew out below the developing flower seldom bloomed (De Swardt, 1989).

Leucospermum growth and development

Leucospermum have different growth habits which give species different forms. They have a long flowering time which stretches from winter to the beginning of summer (Vogts, 1979). Branching is not regular throughout and branches grow indeterminately because the terminal bud is vegetative. The terminal bud is encircled by a number of side buds of which at least two give rise to strong side branches which develop almost at right angles. The side buds can also be inflorescence buds and inflorescences developing from the side buds are skew. Flower production occurs after 2-3 years if there is sufficient moisture available and optimal production is approximately when the plants are 5-6 years old (Vogts, 1979).

Individuals can be inherently vigorous and have longer and more slender branches than another plant in the same population. Two types of shoots should be distinguished, i.e:

i) branches growing fast and vigorously and the majority of which develop into flower branches

ii) branches which sprout at the end of flowering from one or more buds at the bottom, top or next to the old inflorescence.

Vegetative and reproductive growth phases are separate and follow each other in sequence (Wallerstein, 1989). Vegetative growth of new branches takes place during spring and summer and is characterised by strong apical dominance (Jacobs, Napier & Malan, 1986). Plants can not be cut back at any time of the year to stimulate growth as in the rose (Cockshull & Horridge, 1977) as they will be too weak to flower. After shoot growth has terminated in autumn, inflorescences are initiated in the five uppermost axillary buds, and the apical meristem remains vegetative (Wallerstein, 1989). Due to the position where flowers are initiated, flower initiation can only occur after shoot growth has stopped. Shoot elongation can continue until late in March (autumn) (Malan, Cutting & Jacobs, 1994a). Of the 5 inflorescence primordia, the one nearest the terminal bud develops during the winter and blooms in early spring, while the other primordia abort (Wallerstein, 1989).

The vegetative cycle of *Leucospermum* 'Red Sunset' occurs in late spring and summer when extension growth of shoots occurs. Root growth occurs in the winter, this is probably because shoots are the strongest sinks. By the end of February most shoots had stopped growing but did not have the ability to form a flower. The change from vegetative to reproductive growth took place during a relatively short period for long shoots (Jacobs, 1983). The induced state for 'Red Sunset' is attained in the first half of April (autumn) (Jacobs, 1983; Napier, 1985). This is indicated by the development of an inflorescence when shoots are cut back to a completely inhibited axillary bud. Shoot growth occurred when shoots were cut back prior to this date (Jacobs *et al.*, 1986). The ability to initiate a flower was maintained for two months, followed by a gradual loss of the induced state, until the plant returned to the non-induced vegetative state by October (Jacobs, 1985). Flower initiation could only take place when plants were in the induced state and axillary buds are removed from correlative inhibition. Jacobs (1983) found that 'Red Sunset' plants were not in the induced state before April 25. Leaf starch increased during the induced state and could be associated with the inductive state (Napier, 1985)

Retention of the induced state was related to stem size (Jacobs, 1983). The developmental period of secondary flower buds became shorter the later the primary inflorescence was removed due to the rising temperature of spring and summer (Jacobs & Honeyborne, 1979). Disbudding the primary inflorescences too late, resulted in the resumption of shoot growth since the secondary flower buds have aborted (Jacobs, 1983). Loss of the induced state in *Leucospermum* cv. Red Sunset was thought to be due to low light intensity of winter as it corresponded with a decrease in leaf starch (Napier, 1985).

Shoot growth on young 'Red Sunset' plants continued for a longer period than on older plants, which have a more complex shoot system. Vegetative development from a number of axillary buds resumed from shoots on which apical growth ceased before inductive conditions occurred, making these shoots unmarketable (Jacobs, 1985). Non-irrigated plants' shoot growth ceased on 30 March, whereas on irrigated plants most shoots were still actively growing on this date. Water stress is the main reason for the cessation of shoot growth before exposure to inductive short day conditions in the autumn (Malan & Jacobs, 1994).
In experiments done by Napier *et al.* (1986), it was observed that the dry mass of primary inflorescences (PI) increased at an exponential rate. By mid-April the position at which the PI developed was identifiable. The PI developed faster than the surrounding buds and it was seen that the node position at which the PI developed varied. The rate of development of buds situated acropetally and basipetally to the PI decreased, depending on their relative position to the PI. Development rate decreased as the number of nodes between the bud and the PI

increased. A decreasing gradient in the stage of morphological development was attained by buds situated proximal to the PI. Usually only the three buds closest to the PI enter into the floret initiation phase (Malan *et al.*, 1994a).

Axillary buds were correlatively inhibited by developing inflorescences (Jacobs, 1983). The degree of inhibition of axillary buds depended on its position on the shoot. The first few axillary buds directly under the developing inflorescence are only partially inhibited since they developed to ca. 5 mm in diameter. Floret differentiation had progressed to the stage where the perianth initials were visible. Buds lower down on the shoot did not show signs of development and were completely inhibited. When the primary inflorescence is removed, one or more of the uppermost secondary flower buds resumed development (Brits, 1986). The cessation of shoot elongation was the first signal for the gradual loss of correlative inhibition which allowed flower bud initiation in the axillary positions close to the apical bud (Jacobs, 1985).

Growth and development of 'Red Sunset' inflorescences has been divided into four stages by Napier (1985). These are; pre-floret, floret initiation, floret differentiation and enlargement stages. Pre-floret is the initial growth of the bud and lasts until the first week in May. Growth is slow and dry mass accumulation is low. First bracts are formed without floret initials in the axils. These bracts finally make up the involucre covering the peduncle. Floret initiation is marked by the appearance of the first floret initials in the bract axils of later bracts. This lasts until the cessation of floret initiation during the third week of June. Dry mass increase during this phase is slow. Floret differentiation is from the completion of floret initiation to near completion of organ differentiation of basal florets by mid-August, lasting about two months. Growth rate is slow at first but increases rapidly as organ differentiation advances. Enlargement phase is from near completion of organ differentiation in basal florets to anthesis in early October. The growth rate is rapid during this phase (Napier *et al.,* 1986). Criley, Parvin & Lekawatana (1990) in Hawaii, observed that the rate of flower bud length increase in *Leucospermum cordifolium* was gradual until mid-December (winter). Bud diameter increased gradually, increasing slowly until January when it doubled and doubled again just before bud opening.
The first meristematic activity leading to floral primordia appeared in mid-October (autumn) and the apex broadened. By mid-November, three or four cycles of florets had developed and by late November perianth and stamens were initiated. Stamen and pistillate elongation proceeded through December and January (winter). During flower stalk lengthening in late December, there seemed to be a slowing in the development of organ primordia on recent florets. Buds were initiated in October (autumn) but floret primordia were only visibly active three weeks later, about 120 days for flower development (Criley *et al.,* 1990).

Long days had an inductive effect, whereas inflorescence differentiation occurred under short day or a low temperature regime (Wallerstein, 1989). At least 42 natural short day cycles are required for normal flowering (Malan & Jacobs, 1990). Floral differentiation was delayed under long days. During growth under short day conditions, the first florally differentiating meristem inhibited the further development of the other inflorescence primordia (Jacobs *et al.,* 1986). Experiments done by Malan *et al.* (1994b) showed that inhibited distal axillary buds resumed development if shoots were decapitated up to 21 May, when PI was still in the floret initiation phase. Most buds developed vegetatively after the change to long days in mid September.

Leucadendron **growth and development**

Leucadendron growth begins in spring and continues through summer. *Leucadendron* 'Safari Sunset' had a similar growth pattern to *Banksia ashbyi* and *Leucospermum patersonii* (Wallerstein, 1989). The growth cycle included sprouting in spring, cessation of shoot elongation in late summer, inflorescence initiation in autumn, cessation of axillary bud activity in winter and flowering in spring. The ability of *Leucadendron* to initiate an inflorescence depends on the date when elongation stops and or the shoot length at the time. This dependence seems to be common in the three species of Proteaceae and is probably a key to their flowering period (Wallerstein & Nissim, 1992). The fact that axillary buds of *Leucadendron* can sprout but can not elongate during the autumn is similar to the situation found for *Banksia,* and is probably an indication of the positive effect of long days on shoot elongation, as is the case in *Leucospermum* (Wallerstein, 1989).

Control plants of 'Safari Sunset' sprouted in March (winter) in Israel, stopped elongation in July and flowered during the following spring. Pruning plants at the beginning of each month between March and July, was followed by axillary bud sprouting one month later. The new shoots stopped elongating during August and September. Axillary buds of plants pruned between August and October sprouted 2 months after pruning and stopped elongating immediately after sprouting, indicating that elongation ceases between July and October while axillary buds are still able to sprout after pruning but do not elongate more than 3-5 cm. Plants pruned between November and February sprouted during spring when control plants sprouted, indicating that the axillary buds are inactive during winter (Wallerstein & Nissim, 1992).

Banksia **growth and development**

Like many other woody perennials grown from seed, *Banksia* have a juvenile phase during which plants will not flower and early crops are often poor and erratic. Juvenility in most

Banksia lasts 3-4 years (Fuss & Sedgley, 1991). There is a tendency for a reduction in quality of blooms as the season progresses in *Banksia.*

Flower initiation of both *Banksia coccinea* and *Banksia menziesii* occurs in late spring, a time of increasing day length and moderate temperature (Fuss & Sedgley, 1991). Floral development for *B. menziesii* takes 6-8 months and the flowering period extends from February to September with a peak in May (Fuss, Pattison, Aspinall & Sedgley, 1992). The ability of a meristem to initiate an inflorescence depends on the shoot growth rate during spring and summer. Inflorescence development can be accelerated by moderate temperature, especially during the primordial stage (Wallerstein & Nissim, 1992).

Shoot extension growth occurs from the terminal bud during each active growth season until an inflorescence is initiated in the terminal position or the terminal bud is damaged. Upon termination of extension growth new lateral shoots arise from axillary buds. The majority of inflorescences are initiated on two year old wood. Shoots that were floral were longer and thicker than non-floral shoots. Active growth in October, resulted in rapid increase in basal diameter of the previous year's growth and of extension growth from the terminal bud. After February no further increase in shoot length occurred for floral or non-floral shoots, but basal diameter continued to increase. There is a strong correlation between the number of leaves on a shoot, shoot length and basal diameter. *B. coccinea* flowers from July to November, with peak flowering in October. New growth commences and inflorescences are initiated while the bushes are flowering (Fuss *et al.*, 1992). Flower development takes 12 months and there is therefore an overlap between one year's flowering and initiation of the next year's blooms (Fuss & Sedgley, 1991).

In *Banksia baxterii* and *B. hookeriana*, flower initiation is identified by initiation of involucral and common bracts in an irregular arrangement around the apex. Floral development was rapid in *B. baxterii* with immature inflorescences becoming macroscopically visible within the month of flower initiation, then reaching anthesis three months later in mid summer. Microscopic development was slower in *B. hookeriana* than in *B. baxterii,* taking two months from flower initiation to macroscopic appearance. Macroscopic development occurred at a similar rate with anthesis in *B. hookeriana* occurring three months after macroscopic appearance (Röhl, Fuss, Dhaliwal, Webb & Lamont, 1994).

Serruria growth and development

Plants grew vegetatively during spring and summer. Reproductive development occurred during autumn after extension growth had terminated and flowers opened during July and August. *Serruria florida* commenced reproductive development during March and flower initiation was induced by short days (Malan & Brits, 1990).

The number of capitula on a shoot was dependent on shoot diameter with thicker shoots bearing more inflorescences. There was a lower probability of inflorescences occurring at node 2 and 3, possibly due to correlative inhibition by terminal inflorescences. Primordia were initiated during the slow early development of bud bracts. Approximately the first 10 primordia developed into peduncular bracts. Peduncular bract initiation was followed by a flattening of the apical meristem and the rapid initiation of 30-40 bracts and floret primordia. Approximately 15 of the distal florets aborted at an early stage, with approximately 25 florets developing to anthesis. Floret initiation was completed and perianth initials could be distinguished on florets by 4 May (Malan & Brits, 1990).

Summary

Shoot growth, flower initiation and development cycles differ for *Leucospermum* and *Leucadendron*. They are more predictable than that of *Protea* which have a cyclic growth consisting of a number of flushes. *Protea neriifolia* shows differences in extension growth in vegetative and reproductive shoots. Flowering takes place from January to July and shoot growth occurs in spring. In *Protea* cv. Carnival the time of flush depends on the pruning date. The later pruning the smaller the probability that flowering shoots will develop. Carnival needs two consecutive flushes for flower formation, which usually occur from February to April. *Protea* cv. Ivy has no shoot growth or development under short day conditions. Shoot growth occurs in early spring, and the reproductive phase starts at the beginning of December. Flowering takes place from January to April. No shoot elongation takes place during winter but secondary thickening does occur. It is expected that a quantitative induction factor for flower initiation occurs.

Leucospermum have separate vegetative and reproductive growth phases. Vegetative growth occurs in spring and summer and is characterised by strong apical dominance. Inflorescences are initiated after growth has terminated in autumn and flower initiation is induced by short days. Flowering is over a long period. *Leucadendron* sprout in spring, initiate flowers in autumn after

shoot elongation ceases in late summer and flowers in spring. Flower initiation is thought to be dependent on when elongation stops.

Banksia initiate flowers in late spring under long day conditions, floral development varies according to the species. The ability to initiate flowers depends on the shoot growth rate in spring and summer. The majority of flowers were initiated on two-year-old wood, and floral shoots were longer and thicker. *Serruria* grew vegetatively during spring and summer. Reproductive development is during autumn after extension growth has terminated and anthesis reached in August.

Literature cited

Brits, G.J. 1986. Manipulation of flowering time in *Leucospermum cordifolium* with ethephon. *Agroplantae* **9**: 127-130.

Cockshull, K.E. & Horridge, J.S. 1977. Apical dominance and flower initiation in the rose. *Jnl of Hort Sci.* **52**: 421-427.

Criley, R.A., Parvin, P.E. & Lekawatana. S. 1990. Flower development in *Leucospermum cordifolium* "Vlam". *Acta Hort.* **264**: 61-70.

De Swardt, D.C. 1989. Aspekte van die vegetatiewe en reproduktiewe ontwikkeling by geselekteerde *Proteaceae* cultivars. *MSc-thesis.* University of Stellenbosch.

Dupee, S.A. & Goodwin, P.B. 1990. Effect of temperature, daylength and growth regulators on flowering in *Protea, Telopea* and *Leucospermum. Acta Hort.* **264**:79-86.

Fuss, A.M. & Sedgley, M. 1991. Variability in cut flower production of *Banksia coccinea* R. Br. and *Banksia menziesii* R.Br. at six locations in southern Australia. *Aust.Jnl.Expt.Agric.* **31**: 853-858.

Fuss, A.M., Pattison, S.J., Aspinall, D. & Sedgley, M. 1992. Shoot growth in relation to cut flower production of *Banksia coccinea* and *Banksia menziesii* (Proteaceae). *Sci. Hort.* **49**: 323-334.

Gerber, A.I., Greenfield, E.J., Theron, K.I. & Jacobs, G. 1995. Pruning of *Protea* cv. Carnival to optimise economic biomass production. *Acta Hort.* **387**: 99-106.

Greenfield, E.J., Theron, K.J. & Jacobs, G. 1994. Effect of pruning on growth and flowering response of *Protea* cv. Carnival. *J. S. Afr. Soc. Hort. Sci.* **4(1)**: 42-46.

Heinsohn, R.D. & Pammenter, N.W. 1988. Seasonality of shootgrowth and flowering in the fynbos shrub *Protea neriifolia* cultivated in a summer rainfall area. *S. Afr. J. Bot.* **54(5)**: 440-444.

Jacobs, G. 1983. Flower initiation and development in *Leucospermum* cv. Red Sunset. *J. Amer. Soc. Hort. Sci.* **108(1)**: 32-35.

Jacobs, G. 1985. *Leucospermum.* **In**: Halevy A.H. (ed.), Handbook of flowering. pp. 283-286 CRC Press, Boca Raton.

Jacobs, G. & Honeyborne, G.E. 1979. The relationship between heat unit accumulation and the flowering date of *Leucospermum* cv. Golden Star. *Agroplantae* **11**: 83-85.

Jacobs, G., Napier, D.N. & Malan, D.G. 1986. Prospects of delaying flowering time of *Leucospermum*. *Acta Hort.* **185**: 61-65.

Kramer, K.V. & Kozlowski, T. 1979. Internal factors affecting growth **In**: Physiology of woody plants. pp. 546-627. Academic Press. New York.

Little, C.H.A. & Savidge, R.A. 1987. The role of plant growth regulators in forest tree cambial growth. *Plant Growth Regulation* **6:** 137-169.

Malan, D.G., Cutting J.G.M. & Jacobs, G. 1994a. Correlative inhibition of inflorescence development in *Leucospermum* "Red Sunset". *J. S. Afr. Soc. Hort. Sci.* **4(1)**: 26-31.

Malan, D.G., Cutting, J.G.M. & Jacobs, G. 1994b. The role of the developing inflorescences on the loss of responsiveness to flower inducing short days in *Leucospermum* "Red Sunset". *J. S. Afr. Soc. Hort. Sci.* **4(1)**: 32-36.

Malan, D.G. & Brits, G.J. 1990. Flower structure and the influence of day length on flower initiation of *Serruria Florida Knight* (Proteaceae). *Acta Hort.* **264**: 87-91.

Malan, D.G. & Jacobs, G. 1990. Effect of photoperiod and shoot decapitation on flowering of *Leucospermum* "Red Sunset". *J. Amer. Soc. Hort. Sci.* **115(1)**: 131-135.

Malan, D.G. & Jacobs, G. 1994. Influence of day length, irrigation and pruning on shoot growth of *Leucospermum* "Red Sunset". *J. S. Afr. Soc. Hort. Sci.* **4(1)**: 24-25.

Malan, D.G. & Le Roux, R.D. 1995. Preliminary investigation into the effect of time of pruning on shoot growth and flowering time of Protea. *Acta Hort.* **387**: 91-97.

Middelmann, W.J., Gibson, B. & Bell, I. 1989 The commercial perspective **In**: Greyling, T. & Davis, G.W. (eds), A report of the terrestrial ecosystems section. Ecosystem Programmes. The wildflower resource: commerce, conservation and research. Occasional Report No.40.

Napier, D.R. 1985. Initiation, growth and development of *Leucospermum* cv. Red Sunset inflorescences. *MSc - thesis*. University of Stellenbosch.

Napier, D.R., Jacobs, G. Van Staden, J. & Forsyth, C. 1986. Cytokinins and flower development in *Leucospermum*. *J. Amer. Soc. Hort. Sci.* **111(5)**: 776-780.

Röhl, L.J., Fuss, A.M., Dhaliwal, J.A., Webb, M.G. & Lamont, B.B. 1994. Investigation of flowering in *Banksia baxteri* R.Br. and *B.hookeriana* Meissner for improving pruning practices. *Austr. Jnl. Expt. Agric.* **34**: 1209-1216.

Rourke, J.P. 1972. Taxonomic studies on *Leucospermum* R.Br. *J.S.Afr. Bot.* Supplementary volume no. 8. Trustees of the National Botanic Gardens of South Africa. Kirstenbosch. Newlands, Cape Town.

Vogts, M.M. 1979. Proteas: Intensiewe snyblomverbouing Leucospermum-soorte. *Blomme en Sierstruike* **B.12.**

Wallerstein, I. 1989. Sequential photoperiodic requirement for flower initiation and development of *Leucospermum patersonii* (Proteaceae). *Israel Jnl. Bot.* **38**: 25-34.

Wallerstein, I. & Nissim, A. 1992. Control of growth and flowering in *Banksia ashbyi, Leucospermum patersonii* and *Leucadendron* "Safari Sunset". *Acta Hort.* **316**: 73-76.

PAPER 1

Inflorescence initiation and development of two species of the Bruniaceae family (*Brunia albiflora* (Pillans) *and Berzelia galpinii* (Pillans)) as studied with scanning electron micrographs.

Abstract

Twelve species of Bruniaceae are commercially harvested as cut flowers in South Africa and exported to European cut flower markets. Competition with European cut flowers is high. Good quality is therefore required and there needs to be continuity of the product during the marketing period. Research into these species is important in order to select good clonal material and to enable manipulations to be carried out to ensure good quality products are produced. This paper presents a series of scanning electron micrographs which shows, 3-dimensional images of the developmental stages of the shoot apex. The development of the apical meristem of the axillary shoots of two species of Bruniaceae, *Brunia albiflora* (Pillans) and *Berzelia galpinii* (Pillans), were studied in order to determine when inflorescence initiation occurred. It was observed that development of the two species were six months apart with *Brunia albiflora* initiating flowers in October and *Berzelia galpinii* in May.

Introduction

Proteaceae is the dominant family used in the South African indigenous cut flower industry. A large group of plants do not fall into this family and are marketed as the 'Cape Greens' of which the Bruniaceae family forms an important part. The four genera of horticultural importance are *Brunia*, *Berzelia*, *Nebelia* and *Staavia*, however, only 12 of the 74 species are commercially harvested. These are *Brunia albiflora, Brunia alopecuroides, Brunia laevis, Brunia nodiflora, Brunia stokoei, Berzelia galpinii, Berzelia intermedia, Berzelia lanuginosa, Nebelia laevis, Nebelia palacea, Nebelia fragaroides* and *Staavia radiata* (Malan, undated). Some of these species have good potential for cultivation but little is known about cultural requirements and growth and development of the species.

Few of these 12 species are currently being cultivated and production is based on seedling material where variation among plants is high. Competition with European cut flowers is high, demanding uniform products and a continuity of supply. Research into these species is therefore important in order to select clonal material and manipulate plants to ensure that these requirements are met.

The two species discussed in this paper are *Brunia albiflora* (Pillans) and *Berzelia galpinii* (Pillans). The genus *Brunia* has seven species in the Cape, concentrated in the south-western districts and extending eastwards to the Uitenhage district. The genus *Berzelia* has 12 species concentrated in the same areas, but also occurring in Albany near Grahamstown (Dummer, 1912). Anatomically the *Brunia* are distinguished from *Berzelia* in that they have a bilocular ovary and filaments of equal length, which are not longer than the petals. *Berzelia* have a unilocular ovary and stamens that are longer than the petals, which are curved outwards. The filaments are free (Pillans, 1947).

Brunia albiflora is commonly known as the coffee bush and can grow 2-3 m high. It is distinguished from the other seven species in that it has pilose leaves which are furrowed on the ventral surface, the anthers are linear and the upper half of the ovary is glabrous (Pillans, 1947). The inflorescence of *Brunia albiflora* is made up of more than 15 rotund inflorescences, each about 1.5 cm wide. They are surrounded by scale-like leaves and are clustered in corymb-like groups to form an attractive flat-topped conflorescence (Pillans, 1947). Below the inflorescence are a number of leaf-bearing units. The inflorescences develop from lateral positions and the terminal meristem remains vegetative.

Berzelia galpinii, commonly known as baubles, is a smaller plant than *Brunia albiflora*, growing 1.5-2 m high. Characteristics which distinguish it from other species in the genus are leaves that are acuminate and petals that are linear-oblong in the upper half, tapering to the base. The conflorescence is composed of 10 or more rotund inflorescences, each of which are usually 1-1.3 cm wide. The heads increase in size during seed formation. They are globose and are clustered together to give an almost corymbose form (Pillans, 1947).

The objective of this study was to determine when inflorescence initiation takes place and to qualify the progression of inflorescence differentiation and development. This paper presents a series of scanning electron micrographs showing the development of the apical meristem of the shoot apex, relative to the axillary buds of the axillary shoots from the vegetative phase to after anthesis.

Material and Methods

Brunia albiflora and *Berzelia galpinii* were grown from cuttings, from seedling blocks, planted in 1995 on a commercial farm in the Elgin area of the Western Cape, South Africa (19°02'E, 34°08'S). The area is characterised by a Mediterranean climate of cold, wet winters and warm, dry summers. The plant density is 13 000 plants per hectare. The *Brunia albiflora* planting consisted of two blocks 0.47 and 0.43 ha. Plants were drip-irrigated to supplement rainfall and fertigated from August to March according to commercial practices. *Berzelia galpinii* was planted in a trial block and consisted of approximately 100 plants. The first *Brunia albiflora* crop was harvested in 1997 with a total production of 37 000 stems. The following year this increased to 120 330 stems.

Terminal and axillary apices were taken at weekly intervals from 8 April 1997 to 26 February 1998 for *Brunia albiflora* and from 8 March 1997 to 18 November 1997 for *Berzelia galpinii*. Apices were fixed in formaldehyde-acetic acid-alcohol-water (2:1:10:7) (FAA) for storage before being dehydrated in a graded ethanol series. The alcohol concentrations were: 50%, 70%, 85%, 95%, and 100% water free ethanol. The buds were kept at each concentration for a minimum of 3 hours. The apices were then dried by critical point drying with CO_2. The water free 100% alcohol was replaced by CO_2 at a pressure of 75 Bar and 31.1°C. The pressure was increased to 80 Bar and the temperature to 32°C. The CO_2 was gradually released. After drying, the samples were sputter coated with gold for 8 min. at 1kV in an Edwards Auto 306 ion coater. The buds were examined with a Jeol JSM 6100 SEM at a working distance of 12 mm at

an acceleration tension of 5kV. Micrographs were taken using a Joel HR 80018 camera and Agfa 120 mm, 100 ASA film.

Results and Discussion

Flowering shoots of *Brunia albiflora* can be harvested with no inflorescence from the end of August when they are marketed as 'Albigreen'. From mid October to November they are marketed with an immature inflorescence as 'Albiyoung'. Harvesting of 'Albiflora' takes place from December until just before anthesis in March. Heads of 'Albiflora' are fully developed, silver/green in colour and classified according to large, medium and small. Peak harvesting is reached in January (Dücker, unpublished), making the crop very suitable for the overseas market as it falls into a suitable marketing window.

Berzelia galpinii can be harvested before anthesis in the bud stage with small round heads from May to August and after anthesis with larger heads when seed has been formed, from November to May. The latter is the main crop as it falls in the correct marketing window and is a hardier crop for transporting. Anthesis is reached at the end of September in the Elgin area.

Reproductive development of *Brunia albiflora* can be divided arbitrarily into four macroscopically visible stages. The time each stage was reached varied between different plants, as it was not a clonal population.

Stage I The initial phase of tip complexity brought about by precocious development of axillary buds, this stage was clearly visible in August (Fig. 1.1A).

Stage II The elongation of the peduncles, visible from September to December (Fig. 1.1B).

Stage III The enlarging of inflorescence to final size reached in January (Fig. 1.1C, D & E).

Stage IV Anthesis which occurs in February/March (Fig. 1.1F).

A classification of microscopic inflorescence development from vegetative to reproductive stage of the apical meristem of the axillary shoots for *Brunia albiflora* and *Berzelia galpinii* is given in Table 1.1. Schematic diagrams of the vegetative shoot and reproductive shoot are given in Fig. 1.2 and 1.3 respectively, which explains the parts referred to. The development of *Brunia albiflora* (Fig. 1.4-1.8) and *Berzelia galpinii* (Fig. 1.9-1.11) is shown in scanning electron micrographs. These figures illustrate the transition from vegetative to reproductive phase of the apical meristem of the axillary shoots, followed by the development of the florets.

The apical meristem of the shoot apex and sylleptic side shoots (SSS) of *Brunia albiflora* were vegetative in April and May. The size of the meristem of the main shoot was slightly larger than that of the SSS (Fig. 1.4A and 1.4B). Axillary buds were visible in the leaf axils of the terminal part of the main shoot in May (Fig. 1.4C and 1.4D). No axillary buds were visible on the SSS (Fig. 1.4E).

Figure 1.5A shows the main shoot of *Brunia albiflora* before the loss of apical dominance. Stage V1 was the first evidence of reproductive development and was observed microscopically by a precocious development of axillary buds in June for *Brunia albiflora* (Fig. 1.5B) and January for *Berzelia galpinii*. During growth of the main shoot, sylleptic shoots developed at irregular intervals. When shoot growth terminated many upper lateral buds developed which formed inflorescences in the terminal position.

The shoot apex remained vegetative and the axillary shoots elongated past it (Fig. 1.5C). The flower heads therefore occupied a terminal position on upper lateral shoots. From Fig. 1.5C and 1.9A it can be seen that *Brunia albiflora* produces many more axillary shoots than *Berzelia galpinii*.

The apical meristems of the axillary shoots changed rapidly from July to September in *Brunia albiflora* (Fig. 1.5B and 1.5C) and January to April in *Berzelia galpinii*. Size increased, denoting stage V2. By September the apical meristems of the axillary shoots of *Brunia albiflora* were the same size as the terminal meristems (Fig. 1.5C). Not all the axillary buds went through the enlarging and elongation stage (Fig. 1.5C). Elongation commenced in July for *Brunia albiflora* and continued during the initiation of floret primordia. At anthesis, shoots subtending the inflorescences had a final length of approximately 4-5 cm at anthesis. Figures 1.5D-1.5F show the apical meristem of the shoot apex, the apical meristem of the SSS and the apical meristem of the axillary shoot. The variation in size of the different apical meristems at the same stage in August is evident, with the apical meristem of the axillary shoot (Fig. 1.5F) larger than the apical meristem of the shoot apex (Fig. 1.5D). The same meristems are shown for *Berzelia galpinii* in Fig. 1.9B-1.9D in April.

At the end of October, *Brunia albiflora* entered stage R1, evidenced by a flattening of the meristem. This occurred in May for *Berzelia galpinii* (Fig. 1.9D). The many villous hairs covering the meristem made it impossible to see stage R2.

In November, floret primordia were observed in *Brunia albiflora* on enlarged, flattened meristems, the start of stage R3. Involucral, villous bracts subtended the primordia (Fig. 1.6A

and 1.6B). Initiation of the florets took place from the outer edge of the receptacle and continued acropetally, with the peripheral primordia developing the fastest (Fig. 1.6A). *Berzelia galpinii* had floret primordia visible towards the end of May (Fig. 1.10A-1.10C). The meristem of *Berzelia galpinii* was more rounded than that of *Brunia albiflora*.

The development of florets of *Brunia albiflora* and *Berzelia galpinii* were almost identical. Stage P can be seen in Fig. 1.6C and 1.6D for *Brunia* albiflora. Five perianth initials formed in a single whorl of five, the inner whorl of androecium primordia, only just visible, denoted stage A. The androecium of *Brunia albiflora* are seen more clearly in Fig. 1.6E and those of *Berzelia galpinii* in Fig. 1.10D – 1.10F. The shape of the head and the arrangement of the primordia on the meristem are shown for *Brunia albiflora* in Fig. 1.6F and for *Berzelia galpinii* in Fig. 1.11A. Stage P and A took place in December for *Brunia albiflora* and in June for *Berzelia galpinii*.

After the formation of the androecium, cells rose up to form a meristematic ring, which formed the carpel primordia (Fig. 1.7A and 1.7B). The ovary of *B.* albiflora is bilocular and is described by Pillans (1947) as being 'half inferior (and) rounded with two imperfectly formed uniovulate chambers', as seen in Fig. 1.7C.

The developing anthers of *Brunia albiflora* are 425 μm in length (Fig. 1.8A). The pollen grains can be seen in Fig. 1.8B. At anthesis the stamens are of slightly unequal length, they exsert and have introrse anthers of 2 mm in length (Pillans, 1947). Figure 1.8C shows the pistil and anthers enclosed in the perianth. A single flower can be seen in Fig. 1.8D. Its petals are linear elliptic and taper to the base. Villous bracts reaching to the middle of the petals are also evident.

Towards the end of July, pollen of *Berzelia galpinii* had formed in the anthers, which were 1mm long (Fig. 1.11B). The pollen was deposited on the stigma before the filaments extended beyond the perianth (Fig. 1.11C). Anthesis took place in August (Fig. 1.11D), with the florets at the base of the inflorescence extending their styles, continueing acropetally. Figure 1.11D shows the elliptic petals that taper towards both ends. The ovary of *Berzelia galpinii* is inferior and unilocular (Fig. 1.11E). Seed development is shown in Fig. 1.11F.

Conclusion

The set of scanning electron micrographs of the morphological development of apical meristems of the axillary shoots of *Brunia albiflora* and *Berzelia galpinii* provides the basis for describing floral initiation differentiation and growth. Floral initiation was indicated by the widening and flattening of apical meristems of the side shoots. This took place in October for *Brunia albiflora* and in May for *Berzelia galpinii*. It would seem that the development of the two species are six months apart, with floret development of *Brunia albiflora* taking place through the summer and *Berzelia galpinii* in the winter. The reproductive development of *Berzelia galpinii* is similar to that of *Leucospermum* cv. Red Sunset in that reproductive development occurs at the end of March after cessation of shoot growth and that floret development takes place through autumn and winter with anthesis in spring (Jacobs, 1983). Factors playing a role in the induction of flowering in Bruniaceae, are still unknown and require further research.

Literature cited

Dücker, G. Unpublished. Department of Horticulture. University of Hannover.

Dummer, F.A. 1912. An enumeration of the Bruniaceae. *J.Bot.* August **2**.

Jacobs, G. 1983. Flower initiation and development in *Leucospermum* cv. Red Sunset. *J.Amer. Soc. Hort. Sci.* **108(1)**: 32-35.

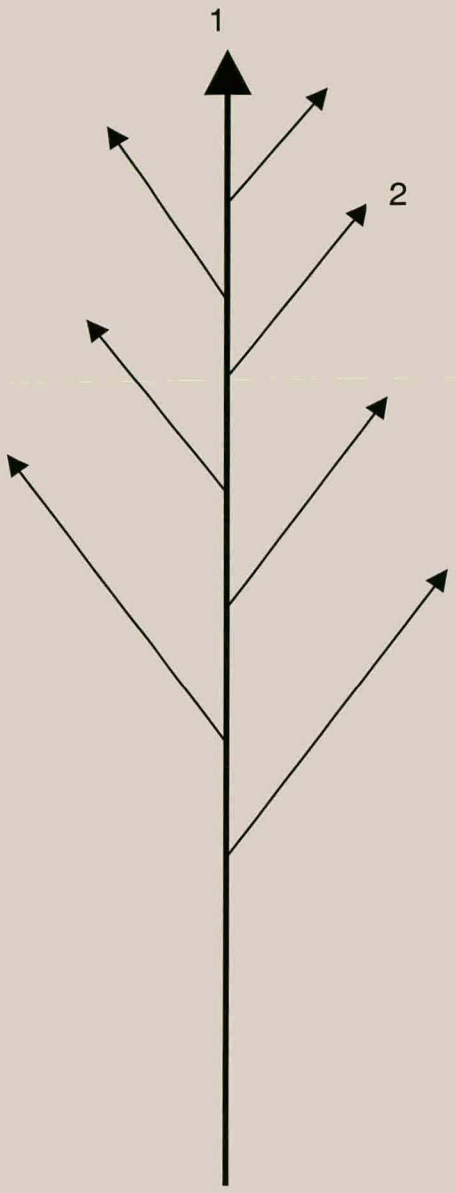
Malan, D.G. Undated. Agricultural Research Council report. The fynbos ornamental industry.

Pillans, N.A. 1947. A revision of Bruniaceae. *J.S.Afr.Bot.* **13**: 121-206.

Figure 1.1. Macroscopic development of *Brunia albiflora*. (A) Stage I: complexing of main shoot tip in August. (B) Numerous shoots in September showing elongation of subtending shoots, stage II. (C) Stage III: reproductive stage, end December, showing the axillary shoots with developing inflorescensces. (D) Reproductive stage in January, further elongation of subtending shoots, stage III. (E) Reproductive stage showing compound inflorescence in February prior to anthesis, stage III. (F) Anthesis of compound inflorescence in March, stage IV.

Table 1.1. Classification of inflorescence development of *Brunia albiflora* and *Berzelia galpinii*.

Stage	Description	Figure	
		Brunia	*Berzelia*
V1	Loss of apical dominance, enlargement of axillary buds	1.5B	
V2	Elongation of axillary shoots, with apical meristem dome shaped	1.5C	1.9A, 1.9B
R1	The dome-shaped apical meristem of axillary shoot widened and flattened		1.9D
R2	Initiation of bract primordia		
R3	Initiation of floral primordia	1.6A, 1.6B	1.10A, 1.10B,10C
P	Perianth initials formed (5)	1.6D	1.10D
A	Androecium initials formed (5)	1.6E	1.10E, 1.10F
G	Gynoecium initials formed	1.7A, 1.7B	
Aa	Anthers visible	1.8A	
Go	Ovule visible	1.7C	1.11E
F	Anthesis		1.11D



1 - apical meristem of shoot

2 - apical meristem of sylleptic shoot (SSS)

Figure 1.2. Schematic representation of vegetative shoot of *Brunia albiflora* and *Berzelia galpinii*

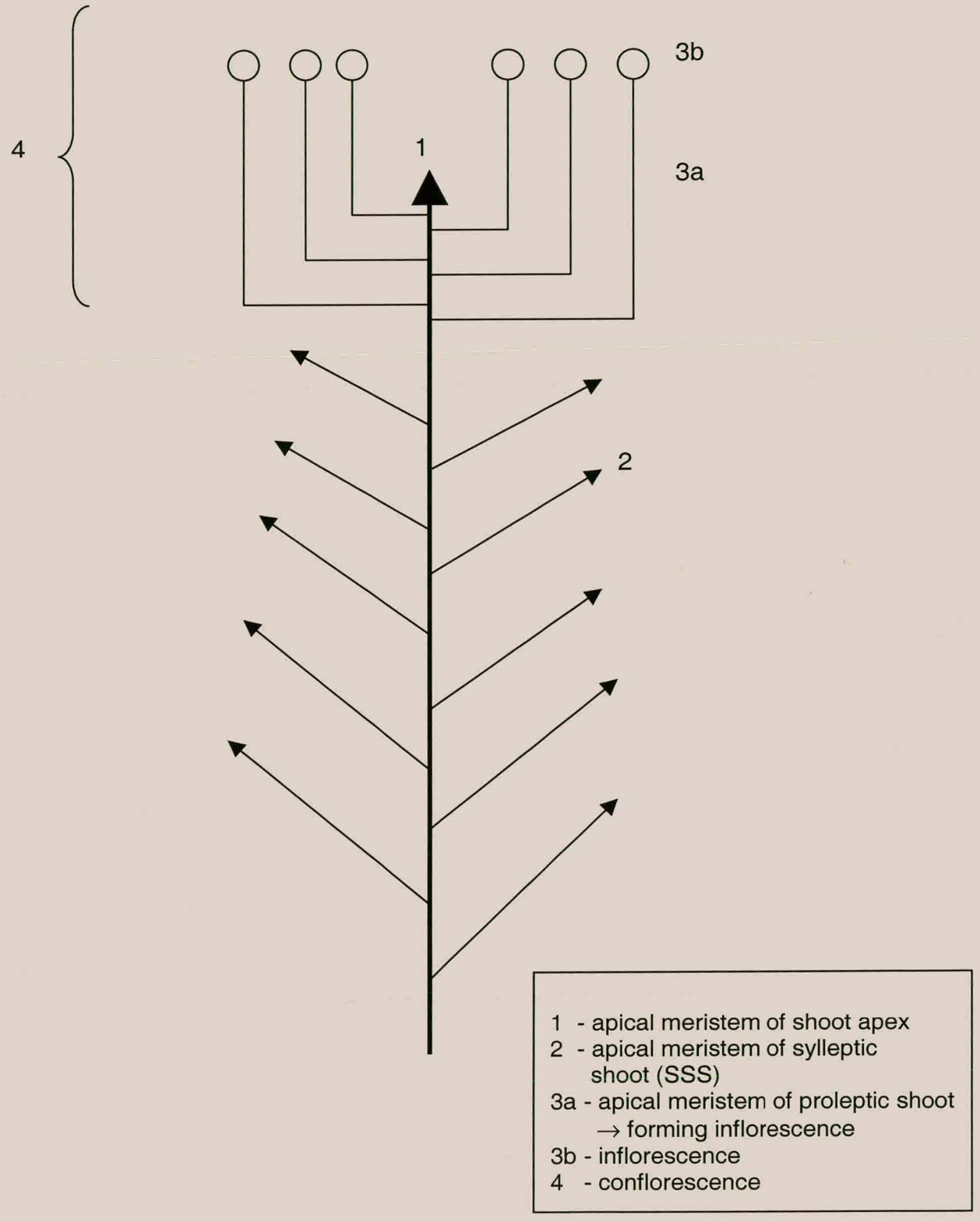


Figure 1.3. Schematic representation of reproductive shoot of *Brunia albiflora* and *Berzelia galpinii*

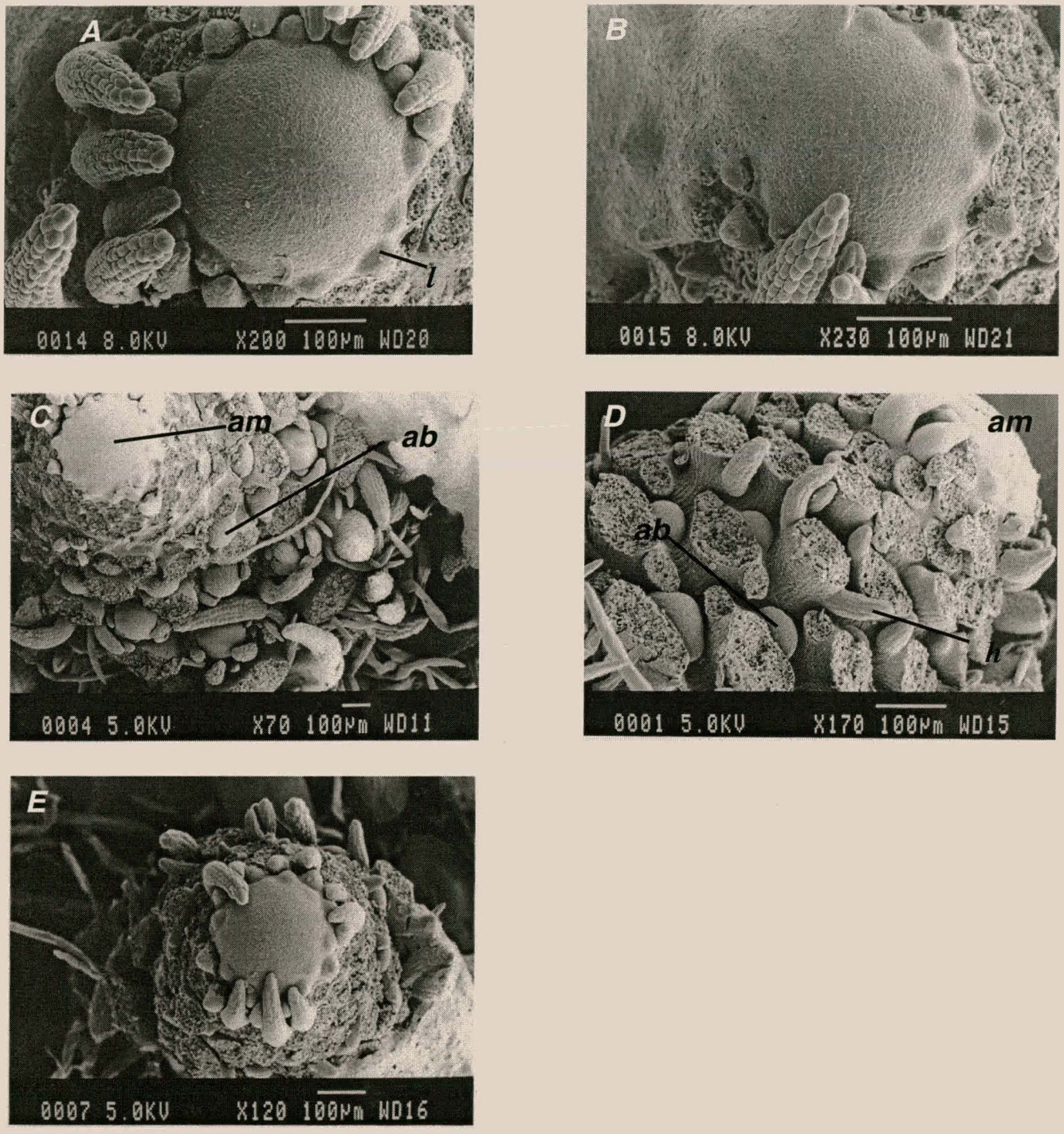


Figure 1.4. Scanning electron micro graphs of the apical meristems of the shoot and sylleptic shoot (SSS) of *Brunia albiflora* in the vegetative stage. (A) Apical meristem of the shoot apex 8/04/97, showing leaf primordia (l). (B) Apical meristem of the sylleptic shoot, 8/04/97, with leaf primordia. (C and D) Main shoot, 20/05/97, with apical meristem (am) and axillary buds (ab) in leaf axils with developing hairs (h). (E) Apical meristem of the sylleptic shoot, 4/06/97.

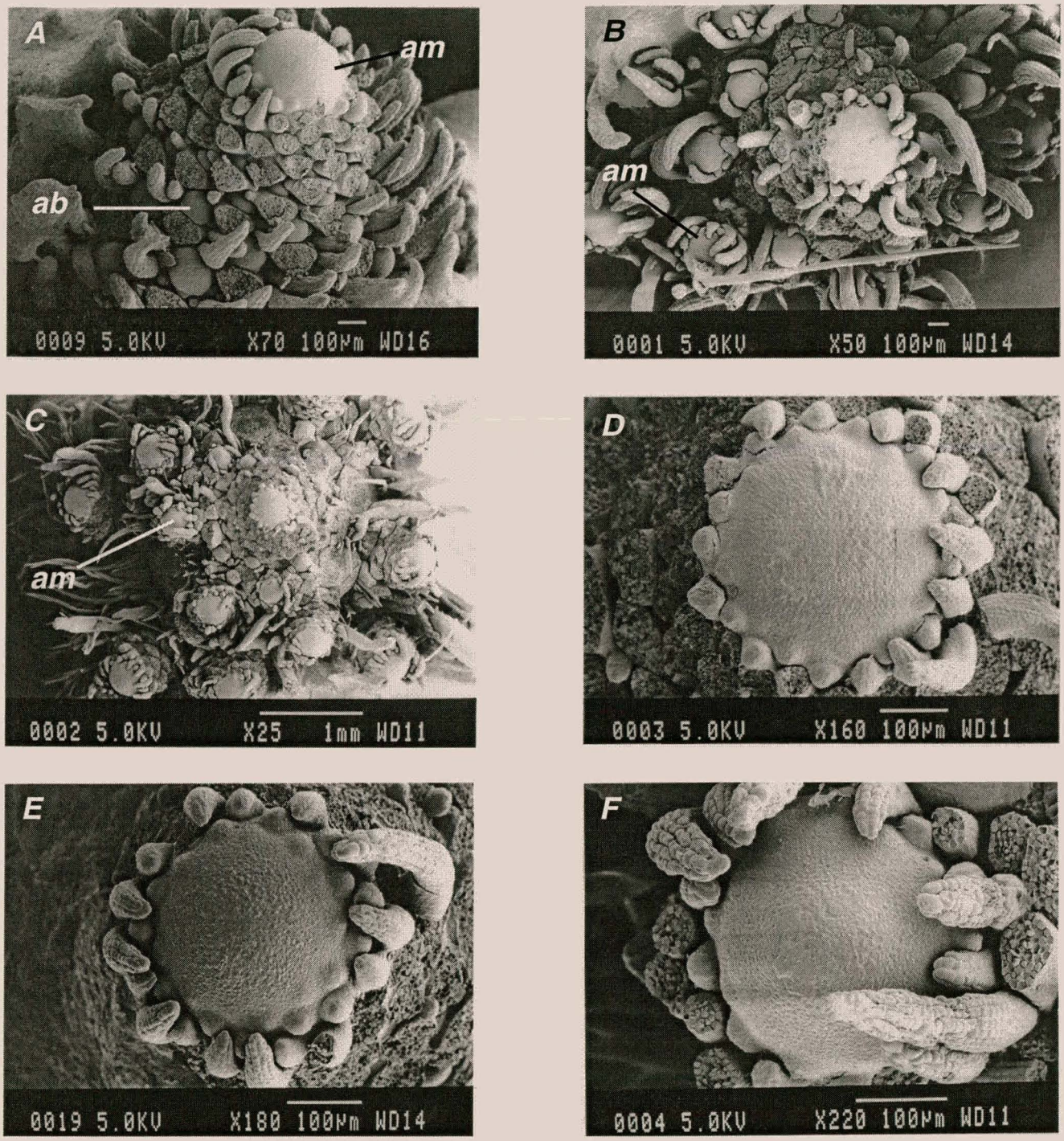


Figure 1.5. Scanning electron micro graphs of the apical meristem of the shoot and axillary shoot of *Brunia albiflora* in the vegetative stage. (A) Main shoot, 16/06/97 before loss of apical dominance with axillary buds (ab). (B) Main shoot, 30/06/97, showing the developing apical meristems of the axillary shoots (am) at stage V1. (C) Main shoot, 13/08/97, showing the terminal apical meristem and the apical meristem of the axillary shoots (am). (D) Terminal apical meristem of the main shoot, 13/08/97, with leaf primordia. (E) Apical meristem of sylleptic shoots, 13/08/97. (F) Apical meristem of the axillary shoots 13/08/97.

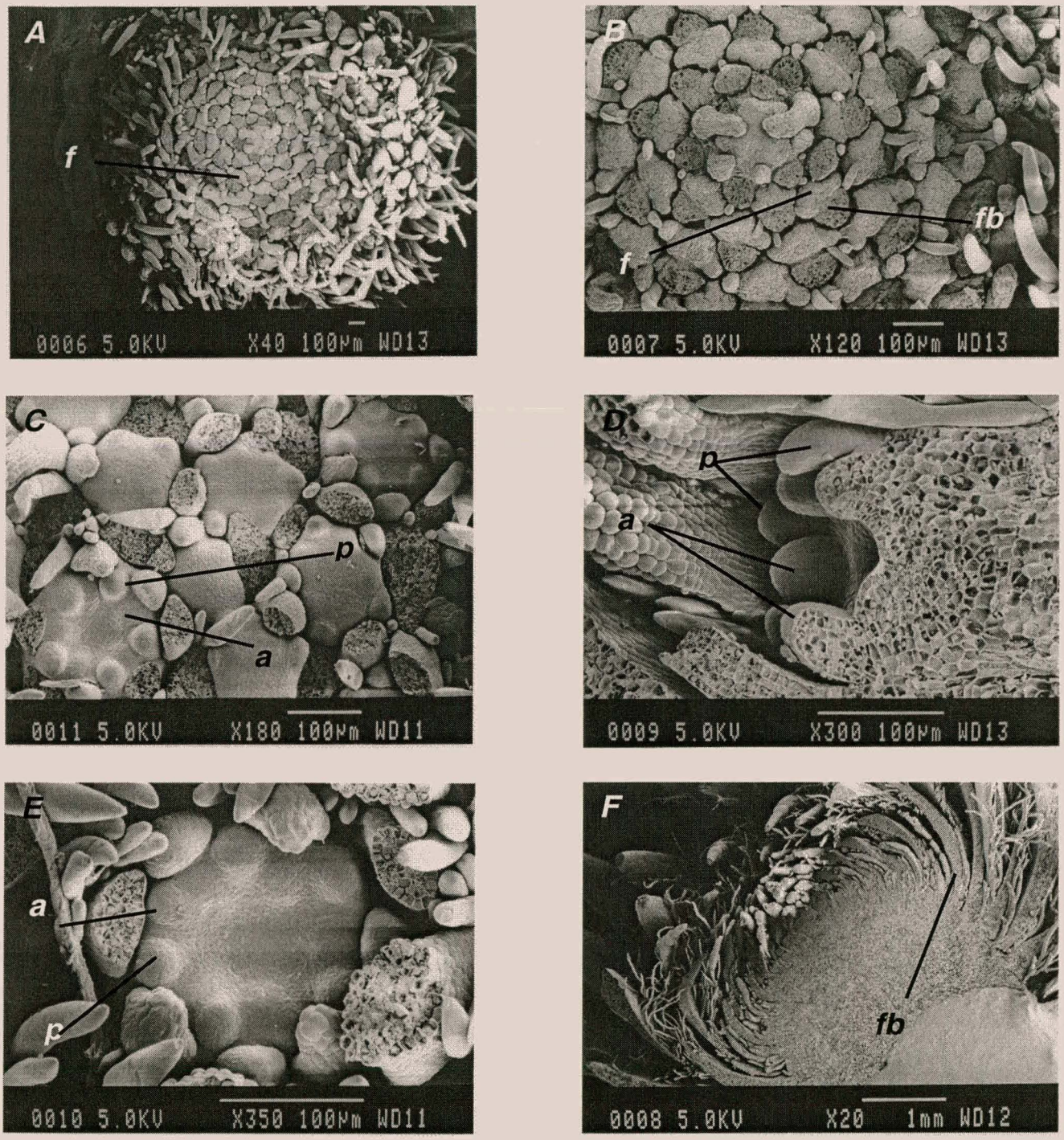


Figure 1.6. Scanning electron micro graphs of the reproductive stage of *Brunia albiflora* from R3 to A. (A) Floret primordia (f) in inflorescence borne terminally on side shoot 4/11/97. (B) Florets (f) in the axils of floral bracts (fb) removed to aid observation. (C) Initiation of perianth (p) initials in whorl of 5 and start of androecium initials (a), also in single whorl of 5, stage P, 2/12/97. (D) Cross section through developing floret, 2/12/97, with perianth (p) and androecium (a) initials visible. (E) Close up of single floret of C. (F) Cross section through inflorescence, showing position of florets in the axils of villous floral bracts (fb)

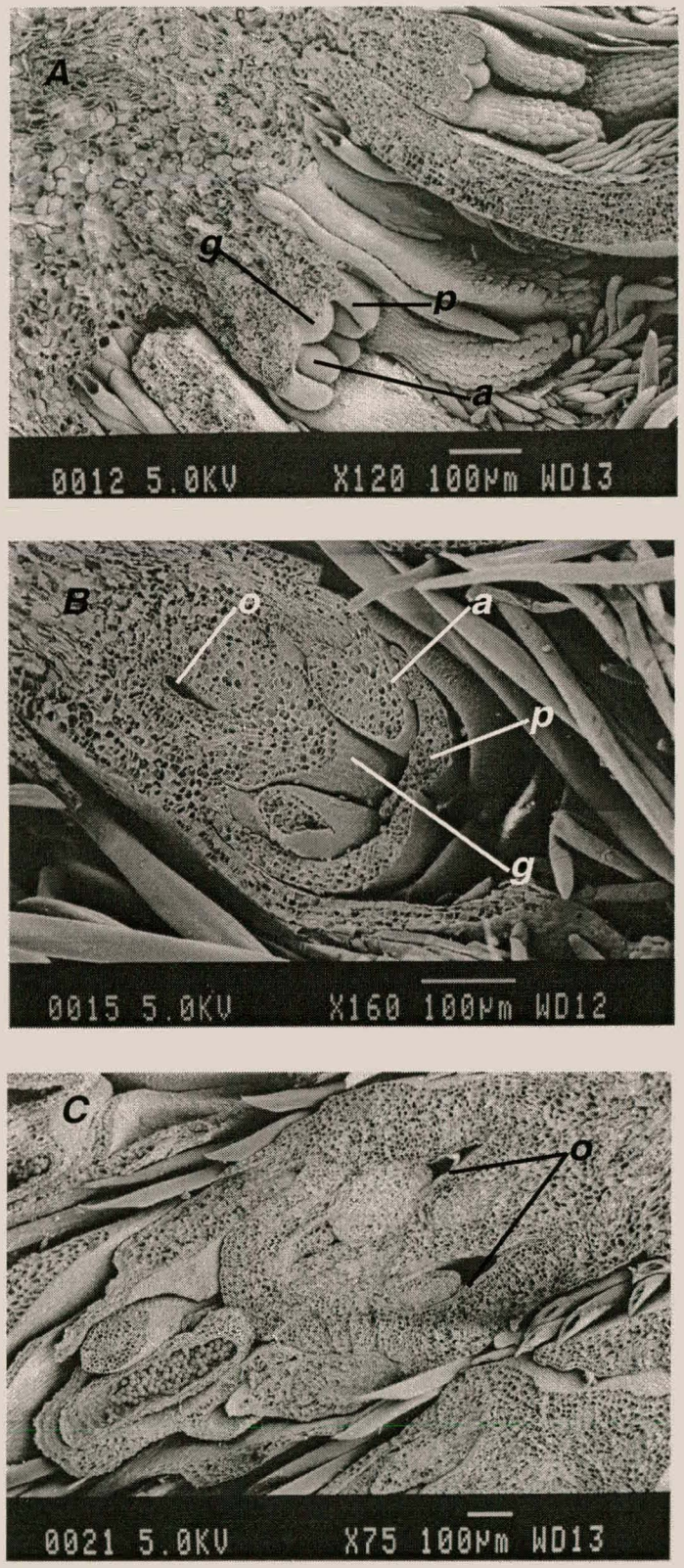


Figure 1.7. Scanning electron micro graphs of the reproductive stage of *Brunia albiflora* from stage G-Go. (A) Floret at stage G, showing perianth (p), androecium (a) as well as gynoecium (g) initials, 16/12/97. (B) Single floret with ovary (o) developing, 30/12/97, with perianth (p), androecium (a) as well as gynoecium (g) initials visible. (C) Bilocular ovary (o) visible, 9/02/98.

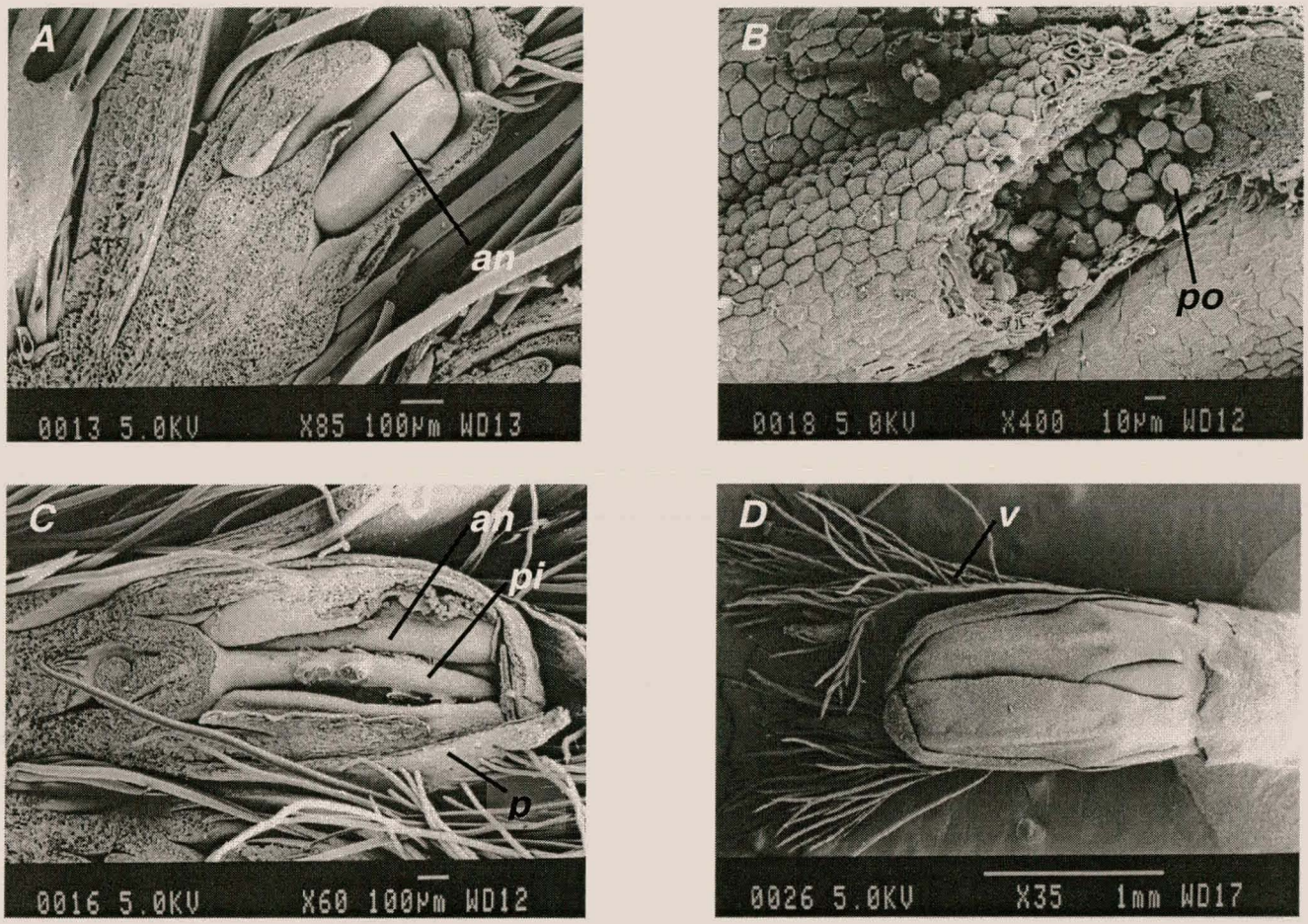


Figure 1.8. Scanning electron micro graphs of the reproductive stage of *Brunia albiflora*. (A) Floret with developing anther (an), 30/12/97. (B) Anther, with pollen (po), 12/01/98. (C) Pistil (pi) visible in single floret, 12/01/98. (D) Single floret prior to anthesis with villous bract (vb), 26/02/98.

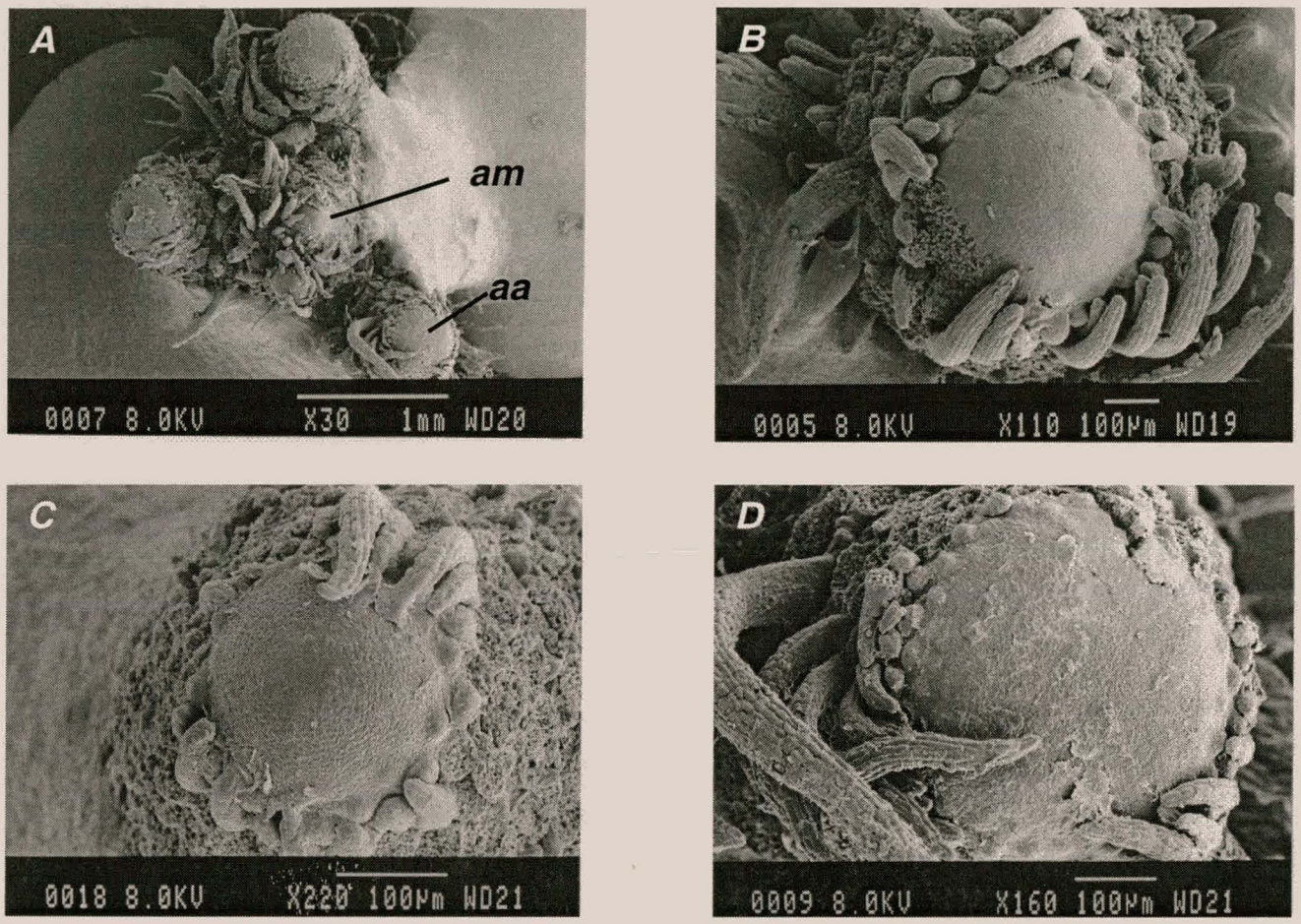


Figure 1.9. Scanning electron micro-graphs of the apical meristems of the main shoot, sylleptic side shoot (SSS) and axillary shoot of *Berzelia galpinii* in the vegetative stage. (A) Arrangement of terminal apical meristem (am) and apical meristems of axillary shoot (aa) 24/04/97. (B) Close up of terminal apical meristem 24/04/97. (C) Apical meristem of SSS 8/04/97. (D) Apical meristem of axillary shoot 24/03/97.

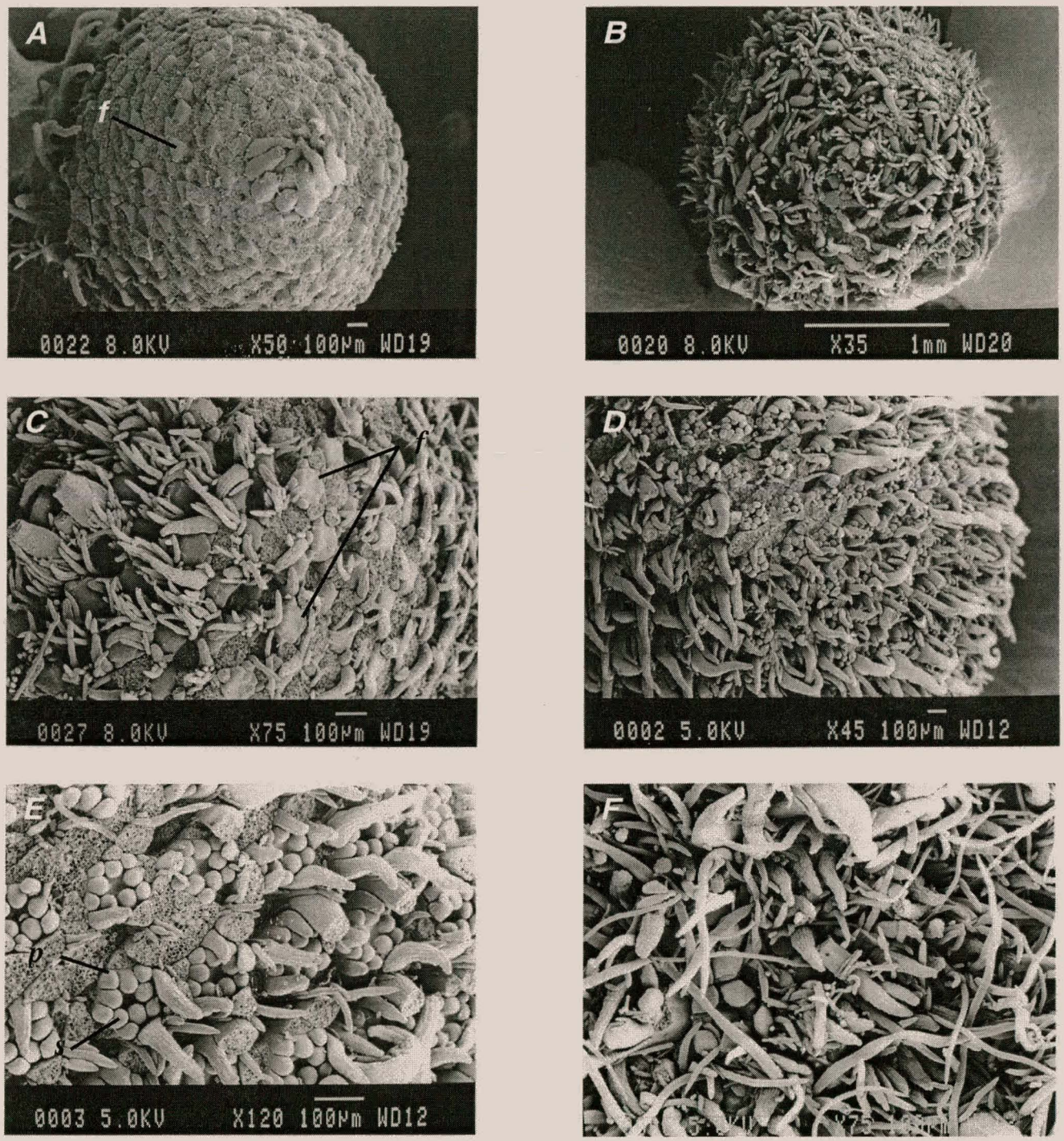
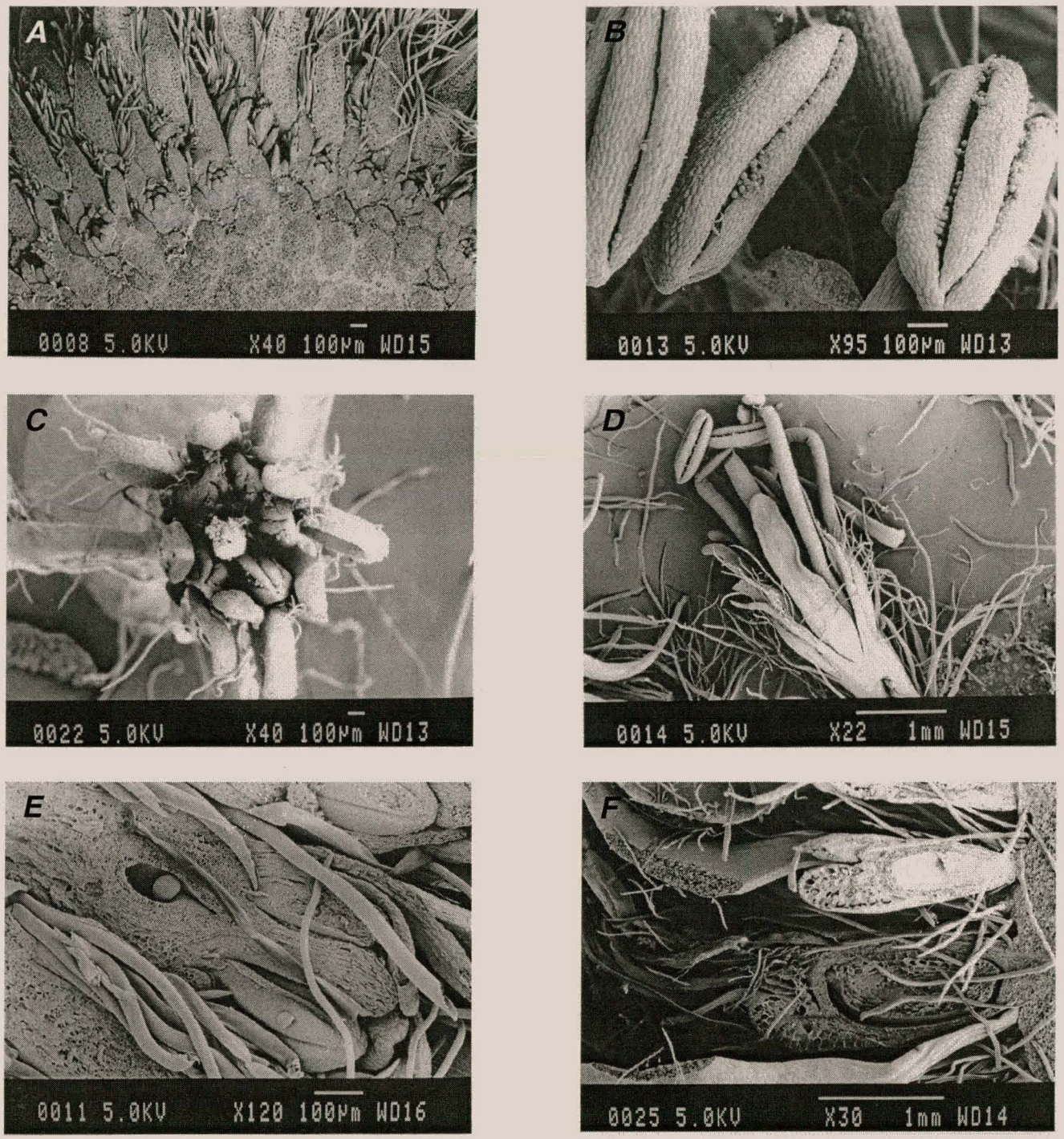


Figure 1.10. Scanning electron micro-graphs of reproductive stage of *Berzelia galpinii* from stage R3 to just prior to F. (A) Initiation of florets (f) in the axils of floral bracts which have been removed 24/04/97. (B) Further stage of development of florets 6/05//97. (C) Close up of florets (f) in axils of floral bracts 6/05/97. (D) Florets in stage S1 4/06/97. (E) Close up of (D) showing perianth initials (p) and androecium initials (s). (E) Hairy floral bracts obscure view of further floret development19/06/97.



Figures 1.11. Floret development of *Berzelia galpinii*. (A) Florets situated in axils of floral bracts 19/06/97. (B) Close up of anthers. (C) Floret showing deposition of pollen on pistil, before filaments exsert 3/08/97. (D) Filaments exserted at flowering 28/07/97. (E) Unilocular ovary, 28/07/97. (F) Developing seed, 18/11/97.

PAPER 2

Seasonal changes in carbohydrate allocation of *Brunia albiflora* (Pillans).

Abstract

Seasonal carbohydrate changes of *Brunia albiflora* (Pillans), which is a fynbos specie used in the South African cut flower industry, were investigated. Shoots which did not flower the previous season (flowering shoots) and shoots sprouting from lateral buds on side shoots left on the plant after the previous harvest (new shoots) were sampled over a one year period in the Elgin area, Western Cape. Starch content of new shoots increased continually while the starch concentration increased until December and then decreased. Sugar content of new shoots paralleled dry matter accumulation, with an increase towards the end of summer. The sugar concentration of new shoots decreased at this time. Side shoots of flowering shoots had a higher starch and sugar content than main shoots after winter. The starch content decreased in side shoots following flower initiation in October. The total sugar content of side shoots reached a maximum in October at flower initiation, after which it also decreased, corresponding with anthesis. It appeared that side shoots were net carbohydrate sources and exported assimilates to the developing inflorescence. The increase in carbohydrates of the inflorescence was higher than the loss in the side shoots and it seems that *B.albiflora* mainly relies on current photosynthates.

Introduction

Brunia albiflora (Pillans) in its natural habitat forms part of the fynbos biome. Generally, photosynthetic rates in the fynbos biome are regarded as low, representative of other sclerophyllous shrubs found in mediterranean type climates (Mooney & Dunn, 1970). The low nitrogen content of mediterranean species is thought to be responsible for this (Mooney, Field, Gulmon, Rundel & Kruger, 1983).

B. albiflora is a sclerophyllous shrub with woody stems. Sclerophylly is thought to be an adaptation to offer the smallest possible transpirational surface for maximal photosynthesis (Van der Merwe, 1992). Sclerophylly, along with the evergreen nature and longevity of leaves, could favour growth on nutrient poor soils by increasing the carbon return per unit of nutrient invested (Stock, Van der Heyden & Lewis, 1992). It has been suggested that sclerophyll leaf metabolism is due to a low nutrient availability, in particular phosphorus (Loveless, 1961). Furthermore, sclerophyllous leaves retain their photosynthetic capacity longer than that of deciduous species (Stock *et al.*, 1992).

Fertilisation of *Protea lepidocarpodendron* increased both stomatal conductance and photosynthetic rate, provided sufficient water was supplied (Stock *et al.*, 1992). Fertilisation is therefore expected to have an effect on the photosynthetic rate of *B. albiflora*.

It is well known that sink strength is altered once a plant becomes reproductive. The high sink strength of flowers and seeds deplete the pool of available carbohydrates, thus inhibiting vegetative growth (Kozlowski, 1992). High carbohydrate levels in woody plants has been related to their tendency to flower, although currently no definite evidence exists to indicate a direct role for carbohydrates in flower initiation. However, it is possible that high carbohydrate levels, in association with as yet undefined biochemical factors, are important in controlling flower initiation (Jackson & Sweet, 1972). Bodson & Bernier (1985) found that assimilate supply could determine the initiation and development of floral organs. This supply will depend on the sink strength of the floral organ, as it will have to compete with vegetative sinks (Kennedy, Fox & Loescher, 1988).

There is a need to understand plant carbohydrate dynamics to enable manipulation of cultural practices for an increased yield. This paper investigates seasonal changes in carbohydrate content of flowering and new vegetative shoots of *B.albiflora* over a one year period (April 1998-March 1999).

Material and Methods

Plant material

Plants grown from cuttings from a seedling block, planted in 1995 on a commercial farm in the Elgin area of the Western Cape, South Africa (34°08' S, 19°02' E) were used in this study. The area is characterised by a Mediterranean like climate of cold, wet winters and warm, dry summers. The *B.albiflora* planting consisted of two blocks 0.47 and 0.43 ha, with a plant density of 13 000 plants per hectare. Plants were drip-irrigated to supplement rainfall and fertigated from August to March according to commercial practices.

Shoot growth

Shoots were tagged in the orchard for monthly length measurements. Ten shoots, which did not flower the previous season (flowering shoots), were tagged on 4 March 1998. The mean shoot length of shoots at the start were 118.80 cm ± 2.53. A further ten new shoots sprouting from lateral buds on side shoots left on the plant after the previous harvest, were also tagged on 4 March 1998. The mean length of these shoots at the start were 19.4 cm ± 1.45. Shoot length was measured monthly until 18 March 1999.

Dry weight

Shoots which did not flower the previous season, and new shoots originating from lateral buds sprouting on side shoots left on the plant after harvesting the flowering shoots, were collected at monthly intervals from April 1998 to March 1999. In order to reduce the variation in shoot length at each harvesting date, shoots corresponding to the length of the shoots in the shoot growth study were selected. At each date, five shoots which did not flower the previous season, as well as five new shoots, were cut off at the point of insertion and brought to the laboratory. Flowering shoots were separated in side shoots, main shoots and inflorescences when present. Samples were frozen at –80°C and lyophyllised under vacuum for 4 days. The dry weight was determined before samples were ground to pass through a 0.25 mm mesh.

Carbohydrate analysis

Samples of 0.40 g were weighed into centrifuge tubes, 1% acetic acid added, tubes then stoppered and shaken overnight (approximately 14 hours). Samples were centrifuged at 3000-4000 rpm for 10 minutes and the supernatant decanted into 100 cm^3 volumetric flasks and made up to the mark with 1% acetic acid. This mixture was filtered through Whatman no.2 filter paper and frozen,

awaiting sugar analysis. The residue of the acetic acid extract was washed into 100 cm^3 volumetric flasks with acetate buffer (200 mg/10 cm^3) and placed in a boiling water bath for two hours. After cooling to below 60°C, 100 µl amyloglucosidase enzyme was added, flasks stoppered and placed in an incubator at 55°C for 18 hours. The solution was filtered into 100 cm^3 volumetric flasks, stored in sample bottles and frozen until starch analysis was carried out. Samples were analysed for sugars and starch separately using a Sanplus segmented flow analysis system from Skalar.

Statistical analysis

The data were analysed by an analysis of variance, using the Statistical Analysis System (SAS) (SAS Institute Inc., 1990). Graphs plotted used an average of two dates to minimise variation.

Results

Growth of new and flowering shoots

After harvest, new shoots originated from axils at the base of syllpetic side shoots low down on the bearer (Table 2.1; Fig. 2.1). Very little resprouting took place from the lower buds on the bearer, especially if these bearers had no leaves remaining (Table 2.2; Fig. 2.2). Resprouting was very irregular. More buds resprouted on longer bearers and sprouting was denser, whereas shorter bearers had bud break occurring over a longer section of the bearer (Fig. 2.2). This resprouting was also delayed.

New shoots grew rapidly until winter, after which growth was slow, with the rate increasing again through spring and summer, reaching a length of 90cm after one years growth (Fig. 2.3). Flowering did not occur. Shoots which did not flower in the first year (flowering shoots) continued growth during late summer and winter until flower initiation occurred in October (Fig. 2.3). There was considerable variation in total side shoot length due to genetic variation in the plant population (data not presented).

Dry mass of new shoots only increased towards the end of summer and autumn (Fig. 2.4) whereas the dry mass of main shoots showed an increase throughout the year (Fig. 2.5). Dry mass of side shoots fluctuated over the period studied (Fig. 2.5). Development of the inflorescence showed a linear increase until anthesis in February/March (Fig. 2.5).

Starch content of new and flowering shoots

Starch content of new shoots seemed to increase continuously, with a steep increase through summer (Fig. 2.6). Starch concentration reached a peak towards the end of December after which it decreased (Fig. 2.7).

Total starch content of side shoots increased at the end of winter (August) and reached a maximum in December after flower initiation whereafter a sharp decrease was observed (Fig. 2.8). Starch content of main shoots showed a more gradual increase and appeared to maintain a relatively constant level from September, decreasing from middle December (Fig. 2.8). Starch content of main shoots was lower than that of side shoots. Starch content of the inflorescence was low and showed a slight increase from October to December after which it remained constant.

Starch concentration was highest in side shoots (Fig. 2.9). It reached a peak during September to January, after which starch concentration decreased. Starch concentration of main shoots had a slight increase at the end of winter (August), remained constant during September to December and decreased at the same time as the concentration in side shoots.

Sugar content of new and flowering shoots

Total sugar content in new shoots was higher than that of starch. It remained relatively constant from June to December (winter and spring) and increased from December (end of summer) (Fig. 2.10). Sugar concentration showed the opposite, decreasing from December until sampling ceased in March (Fig. 2.11).

Total sugar content of side shoots in April was higher than that of main shoots (Fig. 2.12). Total sugar content of side shoots was significantly higher than that of starch ($P>0.05$). A maximum total sugar content for side shoots occurred in October at the time of flower initiation. Total sugar content of side shoots decreased sharply towards anthesis. Total sugar content of main shoots increased until September, after which the levels appeared to remain constant. The developing inflorescence showed a steep increase of total sugars from October through to March (Fig. 2.12).

Sugar concentration of flowering shoots indicated that side shoots had a higher concentration than main shoots (Fig. 2.13). Total sugar concentration of side shoots peaked in October after which it decreased whereas that of the main shoots reached a maximum in September and did not show as steep a decline in concentration (Fig. 2.13).

Discussion

Growth of new and flowering shoots

Shoot growth of *B. albiflora* is continuous, in contrast with proteas, also a fynbos genus which grows in flushes (Malan & le Roux, 1995). During shoot growth of *B. albiflora* sylleptic side shoots develop at irregular intervals. Shoots that develop after harvest reach a length of approximately 40 cm in October (Fig. 2.3), when flower initiation usually occurs, but new shoots failed to initiate flowers. Shoot elongation continued during spring, summer and autumn and in October of the following year, when shoots were approximately 120 cm long, flower initiation occurred. From harvest in March to the next harvest therefore requires two years.

Dry mass accumulation of young developing shoots (main shoots and side shoots) did not increase during the period May to December (Fig. 2.4) and did not reflect the increase in length of the main shoot during this period. This is possibly due to the great variation in number and length (data not shown) of the side shoots. Only by March 1999 did dry mass of the shoot complex increase in relation to the increase in length of the shoot complex. Dry mass of main stems of one year old shoots continued to increase after shoot growth stopped due to flower initiation in October (Fig. 2.5). In contrast, dry matter of side shoots varied during this period.

In Protea, dry mass accumulation of shoots and inflorescences is dependent on current photosynthesis (Greenfield, Theron & Jacobs, 1994) and although dry mass changes in roots were not measured, it is possible that this is also the case with *B. albiflora*. Dry mass of the main shoot increased in particular during the period that inflorescences developed. It appears that the cambium activity is stimulated by inflorescence development.

Starch content of new and flowering shoots

Starch content of new shoots reached the same content in March as flowering shoots sampled in April (Fig. 2.6). Although the total starch content increased until anthesis, the starch concentration increased only until December and then decreased. This could be due to the increased growth of new shoots at this time, causing a dilution effect (Fig. 2.7).

Higher total starch content of side shoots after winter could reflect a higher photosynthetic activity of side shoots. Main shoots had noticeably fewer leaves than that of side shoots (personal observation). The sharp decrease in total starch content in side shoots following flower initiation is

supported by evidence that the flower is a strong sink for carbohydrates (Halevy, 1987; Kozlowski, 1992; Dai & Paull, 1995). It is possible that starch from side shoots was mobilised for flower development as well as for other regions, as the starch content of the inflorescence was low and showed only a slight increase from October to December. The low starch content of the main stems of *B.albiflora* (Fig. 2.8) corresponds with literature on evergreen plants, which do not store much of their carbohydrate reserves in older shoots.

Starch concentration in side shoots (Fig. 2.9) compared well to starch concentrations in older leaves of citrus (0.8-2.5%) (Sanz, Monerri, Gonzalez-Ferrer & Guardiola, 1987). Starch concentrations of *Leucospermum* cv. Red Sunset leaves were slightly higher (1-4%) compared to that of side shoots of *B. albiflora* (Napier, 1985). Starch concentrations in all three parts of *B. albiflora* sampled were higher than that found in either the bark or wood of *Protea* cv. Carnival (Greenfield *et al.*, 1994).

Sugar content of new and flowering shoots

Total sugar content of new shoots paralleled the pattern of dry mass accumulation of new shoots, increasing towards the end of summer when anthesis took place (Fig. 2.10). It could be argued that more sugars were available for new growth or that new shoots had sufficient leaf area to start producing their own carbohydrates. Total sugar concentration of new shoots gradually decreased (Fig. 2.11). The decrease in sugar concentration towards the end of summer could be indicative of the slower growth rate toward winter.

A maximum total sugar content of side shoots occurred in October at flower initiation. The sharp decrease in total sugar content of side shoots towards anthesis may have been due to the use thereof by the developing inflorescence, which showed a steep linear increase from October through March (Fig. 2.12). It appears that side shoots become net carbon sources and then export new assimilates to other parts of the plant. Total sugars in main shoots remained constant during this time, with a slight decrease during anthesis. The sugars of main shoots are not as big a source for the developing inflorescence as the side shoots were.

Citrus leaves showed concentrations of soluble sugars to be lower than starch concentrations in older leaves, but higher in young leaves (Sanz *et al.*, 1987). Sugar concentration in flowering shoots of *B. albiflora* was higher than that recorded by Sanz *et al.* (1987) in older leaves of citrus, but corresponded with the concentrations found in young citrus leaves. Napier (1985) found

Leucospermum leaves to have a sugar concentration of 7% and one-year-old shootsto have 4%. In *Protea*. cv. Carnival, sugar concentrations varied from 2-4% in bark and 0.5-1.2% in wood (Greenfield *et al.*, 1994). These concentrations were in the same range as those found in *B. albiflora*.

The decrease in sugar concentration in main and side shoots corresponded with the increase in sugar content of the inflorescence, with side shoot concentration decreasing first. Sugar concentrations were higher than starch and can be seen as the most important carbohydrate required by the plant, especially during inflorescence development (Fig. 2.13).

Conclusion

Both starch and sugar content in general reflected the dry mass changes of the young developing shoot complex. Deviation was caused by changes in starch and sugar concentrations. Concentration of both starch and sugar declined during the period of maximum dry mass accumulation of the shoot complex. In one-year-old shoots, both starch and sugar content reflected the increase in dry mass of the main stem. Sugar content deviated from the general trend during the period November to March when the sugar content leveled off due to a decrease in concentration of sugars. Starch and sugars did not mirror the changes in dry mass of side shoots, as dry mass of side shoots fluctuated during the period May to March, with no apparent increase in dry mass.

Starch content of side shoots increased from 100-700 mg in May to January due to an increase in concentration from 5 to 20 $mg.g^{-1}$. A similar trend was observed for sugar. The decrease in both starch and sugar content and concentration coincided with an increase in starch and sugar of the inflorescence. It appears, therefore, that mobilisation of carbohydrates from reserves in the side shoots occurred to the inflorescence. However, this contributed a small fraction of the increase in dry mass of the inflorescence (starch content dropped by 5 g and sugars by 5 g). It is, therefore, concluded that dry mass accumulation of the inflorescence is primarily dependent on current photosynthesis and not on carbohydrates stored in the shoots of *B. albiflora*. This is also the case with Proteas where inflorescence dry mass is dependent on current photosynthates. Deciduous fruit store large quantities of carbohydrates in stems, ready for use in spring. This is not the case with *B. albiflora*.

The inability to initiate flowers in October following pruning, is possibly related to an inadequate carbohydrate supply in new shoots in terms of reserves and leaf area to produce current photosynthates. Many plants require relatively high levels of carbohydrates to initiate flowers. The total starch and sugar content of new shoots in October differ significantly from that of flowering shoots, with new shoots containing only 50 mg of starch and 100 mg sugars as compared to 400 mg and 800 mg for starch and sugar respectively in flowering shoots. A similarity with *Protea* cv. Carnival is apparent in that flower initiation occurred more readily on long shoots than on short shoots.

Further research is needed into many aspects of commercial *B. albiflora* production. Before such research can be successfully carried out there is a need to develop clonal material to eliminate some of the variation. The reaction of resprouting after different harvesting times could give insight into the length of time needed for vegetative growth enabling flowering to take place. Carbohydrate studies, which could quantify the carbohydrate content of the side shoots from which resprouting takes place, could give a definite answer to the hypothesis that higher carbohydrate concentrations enable resprouting.

Literature cited

Bodson, M. & Bernier, G. 1985. Is flowering controlled by the assimilate level? *Physiol. Veg.* **23**: 491-501.

Dai, J. & Paull, R.E. 1995. Source-sink relationship and Protea postharvest leaf blackening. *J. Amer. Soc. Hort. Sci.* **120(3)**: 475-480.

Greenfield, E.J. Theron, K.I. & Jacobs, G. 1994. Effect of pruning on growth and flowering response of *Protea* cv. Carnival. *J. S. Afr. Soc. Hort. Sci.* **4(1)**: 42-46.

Halevy, A.H. 1987. Assimilate allocation and flower development. **In**: Atterton J.G. (ed.), Manipulation of flowering. pp. 363-378. Butterworths, London.

Jackson, D.I. & Sweet, G.B. 1972. Flower initiation in temperate woody plants. *Hort. Abstr.* **42**: 9-24.

Kennedy, R.A., Fox, T.C. & Loescher, W.H. 1988. Factors affecting photosynthesis, productivity and yield. *HortScience* **23 (1)**: 33-39.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. *Bot. Rev.* **58:** 109-185.

Loveless, A.R. 1961. A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. *Annals of Botany* **25**: 168-184.

Malan, D.G. & Le Roux, R.D. 1995. Preliminary investigation into the effect of time of pruning on shoot growth and flowering time of Protea. *Acta Hort.* **387**: 91-97.

Mooney, H.A. & Dunn, E.L. 1970. Photosynthetic systems of Mediterranean-climate shrubs and trees of Caliifornia and Chile. *American Naturalist* **104**: 447-453.

Mooney, H.A., Field, C., Gulmon, S.L., Rundel P. & Kruger, F. J. 1983. Photosynthetic characteristics of South African sclerophylls. *Oecologia* **58**: 398-401.

Napier, D.R. 1985. Seasonal and shade induce carbohydrate changes in *Leucospermum* cv. Red Sunset. *MSc Thesis.* Univ. of Stellenbosch. pp 61-69.

Sanz, A., Monerri, C., Gonzalez-Ferrer, J. & Guardiola, J.L. 1987. Changes in carbohydrates and mineral elements in Citrus leaves during flowering and fruit set. *Physiol. Plantarum* **69**: 93-98.

SAS INSTITUTE Inc. 1990. SAS User's guide. Version 6. Fourth edition. Cary, NC.

Stock, W.D., van der Heyden, F. & Lewis, O.A.M. 1992. Plant structure and function. **In**: Cowling, R. (ed.), The ecology of fynbos, nutrients, fire and diversity. pp. 226-239. Oxford University Press.

Van der Merwe, A.M. 1992. A study to determine anatomical and morphological adaptations in the leaves of selected fynbos species. *MSc-thesis.* University of Stellenbosch.

Table 2.1. Sprouting from lateral buds of *Brunia albiflora* on side shoots cut back to different lengths after the previous harvest.

Treatment	Average length in which sprouting occurs (cm)	Number of shoots	Length of shoots (cm)
1 short side shoot	1.5	3	8.5
2 medium side shoot	3.5	4	8.5
3 long side shoot	18	21	3.5

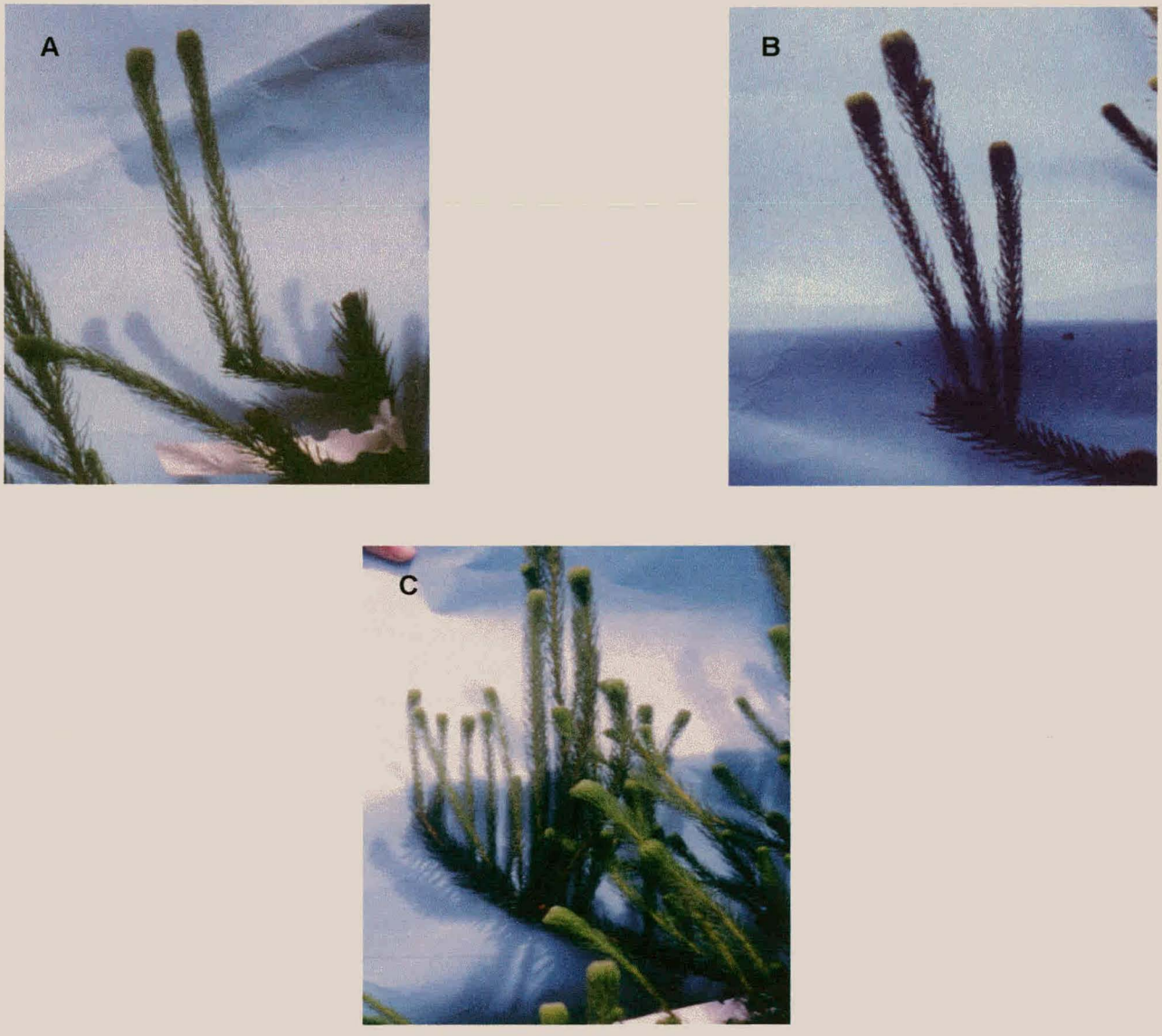


Figure 2.1 Response of lateral buds of *Brunia albiflora* to the cutting back of side shoots left after the previous harvest. A. Treatment 1, short side shoot. B. Treatment 2, medium side shoot. C. Treatment 3, long side shoot.

Table 2.2. Sprouting of buds of *Brunia albiflora*, after six months, from bearers cut back in May 1999.

Treatment	Average length in which sprouting occurs (cm)	Number of shoots	Length of shoots (cm)
1 short bearer	0-10	0-10	starting-5
2 medium bearer	21-71	0-39	starting-15
3 long bearer	2-6	11-16	2-15

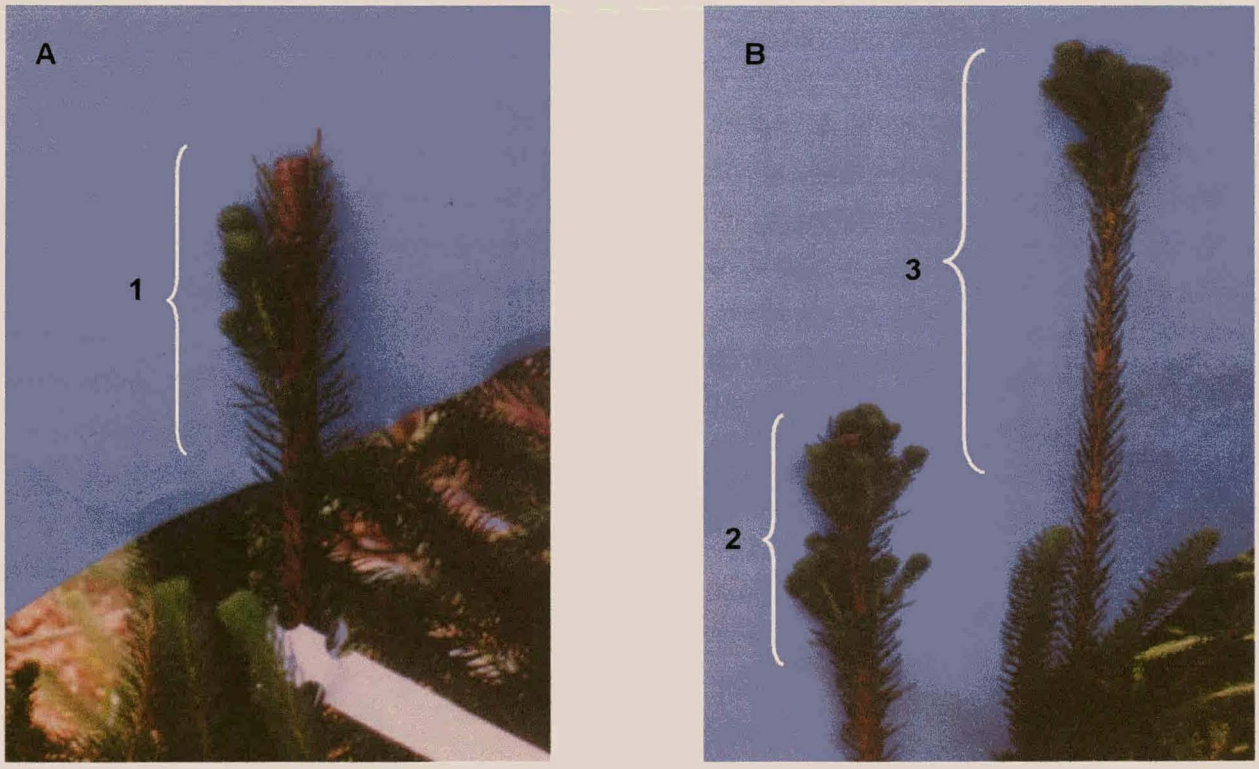


Figure 2.2. Response of pruning *Brunia albiflora* in May 1999, after six months. A. Treatment 1, short bearer. B. Treatment 2, medium bearer and Treatment 3, long bearer.

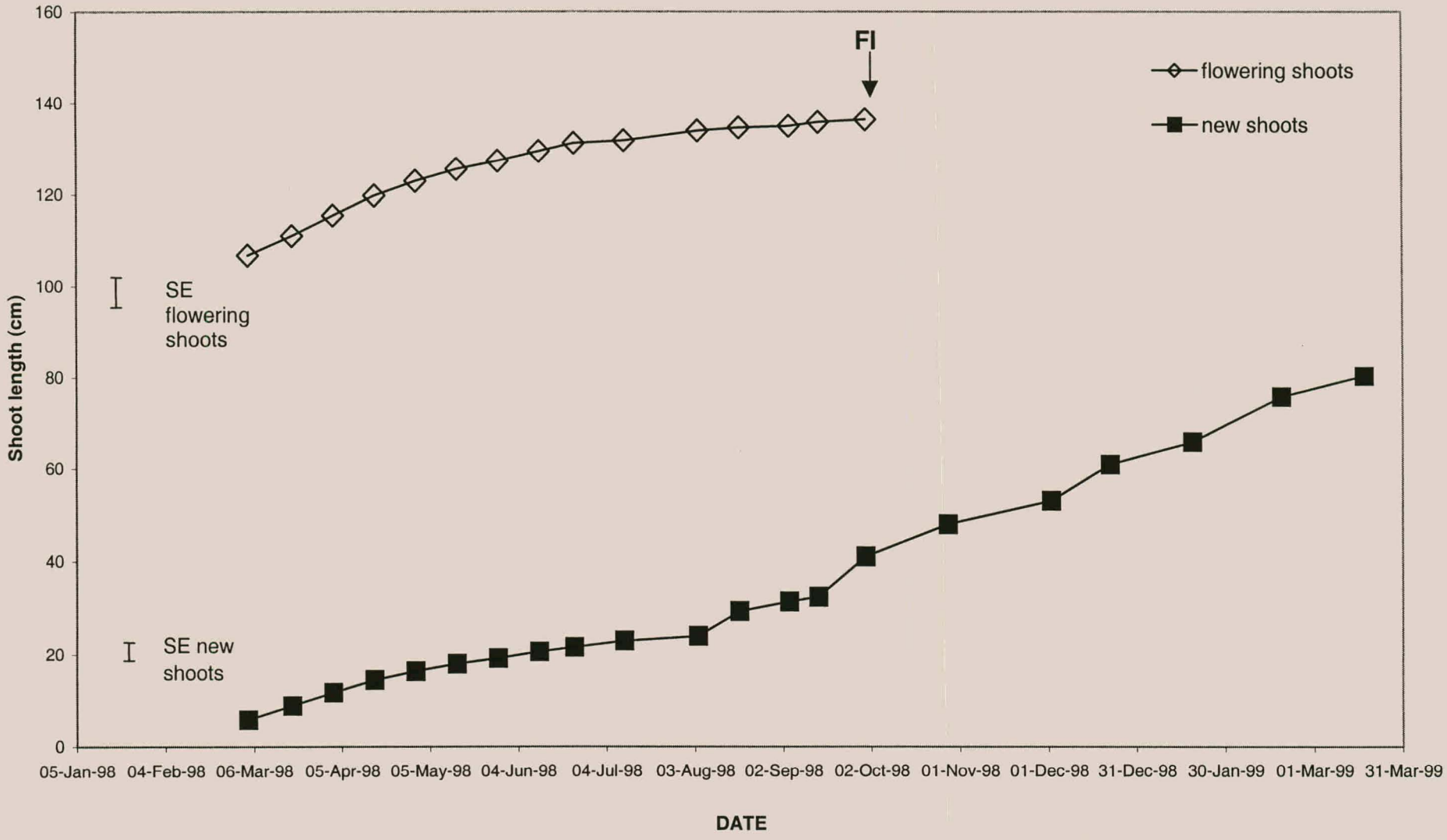


Figure 2.3. Average length of ten tagged shoots which did not flower the previous year (flowering shoots) and shoots that resprouted after harvest (new shoots) of *Brunia albiflora* over time.

FI - flower initiation

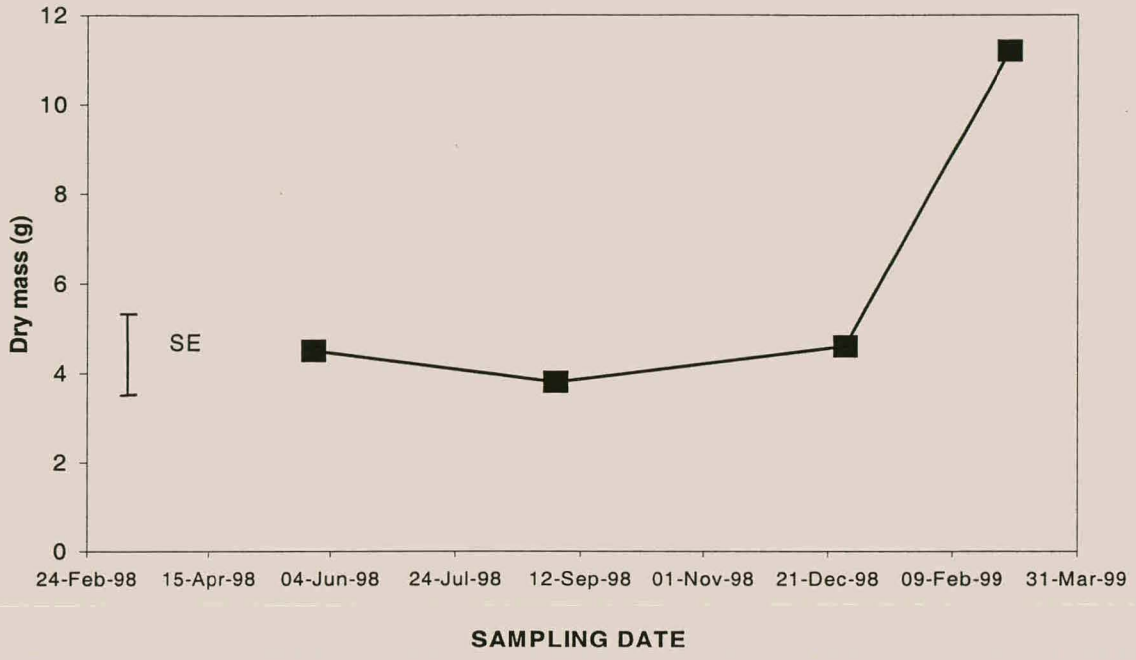


Figure 2.4. Changes in dry mass (g) of new shoots from regrowth following harvest of *Brunia albiflora* with sampling date.

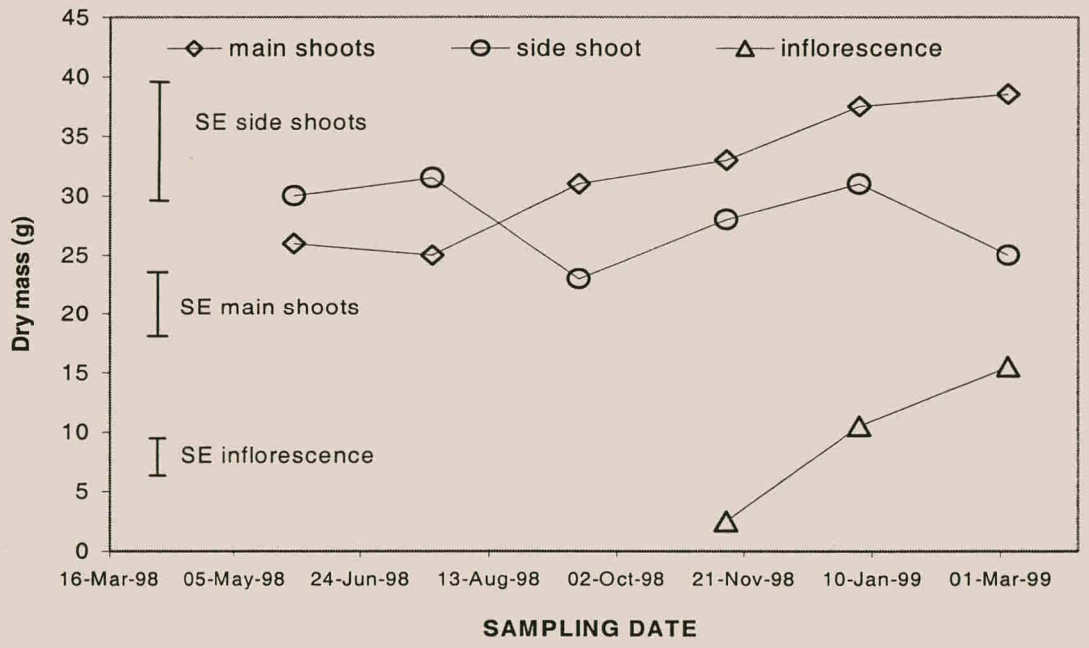


Figure 2.5. Changes in dry mass (g) of main shoots, sylleptic side shoots and inflorescences of flowering shoots of *Brunia albiflora* with sampling date.

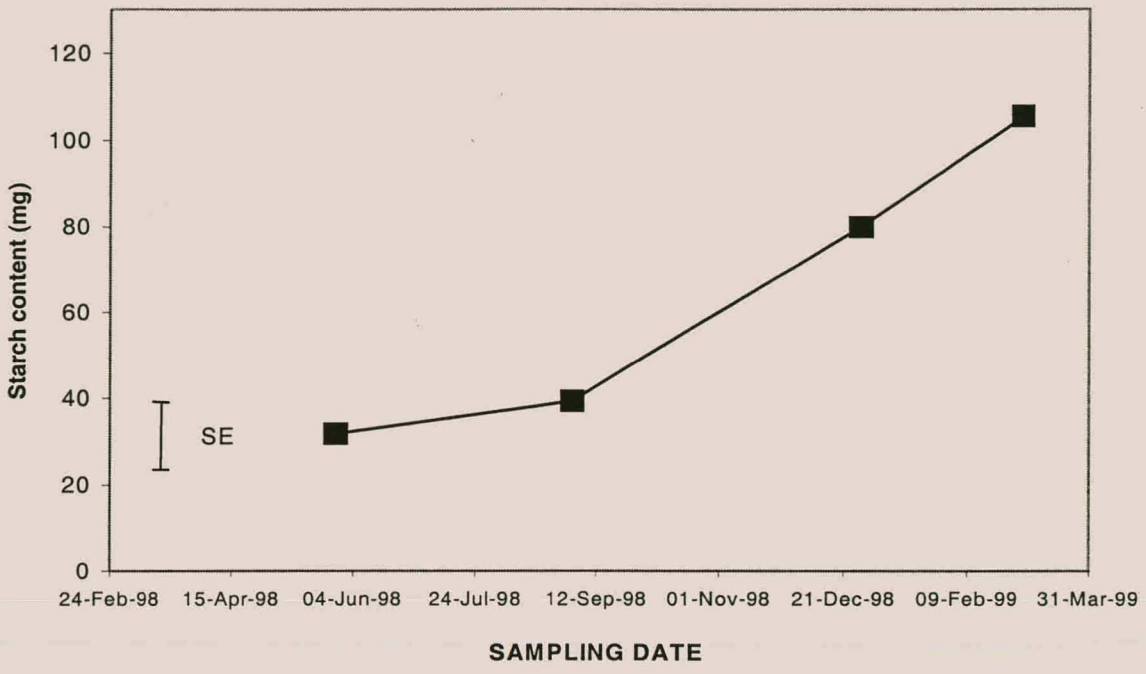


Figure 2.6. Starch content (mg) of new shoots from regrowth following harvest of *Brunia albiflora* with sampling date

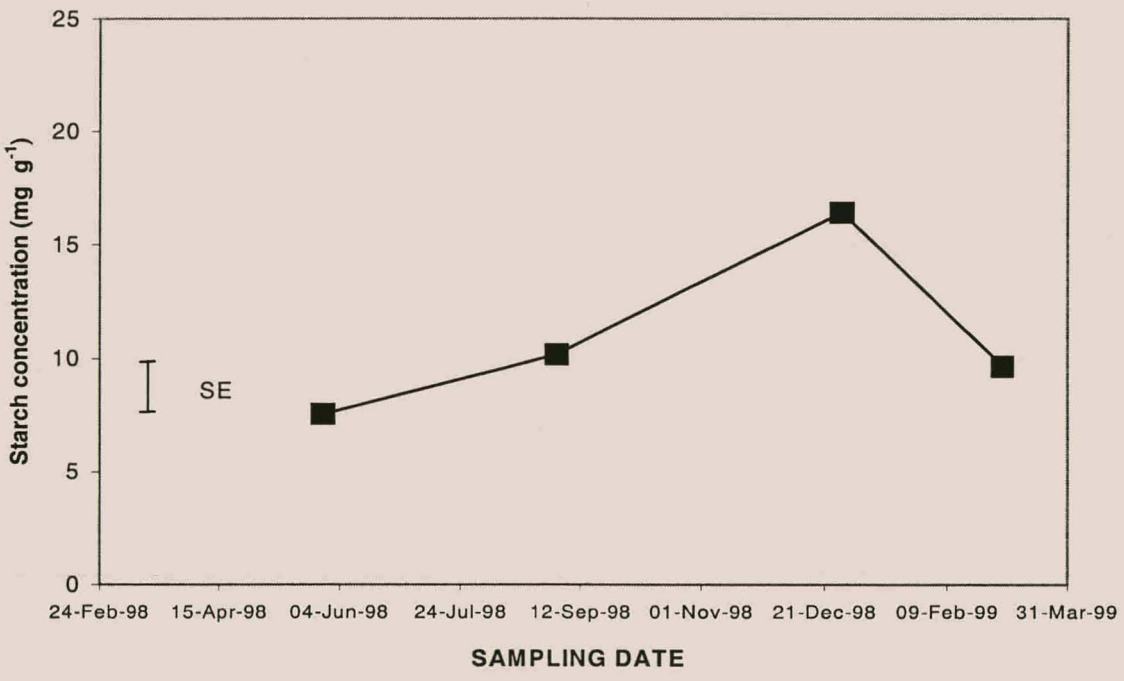


Figure 2.7. Starch concentration (mg g^{-1}) of new shoots from resprouting after harvest of *Brunia albiflora* with sampling date.

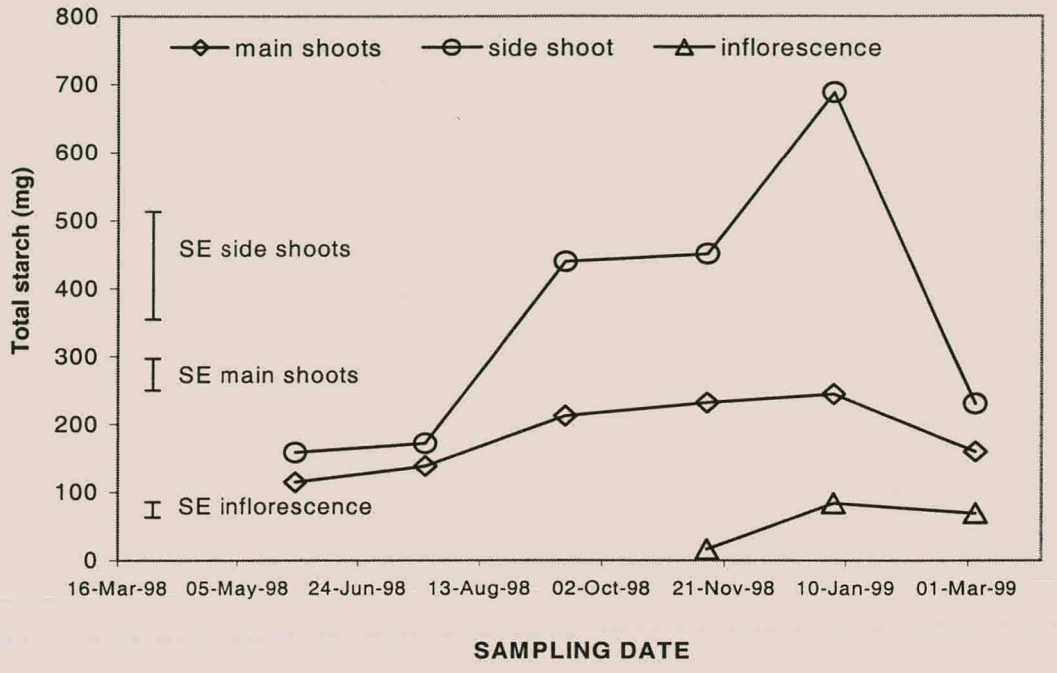


Figure 2.8. Changes in starch content (mg) of main shoots, sylleptic side shoots and inflorescence of flowering shoots of *Brunia albiflora* with sampling date.

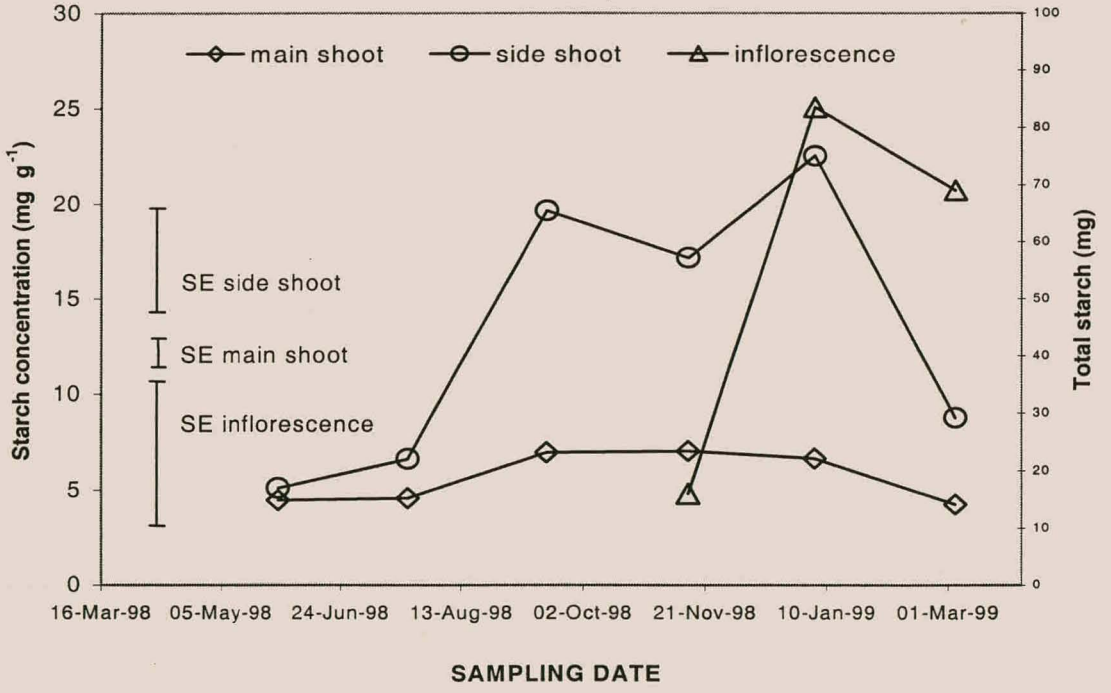


Figure 2.9. Changes in starch concentration (mg g^{-1}) of main shoots, sylleptic side shoots and starch content of inflorescences (secondary axis) of flowering shoots of *Brunia albiflora* with sampling date.

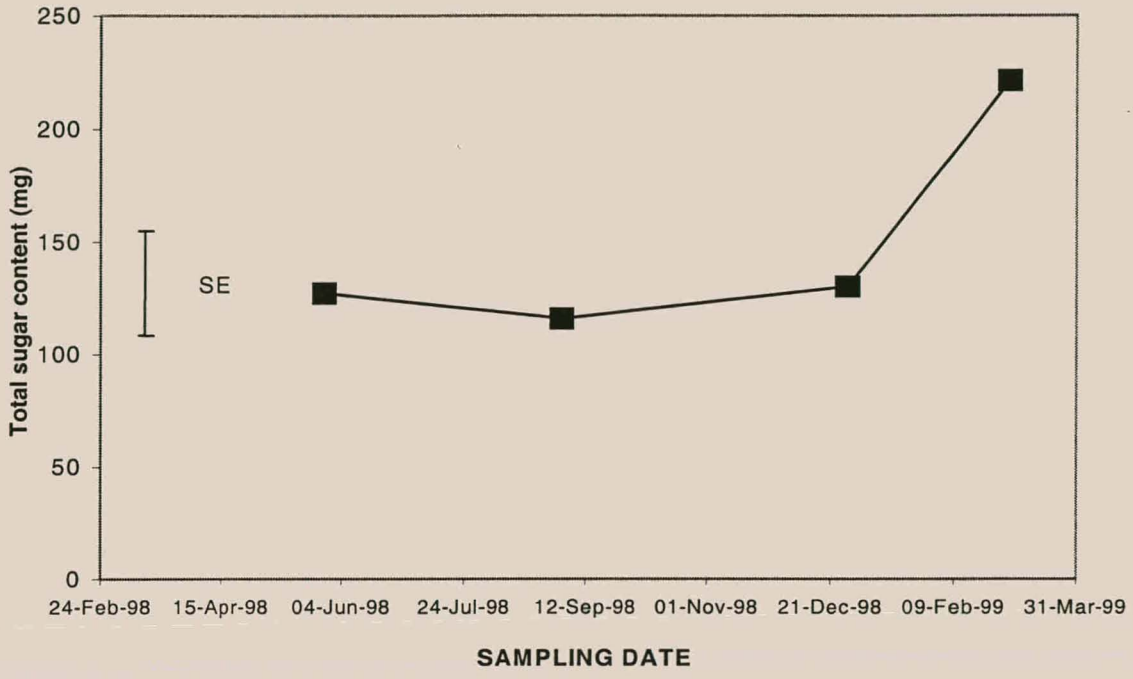


Figure 2.10. Changes in total sugar content (mg) of new shoots from regrowth after harvest of *Brunia albiflora* with sampling date.

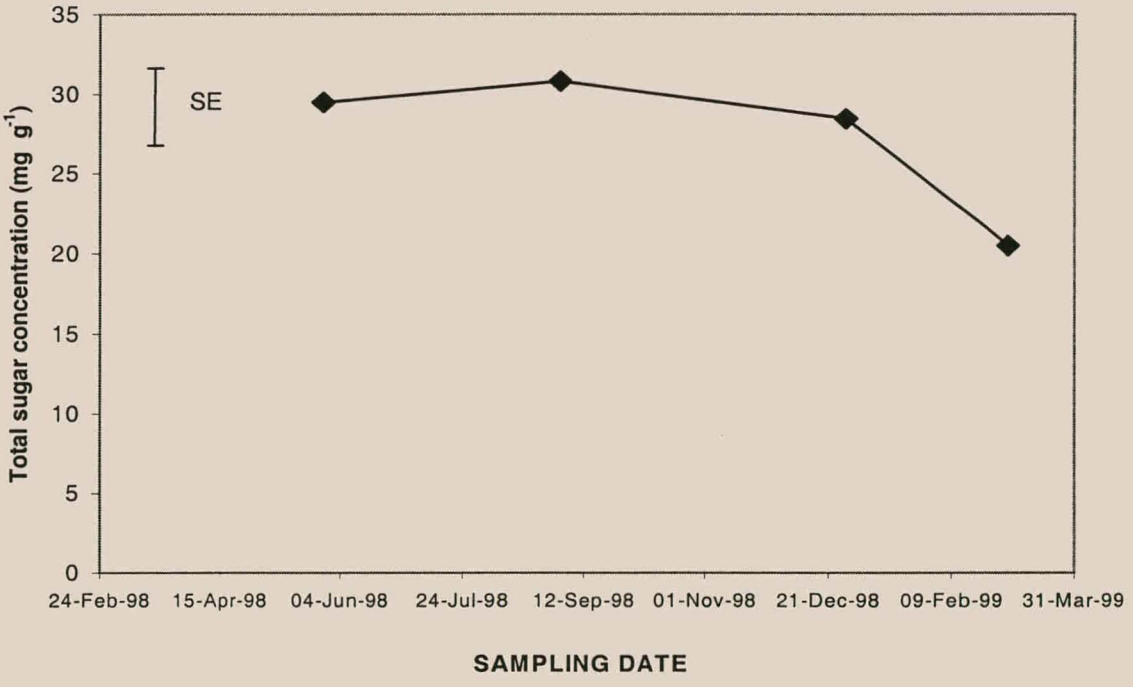


Figure 2.11. Changes in total sugar concentration (mg g^{-1}) of new shoots from resprouting after harvest of *Brunia albiflora* with sampling date.

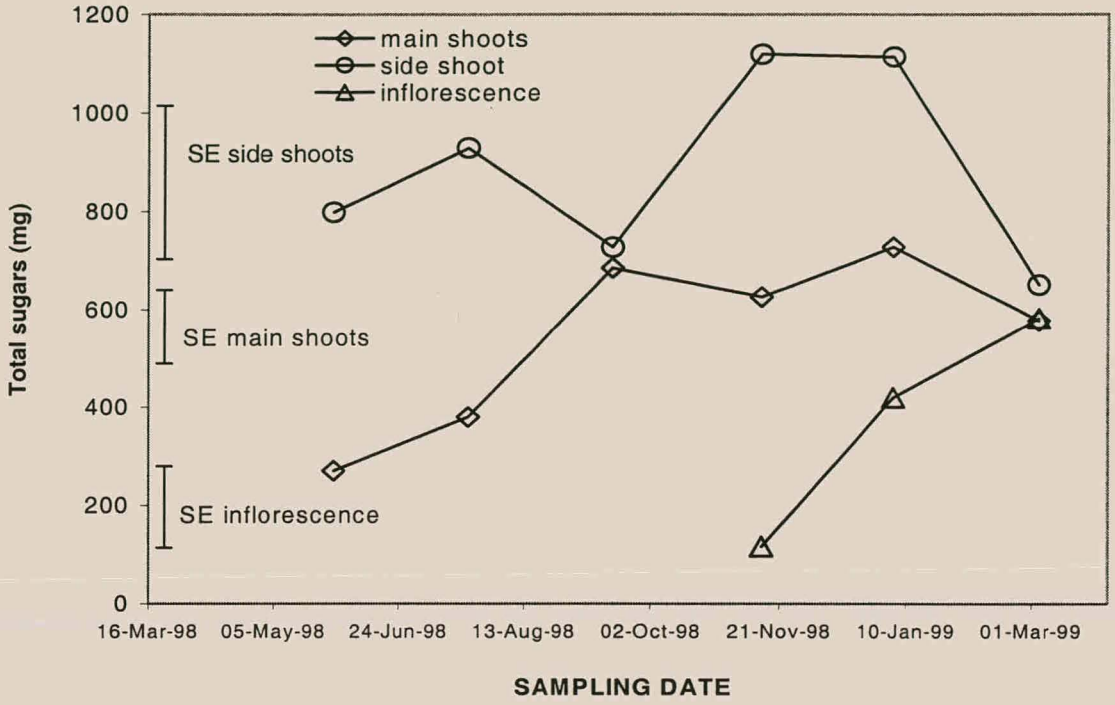


Figure 2.12. Changes in total sugar content (mg) in main shoots, sylleptic side shoots and inflorescences of flowering shoots of *Brunia albiflora* with sampling date.

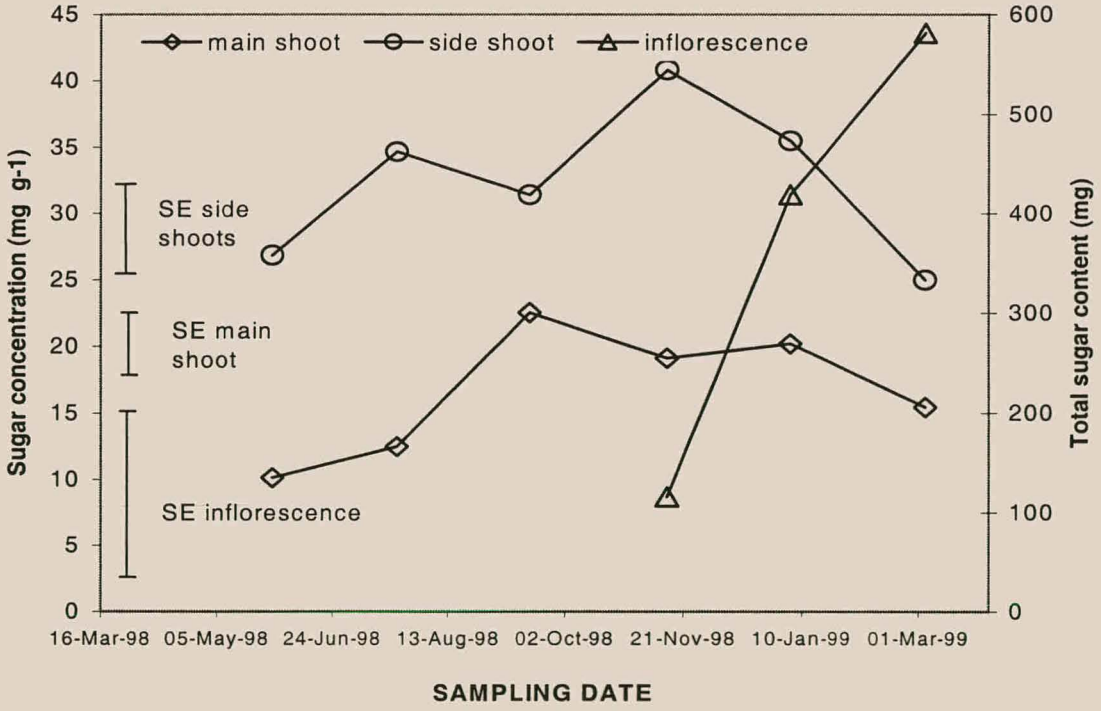


Figure 2.13. Changes in total sugar concentration (mg g^{-1}) of main shoots and sylleptic side shoots of flowering shoots of *Brunia albiflora* with sampling date. Total sugar content of inflorescence on secondary axis.

PART TWO

SOIL SCIENCE

LITERATURE REVIEW II

The edaphic and nutritional requirements of Western Cape Fynbos

Introduction

Soils of the fynbos biome vary considerably as the parent material from which the soils are derived varies over the biome as does topography. The landscape of the fynbos biome is dominated by mountains of the Cape Fold Belt, which consist of hard quartzitic rocks belonging to the Table Mountain and Witteberg Group. These rocks give rise to medium sands and loamy sands which commonly have gravelly subsoils of weathered sandstone, shales or granites (Campbell, 1983). Soils derived from Table Mountain quartzite are very acidic (pH (KCl) ≈ 3.2-4.5), have low exchangeable cations, N and available P although soils vary considerably. The pH (KCl) of soils derived from granites and shales is higher, 4.0-4.6 and 5.8, respectively. Soil nutrients and soil moisture have been implicated in determining the distribution of fynbos (Stock & Allsopp, 1992). Fynbos vegetation is found at sites with a precipitation of greater than 700 $mm.yr^{-1}$ (Stock & Allsopp, 1992).

Fynbos vegetation has developed special adaptations to the nutrient poor soils. This has resulted in little research on nutritional aspects of the plants. Most research has been carried out on the Proteaceae family, which is the family most cultivated for the export market and justifies the extra nutritional inputs. Unfortunately the research that has been done is very fragmented and little nutritional data has been published for other species of fynbos cut flowers. The nutritional requirements of South African Proteaceae are unfortunately not well defined.

There is a lack of data on fynbos environments and this has led to a number of myths which are discussed by Campell (1983). Another problem is that most of the research has been undertaken in the south-western area of the Western Cape Province and the generalisations made do not hold for other areas in the biome.

Plant adaptations

Plants of the fynbos biome have adapted to the low nutrient environment and compete more effectively than plants with a higher nutrient requirement on these soils. Lewis & Stock (1978)

found that N metabolism of fynbos was low in comparison with plants adapted to more favourable soil N nutritional conditions. The low N metabolism also corresponded with the slow growth habit of these plants and is probably an adaptation to the poor nutrient status of the soil. The sclerophyllous nature of the leaves is thought to be another adaptation, because it allows an increased carbon return per unit of nutrient invested (Orions & Solbrig, 1977). Many species also withdraw N and P from leaves prior to senescence (Jongens-Roberts & Mitchell, 1986). Fire is an important factor in this biome for returning mineral elements to the soil. Litter decomposition is low because of the unfavourable climatic conditions and poor litter quality (Brown & Mitchell, 1986, Stock & Lewis, 1986).

Plants of the fynbos biome have developed specialised root systems to allow maximal nutrient uptake. Proteaceae produce clusters of 'proteoid rootlets', densely covered with root hairs that effectively increase the absorptive surface (Read, Field, Gulmon, Jongens-Roberts, Lewis, Mitchell & Oechel, 1983). These rootlets form mainly in the organic topsoil and could facilitate the utilisation of sources of organic P (Read *et al.*, 1983) and fulfil an important function in the P uptake at the low pH values found in fynbos soils (Vorster & Jooste, 1986). Factors causing their formation are still unknown, however, age of plants, soil type and season are all factors controlling their formation (Lamont, 1983). Rootlet formation was suppressed at high P supply (Dinkelaker, Hengeler & Marschner, 1995). A few studies have been carried out on the variation of soil P in the fynbos biome. It was found that lowest available P was found in soils of mountain fynbos because of steep slopes and high rainfall and that Swartland soils had a similar P status to those of granite derived soils (Witkowski & Mitchell, 1987). It was also found that P was depleted in the middle layers while the surface was enriched by litterfall (Mitchell, Brown & Jongens-Roberts, 1984). The low P status of the soils of the fynbos biome were similar to those of Australian heathlands (Groves, 1983).

Mycorrhizal associations (ecto and endo infections) have been found in the Ericaceae family. This association increases the uptake of NH_4-N and P and allows the use of simple organic N compounds (Stribley & Read, 1980). Nitrogen fixation in symbiotic associations also occurs, mainly with Aspalathus. Nitrogen fixation rate is highest in the early stages of plant colonisation (Dunn, Debano & Eberlein, 1979). The fynbos biome also has a number of resprouters which have an extensive secondary root system allowing rapid sprouting after fires (Kummerow, Krause & Jow, 1978).

Nutritional studies

The general belief is that plants belonging to the Proteaceae family are unresponsive to fertilisation and are sensitive to high P concentrations. Nutritional concentrations in tissue of certain Proteaceae species grown in Australia have been published (Price, Cresswell & Handreck, 1997). Nutrient concentrations are given for different growth stages and plant parts, sampled with the aim of providing a starting point from which researchers can further investigate the nutritional status of species and refine data. South Africa is lacking in such data, despite the serious need for this by the growing industry, which is highly dependent on the production of high quality products.

Appropriate fertiliser applications to commercial plantings are becoming more important as production areas increase and competition demands better quality products. Although fynbos have adapted to low nutrient environments for survival, this does not mean they are unable to tolerate higher levels which could increase production and quality. Witkowski (1989) found that with increased fertiliser application to *Leucospermum parile* and *Phylica cephalantha* the mortality pattern did not change and that the vegetation seemed resilient to nutrient additions. Claassens (1986) found high nutrient concentration in culture medium had no negative influence on plant growth.

Most research has centred around fertilising with N and P due to the assumption that high levels of P are toxic (Parvin, 1986) and due to the seemingly low P requirement of Proteas (Prasad & Dennis, 1986). Phosphorus was thought to limit vegetative growth in edaphically similar Mediterranean and other heathlands of Australia (Specht, 1981). It has been hypothesised (Clarkson, 1967), that the adaptations of fynbos plants to nutrient poor soils have resulted in slower growth rates which do not reflect current nutrient availability of soils. When nutrient availability is increased, it is thought that plants store nutrients (luxury consumption) which can be used during periods of reduced availability (Stock, Sommerville & Lewis, 1987). It seems that fynbos is better adapted to P rather than N conservation by enhanced luxury consumption of P and greater withdrawal prior to senescence and leaf abscission (Specht, 1981). It was demonstrated for *Leucadendron salignum* that excess K and P are taken up when soil nutrient concentrations of these elements increase and that they are then stored for later growth when supply becomes limiting (Heinsohn & Pammenter, 1986).

Phosphorus has been reported as a factor in death rates of Western Australian Banksias (Ellyard & McIntyre, 1978) and decreased yield of *Leucospermum* roots in sand culture (Claassens, 1986). Nichols & Beardsell (1981) reported symptoms of P toxicity in some native Australian Proteaceae but high concentrations of soluble P were used (300 mg l^{-1}). It was shown that high Ca concentration aggravated the necrotic leaf symptom of high P, while high N and K alleviated them (Nichols & Beardsell, 1979). *Leucadendron* cv. Safari Sunset in New Zealand (Prasad & Dennis, 1986) and Israel (Silber, Ganmore-Neumann & Ben-Jaacov, 1998) showed no toxicity resulting from high P uptake, but impeded growth did occur because of low levels. Heihnsohn & Pammenter (1986) found that P supply of *Leucadendron salignum* did not affect P uptake except at the highest levels where there was an increase in P concentration. The presence of other nutrients did not affect the uptake of P. In experiments with *Protea repens,* Lamb & Klaussner (1988) found the opposite effect with an increased growth response to P. It would appear that certain species are more tolerant to high P concentrations. Phosphorus additions to sand-plain lowland fynbos decreased growth, however these were short duration studies (Witkowski, 1989; Witkowski & Mitchell, 1989; Witkowski, Mitchell & Stock, 1990). More long term studies need to be carried out due to the long residence time of P in soils. It would appear that certain species are more tolerant to P and that the general view of all Proteaceae being sensitive to P is unfounded.

The responses observed were small and it seems unlikely that low concentration single event nutrient additions are likely to cause major changes in productivity (Stock & Allsopp, 1992). The contradicting results could be due to specific intolerances of different species or wrong assumptions due to lack of knowledge. Claassens (1986) found considerable differences in response of nutrient elements in sand culture, particularly N-supply, between Protea species and even within the same specie collected from different sites.

Contrasting views exist for nitrogen. The N demand of fynbos species have been said to be low (Stock & Lewis, 1986) and yet Claassens (1986) reported that nitrogen is a nutrient of particular importance in Protea cultivation. Claassens (1986) found more favourable growth associated with increasing N supply, particularly NH_4. *Protea neriifolia* and *Leucospermum cordifolium* could both use NH_4 –N even at levels which may be harmful to other plants. *Leucospermum patersonii* and *Protea repens* could use NO_3 to some extent but NH_4 was preferable in most cases. The preference for NH_4-uptake and assimilation could be due to the passive absorption of NH_4, which occurs at greater rates than for NO_3. No chemical transformation is required and therefore less energy is needed for plant assimilation. *Protea* cv. Ivy (*P. longiflora x P. lacticolor*) failed to grow

with only NO_3. Heinsohn & Pammenter (1986) observed in *Leucadendron salignum* that N concentrations increased with increasing supply of NH_4 and high NO_3 levels depressed N and K absorption. They suggested that high levels of NH_4-N combined with moderate levels of P and K, were optimum for growth as varying P and K levels did not influence N absorption. Witkowski *et al.* (1990) found that applications of inorganic N, whether NH_4 or NO_3, was rapidly utilisd but that N remained significantly higher in the soil for one year. Immobilisation of N and P by micro-organisms can occur in nutrient poor soils and nutrients are released slowly because of the high carbon to mineral nutrient ratios.

Walters, Jooste & Raitt (1991) looked at the effect of Na:K ratio on *Leucadendron salignum*. It was observed that sodium could substitute for a portion of the potassium in *L. salignum* and that the species was not very sodium sensitive. Claassens (1986) found that the inclusion of Na in the nutrient medium improved growth of certain species, particularly at excessively high NH_4 -levels. This could be due to Na lowering the relatively high and harmful rate of NH_4 uptake. *Leucadendron* cv. Safari Sunset showed no increased K in plant tissue in response to increased concentration of K in the nutrient solution. The K content was low compared to that of other plants and compared to Na concentrations, but there were no visible signs of damage (Silber *et al.*, 1998).

Conclusion

Caution should be taken in the interpretation of results of fertiliser applications to natural fynbos stands, as soil interactions could play a significant role in reducing or exacerbating the effects of nutrient additions. Different growth mediums have been used in the nutrient studies which provide a more controlled environment.

Work has been carried out to try and understand the nutritional requirements of fynbos. However, species seem to vary in their response to nutrient additions. This highlights the need for systematic studies on nutrient requirements, possibly grouping species according to their natural climate or growth on specific soil types.

Literacture cited

Brown, G. & Mitchell, D.T. 1986. Influence of fire on the soil phosphorus status in Sand Plain Lowland Fynbos, south western Cape. *S.Afr.J.Bot.* **52**: 67-72.

Campell, B.M. 1983. Montane plant environments in the fynbos biome. *Bothalia* **14(2)**: 283-298.

Claassens, A.S. 1986. Some aspects of the nutrition of Proteas. *Acta Hort.* **185**: 171-179.

Clarkson, D.T. 1967. Phosphorus supply and growth rate in species of Agrostis L. *J. Ecol.* **55**: 111-118.

Dinkelaker, B. Hengeler, C. & Marschner, H. 1995. Distribution and function of Proteoid roots and other root clusters. *Bot. Acta* **108**: 183-200.

Dunn, P.H., Debano, L.F. & Eberlein, G.E. 1979. Effects of burning on chaparral soils. II. Soil microbes and nitrogen mineralization. *Proc. Soil Sci. Soc. Am.* **43**: 509-514.

Ellyard, R.K. & McIntyre, D.K. 1978. Effect of superphosphate and high levels of lime on the growth of Western Australian Banksia. *IPPS Comb. Proc.* **28**: 450-453.

Groves, R.H. 1983. Nutrient cycling in Australian heath and South African fynbos. **In**: Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. (eds), Mediterranean-type Ecosystems. The Role of Nutrients. **43**: 179-191. Ecological Studies Springer, Berlin.

Heinsohn, R.D & Pammenter, N.W. 1986. A preliminary study of interactions between nitrogen, potassium and phosphorus in the mineral nutrition of seedlings of *Leucadendron salignum Berg.* (Proteaceae). *Acta Hort.* **185**: 137-143.

Jongens-Roberts, S.M. & Mitchell, D.T. 1986. The distribution of dry mass and phosphorus in an evergreen fynbos shrub species, *Leucospermum parile* (Salisb.) (Proteaceae), at different stages of development. *New Phytologist* **103**: 669-683.

Kummerow, J., Krause, D., & Jow, W. 1978. Seasonal changes of fine root density in southern Californian chaparral. *Oecologia* **37**: 201-212.

Lamb, A.J. & Klaussner, E. 1988. Response of the fynbos shrubs *Protea repens* and *Erica plukenetii* to low levels of nitrogen and phosphorus applications. *S.Afr.J.Bot.* **54(6)**: 558-564.

Lamont, B. 1983. Proteoid roots in the South African Proteaceae. *J. S. Afr. Bot.* **49(2)**: 103-123.

Lewis, O.A.M. & Stock, W.D. 1978. A preliminary study of the nitrogen nutritional status of members of the South African Proteaceae. *J. S. Afr. Bot.* **44(2)**: 143-151.

Mitchell, D.T., Brown, G. & Jongens-Roberts, S.M. 1984. Variation of forms of phosphorus in the sandy soils of coastal fynbos, South-western Cape. *J. Ecol.* **74**: 977-993.

Nichols, D.G. & Beardsell, D.V. 1981. Interactions of calcium, nitrogen, and potassium with phosphorous on the symptoms of toxicity in Grevillea cv 'Poorinda Firebird'. *Plant and Soil* **61(3)**: 467-445.

Orions, G.H. & Solbrig, O.T. 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *American Naturalist* **111**: 677-690.

Parvin, P.E. 1986. Use of tissue and soil samples to establish nutritional standards in Protea. *Acta Hort.* **185**: 145-153.

Prasad, M. & Dennis, D.J. 1986. Phosphorus nutrition of Leucadendron 'Safari Sunset'. *Acta Hort.* **185**: 155-159.

Price, G.H., Cresswell, G.C. & Handreck, K.A. 1997. Ornamentals. **In**: Plant analysis: an interpretation manuel. Martinelli, L. (ed.), pp. 467-485. CSIRO Publishing. Collingwood, VIC 3066. Australia.

Read, D.J., Field, C.B., Gulmon, S., Jongens-Roberts, S.M., Lewis, O.A.M., Mitchell, D.T. & Oechel, W. 1983. **In**: Day, J.A. (ed.), Mineral nutrients in Mediterranean ecosystems. pp. 33-53.

Silber, A., Ganmore-Neumann, R. & Ben-Jaacov, J. 1998. Effects of nutrient addition on growth and rhizosphere pH of *Leucadendron* 'Safari Sunset'. Plant and Soil **199**: 205-211.

Specht, R.L. 1981. Nutrient release from decomposing leaf litter of *Banksia ornata*, Dark Island heathland, South Australia. *Aust.J.Ecol.* **6**: 59-63.

Stock, W.D. & Allsopp N. 1992. Plant structure and function. **In**: Cowling, R. (ed.), The ecology of fynbos, nutrients, fire and diversity. pp. 145-257. Oxford University Press.

Stock, W.D. & Lewis, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *J. Ecol.* **74**: 317-328.

Stock, W.D., Sommerville, J.E.M. & Lewis, O.A.M. 1987. Seasonal allocation of dry mass and nitrogen in a fynbos endemic Restionaceae *species Thanmochortus punctatus*. Pill. *Oecologia* **72**: 315-320.

Stribley, D.P., & Read, D.J. 1980. The biology of mycorrhiza in the Ericaceae. VII. The relationship between mycorrhizal infection and the capacity to utilize simple and complex organic nitrogen sources. *New Phytol.* **86**: 365-371.

Vorster, P.W. & Jooste, J.H. 1986. Potassium and phosphate absorption by excised ordinary and proteoid roots of the Proteaceae. *S. Afr. J. Bot.* **52(4)**: 277-281.

Walters, C.M., Jooste, J.H & Raitt, L.M. 1991. Aspects of the sodium and potassium nutrition of the fynbos shrub *Leucadendron salignum* L. (Proteaceae). *S.Afr.J.Bot.* **57(4)**: 181-185.

Witkowski, E.T.F. 1989. Response to nutrient additions by the plant growth forms of sand-plain lowland fynbos, South Africa. *Vegetatio* **79**: 89-97.

Witkowski, E.T.F, & Mitchell, D.T. 1987. Variations in soil phosphorus in the fynbos biome, South Africa. *J Ecol.* **75**: 1159-1171.

Witkowski, E.T.F. & Mitchell, D.T. 1989. The effects of nutrient additions on above-ground phytomass and its phosphorus and nitrogen contents of sand-plain lowland fynbos. *S.Afr.J.Bot.* **55(2)**: 243-249.

Witkowski, E.T.F., Mitchell, D.T. & Stock, W.D. 1990. Response of a Cape fynbos ecosystem to nutrient additions: Shoot growth and nutrient contents of a proteoid (*Leucospermum parile*) and an ericoid (*Phylica cephalantha*) evergreen shrub. *Acta Ecologica* **11(3)**: 311-326.

PAPER 3

Soil and nutrient requirements of *Brunia albiflora* (Pillans)

Abstract

Soil and plant nutrient requirements of *Brunia albiflora* (Pillans) were investigated by selecting three localities in the Western Cape where commercial harvesting of *B. albiflora* takes place. Variation in terms of growth performance was large and it was hypothesised that a nutritional explanation could be found for these differences by studying the relation of soil nutrients and the nutrient status of the plant. At each locality, plants corresponding with different growth categories, presumably caused by different soil types, were selected. Five of the youngest side shoots of approximately 10 cm were sampled randomly just after harvest (February 1998) and at the resumption of vegetative growth (April 1998). Plant samples were analysed for macro and micro elements. Soil samples at each plot were taken for complete analysis. Soil types at each locality varied greatly and it was observed that Ca in topsoils showed a significant negative correlation with plant performance, whereas soils with higher exchangeable Na showed good plant performance. Soils with a high clay content seem to be unsuitable for *B. albiflora,* possibly due to poor aeration. Positive correlations were also found with organic carbon, N, P and K, as well as acidity and exchange capacity of the B horizon. This is possibly the result of a tendency towards podzolic character of certain B horizons, aiding the retention of P, K and Na.

Introduction

Brunia albiflora (Pillans) is harvested for its conflorescence, which forms an attractive flat topped head. This product can be harvested from October through to February before anthesis, and before this without an inflorescence. It comprises an important percentage of the 'Cape Greens' which are exported to Europe. The demand for the cultivation of South African 'fynbos' is increasing as natural stands can no longer support the growing industry and therefore a knowledge of these plants is critical to enable successful cultivation. In its natural habitat *B. albiflora* occurs in seepage areas. Due to the demand for this product they are increasingly being cultivated outside of these natural conditions and growth is not always as good as in the natural habitat.

At present, harvesting of *B. albiflora* takes place from natural plant populations, from plants that were established by broadcast sown seed, and from plants grown from non-clonal cuttings planted in rows in orchards with fertigation. Plants in natural populations and those broadcast sown, show much variation and the quality of flowers is therefore very varied. To compete on the export flower market, good quality products have to be produced and this can only be accomplished with clonal material grown in an orderly fashion in orchards where cultural practices can be carried out. This implies taking the plants away from their natural habitat and requires a better understanding of the soil and nutritional requirements of the plant.

Soils of the fynbos biome vary considerably as the parent material from which the soils are derived varies over the biome, as does the topography. The landscape of the fynbos biome is dominated by mountains of the Cape Fold Belt, which consist of hard quartzitic rocks belonging to the Table Mountain and Witteberg Group. These rocks give rise to medium sands and loamy sands which commonly have gravelly subsoils of weathered sandstone, shales or granites (Campbell, 1983). Soils derived from Table Mountain quartzite are very acidic (pH (KCl) $\approx$ 3.2-4.5), have low exchangeable cations, N and available P, although soils vary considerably. The pH (KCl) of soils derived from granites and shales is higher, 4.0 - 4.6 and 5.8, respectively. Soil nutrients and soil moisture have been implicated in determining the distribution of fynbos (Stock & Allsopp, 1992). Fynbos vegetation is found at sites with a precipitation greater than 700 $mm.yr^{-1}$ (Stock & Allsopp, 1992).

To gain more knowledge of the soil demands of *B. albiflora,* a study was undertaken where *B. albiflora* is harvested at three localities in the coastal zone of the Western Cape, which have

different meso-climates and management strategies. Variation in terms of growth performance was large at each locality and it was hypothesised that a nutritional explanation could be found for these differences by studying the relationships between soil characteristics, plant performance and nutrient status of the plants. Knowledge of the natural conditions this specie prefers was thought to give an indication of the cultural conditions to be adopted in commercial plantations.

Materials and Methods

Localities

Three localities in the coastal zone of the Western Cape, South Africa, where harvesting of *B. albiflora* take place, were used for this study (Fig. 3.1). The Western Cape is characterised by a Mediterranean climate of cold, wet winters and warm, dry summers. The three localities had different cultivation methods. At Rooi Els (L1), with a westerly aspect, *B. albiflora* occurs in its natural habitat. Plant age varied, as it was a natural population with new seedlings every year, and were situated less than 1 km from the sea. Plants were not subjected to commercial practices except harvesting. Kleinmond (L2) was approximately 2 km from the sea and had a southerly aspect. Plants were grown from broadcast sown seed without irrigation. Plant age could not be assessed accurately as it was a seedling stand, but were estimated to be approximately 4-5 years old. Plants were fertilised in June and November of 1997 and in June 1998, by hand sowing urea-formaldehyde (38% N), KCl (50% K), $MgSO_4$ (10% Mg) and MAP (12% N; 26.7% P). The elements N, P, K and Mg were applied in the ratio of 15:1:10:4 with approximately 300 $kg.ha^{-1}$ per application. Grabouw (L3) was in a mountain basin at an altitude of 450 m and more than 10 km from the sea. Plants were grown from cuttings from a seedling block and were planted in 1995 at a density of 13 000 plants per hectare. Plants were drip-irrigated to supplement rainfall, and fertiliser was applied through the irrigation system from August to March in the form of NH_4SO_4 (21% N) MAP (12% N; 26.7% P), K_2SO_4 (42% K) and $MgSO_4$ (10% Mg). The elements N, P, K and Mg were applied in a ratio of 15: 1: 10: 4, with 400 $kg.ha^{-1}$ of this mixture irrigated over the season. Pest and disease control was also carried out by spraying at monthly intervals with iprodione fungicide in October and November and with a pyrethroide (lambda-cyhalothrin) insecticide at monthly intervals for the period December to April.

Growth categories

At each locality, plots were selected corresponding with different categories of plant growth, presumably caused by different soil types. There were two replicates for each category or soil type.

Rooi Els (L1) had two soil types and two growth categories, ie. strong (C1) and poor growth (C2). Kleinmond (L2) and Grabouw (L3) each had three soil types or growth categories of which one had good growth (C1) and the other two supporting poor growth (C2 & C3). Soils at C2 plots were grey and those at C3 plots yellowish. To quantify plant growth, plant volume was determined using the Braun-Blanquet 5 point scale in 1 m^2 plots (Table 3.1, Wratten & Fry, 1980). Density of plants was estimated by the number of plants per 1 m^2. Plant volume was a better estimate of plant performance and was used for correlations with plant and soil properties.

Plant material

Sampling:

B. albiflora is characterised by pilose leaves about 1 cm in length and 2 mm basal width, which were too small to sample individually. Consequently, five of the youngest side shoots of approximately 10 cm were taken from five randomly selected plants in each plot just after harvest (26 February 1998). The stems from which samples were taken had inflorescences which had reached anthesis. This sampling was repeated on 30 April 1998 at the resumption of vegetative growth, using the youngest fully matured side shoots from stems that were vegetative. The side shoots were rinsed in distilled water and dried on paper towels. The leaves were stripped from side shoots and leaves and stems were analysed separately.

Analysis:

Side shoot stems and leaves were dried in an oven for 2-3 days at 80°C. Dried samples were weighed and ground to <1 mm, using a coffee mill, and stored in plastic bottles with airtight lids. Samples were ashed at 500°C for five hours, taken up in HCl for analysis of all elements, except nitrogen, using an automated system for phosphorus (P) and boron (B) and flame photometer for the other metallic cations (Du Preez, Carstens & Van Wyk, 1981).

For total N, Se catalyst was added to samples and digested with concentrated sulphuric acid in digestion tubes in an aluminium block. Total nitrogen was measured as an ammonia-salicylate complex on an automated analyser system (Lambrechts, 1993).

Soils

Sampling:

Soil profile pits were dug in each plot at Kleinmond (L2) and Grabouw (L3) and profiles described. The soils were classified according to the South African Binomial system (MacVicar, 1991). At

Rooi Els (L1), constant water logging necessitated the use of an auger for sampling and to classify horizons. Composite soil samples of each horizon per plot were obtained by combining and thoroughly mixing subsamples from each face of the profile pit for each horizon (Appendix A).

Analysis:

Soil samples were immediately air-dried at room temperature, sieved to separate the coarse fraction (>2 mm) and stored in plastic bags until further analysis. Soil pH was measured in 1M KCl using a soil:solution ratio of 1:2.5. Total organic carbon (C) was determined by the Walkley-Black method (Hesse, 1971) and humified organic carbon determined by selective dissolution with sodium pyrophosphate at pH 10 (Anon, 1990). Total N content was determined using the macro-Kjeldahl method (Bremner, 1965). Extractable cations were determined by standard methods, using 0.2M NH_4Ac (pH 7) as extractant and atomic absorption spectrophotometry (Anon, 1990). Cation exchange capacity was determined using a 0.2M K_2SO_4 solution for the second leaching and the macro-Kjeldahl method of determining leached NH_4^+ (Anon, 1990). Plant available phosphorus was determined using 1% citric acid as extractant and P spectrophotometrically determined after colour development with ammonium molybdate (Jackson, 1958). Exchangeable acidity was determined using the method of Eksteen (Eksteen, 1969). Total iron oxide (Fe_{dcb}) was extracted using the dithionite-citrate-bicarbonate (DCB) method (Anon, 1990). Iron (Fe_p) and aluminium (Al_p) were selectively extracted with a sodium pyrophosphate solution buffered at pH10 to determine the podzolic character of soils (Anon, 1990). The trace elements Cu, Zn and Mn were extracted using EDTA and determined with atomic absorption spectrometry (Beyers & Coetzer, 1971). Particle size fractions were determined by a combination of the pipette method for silt and clay, and sieving for the sand fractions (Day, 1965).

Statistical methods

Soil data were analysed by means of analysis of variance, using the Statistical Analysis System (SAS) (SAS Institute Inc., 1990). Correlation coefficients were calculated using Pearsons correlation coefficient (SAS Institute Inc., 1990).

Results and Discussion

Plant performance and soils

Plant performance (Table 3.1) did not show large variation between localities, but differences were large between categories at each locality, possibly due to the different soil types. There were numerous interactions between soil chemical properties of localities and plant performance category plots, making interpretation too complex. Average soil chemical values for main effects are therefore given in Table 3.2, with textural analysis data in Table 3.3. Localities were statistically analysed separately and soil chemical data is given in Tables 3.4A and 3.4B. The soils of all localities were characterised by low N contents (Table 3.4A), as is also indicated by the presence of *Drosera* spp (Vorster, 1965) in the undisturbed soil at Rooi Els (L1) (data not shown). The soils of all localities had low pH, common in sandy soils supporting Cape Coastal fynbos vegetation (Taylor, 1969).

Rooi Els:

The soils at Rooi Els (L1) developed from Table Mountain sandstone and were classified as organic rich Fernwood forms according to the South African Binomial system (MacVicar, 1991). These soils have a dark coloured sandy orthic A horizon followed by a strongly leached, grey, sandy E horizon (Table 3.3). The soils are nutrient poor but with a higher organic carbon content at C1 plots compared to C2 plots, which explains the higher exchange capacity at these plots (Table 3.4A).

The soils (C1 and C2) are excessively wet, even in summer, due to some summer rains, condensation from clouds, but primarily from seepage. The water table at C1 plots was present at the surface in winter, subsiding to 50 cm below the surface in summer, making the study of profile pits impossible. The C2 plots were slightly drier, with the water table within 7 cm from the surface in the winter and 80 cm below the surface in summer. Oxygen content of the water was not measured, but for the plants to survive, it is assumed that the water must be lateral moving and oxygenated.

Leaves of *B. albiflora* are very hairy and it has been demonstrated that this enables plants to condense considerable quantities of moisture out of south easterly mists (Boucher, 1978). Moisture laden winds often occur at Rooi Els (L1) and due to its proximity to the sea, sea spray will also have an effect on moisture and salts, Na, Mg and Ca, being intercepted (Lull, 1964). Salts

could be absorbed by the plant or return to the water table, thereby enriching the nutrient content of the water table. The soils at Rooi Els (L1) seem to be enriched in Mg and Na, judging from their saturation percentage compared to that of the other two localities (Table 3.4A).

Kleinmond:

The soils at C1 plots at Kleinmond (L2) were situated on grey soils, developed from Table Mountain sandstone and classified as Houwhoek form. They were characterised by a sandy orthic A horizon on a grey sandy E horizon on a podzol B horizon on saprolite without signs of wetness (Table 3.3). The E horizon at C1 plots was within 200 mm of the surface and the podzol B at a depth of about 400 mm.

The soils of the two C2 plots on grey soil also developed from Table Mountain sandstone and were classified as Concordia form, tending toward Lamotte form, and Constantia form, tending towards Concordia form. The Concordia form soil consisted of a sandy orthic A horizon on a sandy, grey E horizon on a coarse gravelly podzol B horizon on unconsolidated gravel and stone material without signs of wetness. The Lamotte soil is similar to the Concordia soil, but have unconsolidated gravel and stone material with signs of wetness under the podzol B horizon. The Constantia soil had a sandy orthic A horizon on a sandy E horizon on a coarse gravelly apedal yellow-brown B horizon with podzolic character under the B horizon.

The soils at the two C3 plots were yellowish, also developed from Table Mountain sandstone and were classified as Glenrosa and Cartref forms. These weakly developed soils both had a gravelly, sandy orthic A horizon on a yellowish, stony, lithocutanic B horizon, which were not hard and had no signs of wetness. In addition, the Cartref soil had a gravelly, sandy, yellow E horizon. The lithocutanic horizons were shallow (250 mm below surface) and had a large percentage of coarse angular gravel and stones (Table 3.3).

Grabouw

Here the soils also developed from Table Mountain sandstone and were ripped before planting, which was visible to a depth of approximately 600 mm. The soil at C1 plots was Houwhoek form soil, with a rocky, sandy orthic A horizon on a grey, rocky, sandy, E horizon on a coarse gravel and angular stony podzol B horizon on saprolite (weathered sandstone without signs of wetness (Table 3.3)). The podzol B at C1 plots at Grabouw (L3) was less prominent than those of C1 plots at Kleinmond (L2). Contrary to expectation, organic carbon (Table 4A) and iron oxides (Fe_{DCB}) (Table

3.4B) were not significantly higher in the podzol B at C1 plots compared to that of the E horizon. This could be due to mixing by soil preparation. The Houwhoek form C1 plots were situated on a straight slope compared to C2 plots on Cartref form soils, which were located on a convex landscape position. The Cartref form soils do not however appear to be poorer than the Houwhoek form soils (Table 3.4A).

The soil of C2 plots were classified as Cartref form, differing from C3 plots at Kleinmond (L2) in that the E horizon was grey, implying more advanced leaching from this horizon. The lithocutanic B horizon was not hard and had many angular coarse gravel fragments and boulders. The soil was sandy with a low clay content (<5%) (Table 3.3).

The soil of C3 plots were yellowish, classified as Klapmuts form, with a sandy loam orthic A horizon on a sandy loam, yellow E horizon, on a silty clay, non-red, pedocutanic (subangular block structured) B horizon. The higher exchange capacity of the soil (Table 3.4A) can be ascribed to the heavier texture (Table 3.3). The organic carbon content was higher than that of C1 and C2 plots throughout the profile, with corresponding higher iron oxide contents (Fe_{DCB}) (Table 3.4B).

Effect of soil characteristics

Correlation coefficients of plant volume with soil chemical properties, given in Table 3.5, show very few significant relationships. Soil samples were only taken at one sampling date which could give a biased picture of the availability of certain nutrients, such as N and P, which are controlled by biotic factors and will vary seasonally according to water and temperature limitations. In addition, each locality had its own meso-climate and were exposed to different cultural practices. Plant populations also differed in terms of age and method of establishment, causing a complex situation when soil chemical properties are related to plant performance.

It would appear that plant performance is positively related to the C, N, P, K and Na content as well as acidity and exchange capacity of the third horizon (Table 3.5). This is possibly the result of a tendency toward podzolic character of certain B horizons, aiding the retention of P, K and Na. A tendency towards positive effects of Na and Cu in the topsoil were also evident, whereas Ca and Al seemed to have negative effects (Table 3.5).

Organic carbon and the exchange complex are interdependent and would be expected to show the same trends. Organic carbon not only affects the exchange capacity but can form complexes with

inorganic soil constituents like metal ions, hydrous oxides and clay minerals. These can affect chemical, physical and biological properties of soils (Schnitzer, 1969) and could be a determining factor in good plant performance.

The soil chemical properties at Rooi Els (L1) (Table 3.4A & B) corresponded with the trends shown in Table 3.5, except for exchangeable K in the B horizon which showed no significant differences (Table 3.4A). The C1 plots at Rooi Els (L1) also had significantly lower pH in the first and third horizons compared to C2 plots (Table 3.4A), which could benefit the growth of mycorrhiza as fungi dominate at low soil pH in the soil and rhizosphere. Preliminary studies on *B. albiflora* have shown that there is an association with a vesicular arbuscular mycorrhiza (Poole, 1998, unpublished data). The presence and activity of mycorrhiza could assist growth of these plants on poor soils as they can modify the ability of plant roots to absorb P and other nutrients from soil. Exchangeable Mg was higher in all horizons at C1 plots at Rooi Els (L1) compared to C2 plots (Table 3.4A). This was not the case at the other two localities and questions the industries fertilisation programme which seems to focus on Mg. Exchangeable Ca and Ca saturation, which was significantly lower at C1 plots, suggests a possible intolerance of *B. albiflora* to relatively high Ca levels in the soil.

Differences between chemical properties of well (C1) and poorly performing plots (C2 & C3) at Kleinmond (L2), also reflected the trends observed for the soil chemical properties showing significant correlations in Table 3.5 (Table 3.4A & B). This was the only locality showing exchangeable K to be significantly higher in the B horizon at C1 plots and was probably mainly responsible for the positive correlation of K in this horizon with plant performance (Table 3.5).

Differences in soil chemical properties of C1, C2 and C3 plots at Grabouw (L3), showed little conformity with the trends in Table 3.5, with organic carbon, total N, exchangeable acidity and the exchange capacity lower at C1 plots, compared to that of C3 plots (Table 3.4A & B). The C3 plots at Grabouw (L3), despite having a higher exchange capacity throughout the profile, induced poor plant performance. The relatively high exchange capacity is evidently the result of the higher clay content (Table 3.3) and not solely because of a higher organic carbon content of the soils (Table 3.4A). *B. albiflora* seems to prefer lighter textured soil possibly due to better aeration.

In general, the indications are that good growth performance of the plants seems to be associated with sandy soils with a podzol B horizon or tending towards podzolic character. Where the podzol B is lacking, namely Rooi Els (L1), organic carbon appears to be most prominent. Iron oxides in

the podzol B would influence the anion and cation adsorption, surface area and water holding capacity of soils (Sumner, 1963). In acid soils podzol B horizons are also associated with a higher total P (Schnitzer, 1969). Plant available P was highest in the B horizons of C1 plots at Rooi Els (L1) and Kleinmond (L2) and could be important in achieving deep rooting. Comparative root studies were however lacking. Organic matter extracted from podzol horizons has been found to be essentially fulvic acid, which forms more stable complexes with Fe and Al than divalent cations (Schnitzer, 1969). Fulvic acids occur in all soils and it is therefore likely to affect the supply and availability of nutrients to plant roots. It can also enter the plant and influence plant metabolism. The higher organic carbon and related exchange capacity as well as higher P in podzol B horizons seem to be important factors influencing plant growth performance. Additional positive characteristics of the podzol B could be that of increased surface area and water holding capacity.

Conclusion

Plant and root growth is governed by many soil-related factors, such as soil atmosphere, mechanical restrictions, water content and retention and nutrient content. It is difficult to quantify the availability of nutrients as this requires knowledge of the individual plant requirements and what the plant's capacity is to extract nutrients.

Plant performance varied widely at each locality, corresponding with different soil types. Plant performance showed a positive correlation with C, N, P, K and Na contents of soil as well as acidity and exchange capacity of the B horizon, possibly due to a podzol B horizon or soils tending towards podzolic character. Where there was no podzolisation, organic matter seemed to play a prominent role. The positive effect of the higher exchange capacity associated with high organic carbon in the deeper horizons could be due to the increased retention of nutrients and water.

Other trends observed in terms of soil factors affecting growth were high Ca in the A horizon, being a factor associated with poor growth performance. It can therefore be assumed that *B. albiflora* will perform better on soils with more Ca leached horizons. Soils with higher exchangeable Na in the A and B horizon also showed good plant performance, suggesting that where there is higher Na in the soil, plants will use it. This element definitely needs more research in terms of Bruniaceae and Proteaceae.

Grabouw (L3) differed from the other two localities, possibly due to the additional fertilisers and irrigation applied at this locality. Poor growth on grey soils and yellow soils were influenced by different factors. The main factor influencing poor growth on yellow soils seems to be the high clay content. Soils with high clay contents (>20%) seem to be unsuitable for *B. albiflora,* which prefer lighter textured soils, possibly due to better aeration. Plants at Grabouw (L3) could have developed different uptake mechanisms due to increased nutrient levels. Good growth on grey soils seemed to be associated with the podzolic character of the soils.

B. albiflora seem to thrive on leached soil material, but do not respond negatively to fertiliser application such as those applied at Kleinmond (L2) and Grabouw (L3). Adaptation to low nutrient conditions does not necessarily mean that plants cannot tolerate higher nutrient concentrations.

Literature cited

Anon. 1990. Handbook of standard soil testing methods for advisory purposes. Soil Science society of South Africa. PO Box 30030, 0132 Sunnyside, RSA.

Beyers, C.P. De L. & Coetzer, F.J. 1971. Effect of concentration, pH and time on properties of di-ammonium EDTA as a multiple soil extractant. *Agrochemophysica* **3**: 49-54.

Boucher, C. 1978. Cape Hangklip area. II. The vegetation. *Bothalia* **12(3)**: 455-497.

Bremner, J.M. 1965. Inorganic forms of nitrogen. **In:** Black, C.A. *et al.* (eds), Methods of soil analysis. pp 1179-1237. *Am. Soc. Agron.* Inc., Madison, Wis.

Campell, B.M. 1983. Montane plant environments in the fynbos biome. *Bothalia* **14(2)**: 283-298.

Day, P.R. 1965. Particle fractionation and particle size analysis. **In:** Black, C.A. *et al.* (eds), Methods of soil analysis pp. 545-567. *Am. Soc. Agron.* Inc., Madison, Wis.

Du Preez, M., Carstens, J. & Van Wyk, E. 1981. Navorsingsinstituut vir Vruge en Vrugte – tegnologie (NIVV). Inligtingsbulletin Nr. 10- Blaarontleding., Stellenbosch (23:1) NIVV prosedure en tegniese nommer 32 voorbereiding en droogverassing van blaarmonsters vir ontleding.

Eksteen, L.E. 1969. The determination of lime requirement of soils for various cropas in the Winter Rainfall Region. *Fertilizer Society of South Africa Journal* **2**: 13-14.

Hesse, D.R. 1971. A textbook of soil chemical analysis. John Murray, London.

Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J.

Lambrechts, M.H. 1993. Determination of total nitrogen in plant material. Adapted from Technicon Industrial Method. Department of Horticulture Stellenbosch University.

Lull, H.W. 1964. Ecological and silvicultural aspects. **In:** Chow, T.V. (ed.), Handbook of applied hydrology. pp. 6-7. McGraw-Hill book company, New York.

Macvicar, C.M. 1991. Soil Classification working group. Soil classification-a taxonomic system for South Africa. Department of Agricultural Development. Memoirs of the Natural Agricultural Resources of South Africa No.15, Pretoria.

SAS INSTITUTE Inc. 1990. SAS User's guide. Version 6. Fourth edition. Cary, NC.

Schnitzer, M. 1969. Reactions between Fulvic Acid, a Soil Humic Compound and Inorganic Soil Constituents. *Soil Sci. Soc. Amer. Proc.* **33**: 75-81.

Stock, W.D. & Allsopp N. 1992. Plant structure and function. **In**: Cowling, R. (ed.), The ecology of fynbos, nutrients, fire and diversity. pp. 145-257 Oxford University Press.

Sumner, M. E. 1963. Effect of iron oxides on positive and negative charges in clays and soils. *Clay Min. Bull.* **5**: 218-226.

Taylor, H.C. 1969. A vegetation survey of the Cape of Good Hope Nature Reserve. *M.Sc thesis*, University of Cape Town.

Vorster, A. 1965. Inseketende plante. *Archimedes* **7(3)**: 5-6.

Wratten, S.D. & Fry, G.L.A. 1980. Field and laboratory exercises in ecology. Edward Arnold (Publishers) Limited. 41 Bedford Square, London WC1B3DQ.

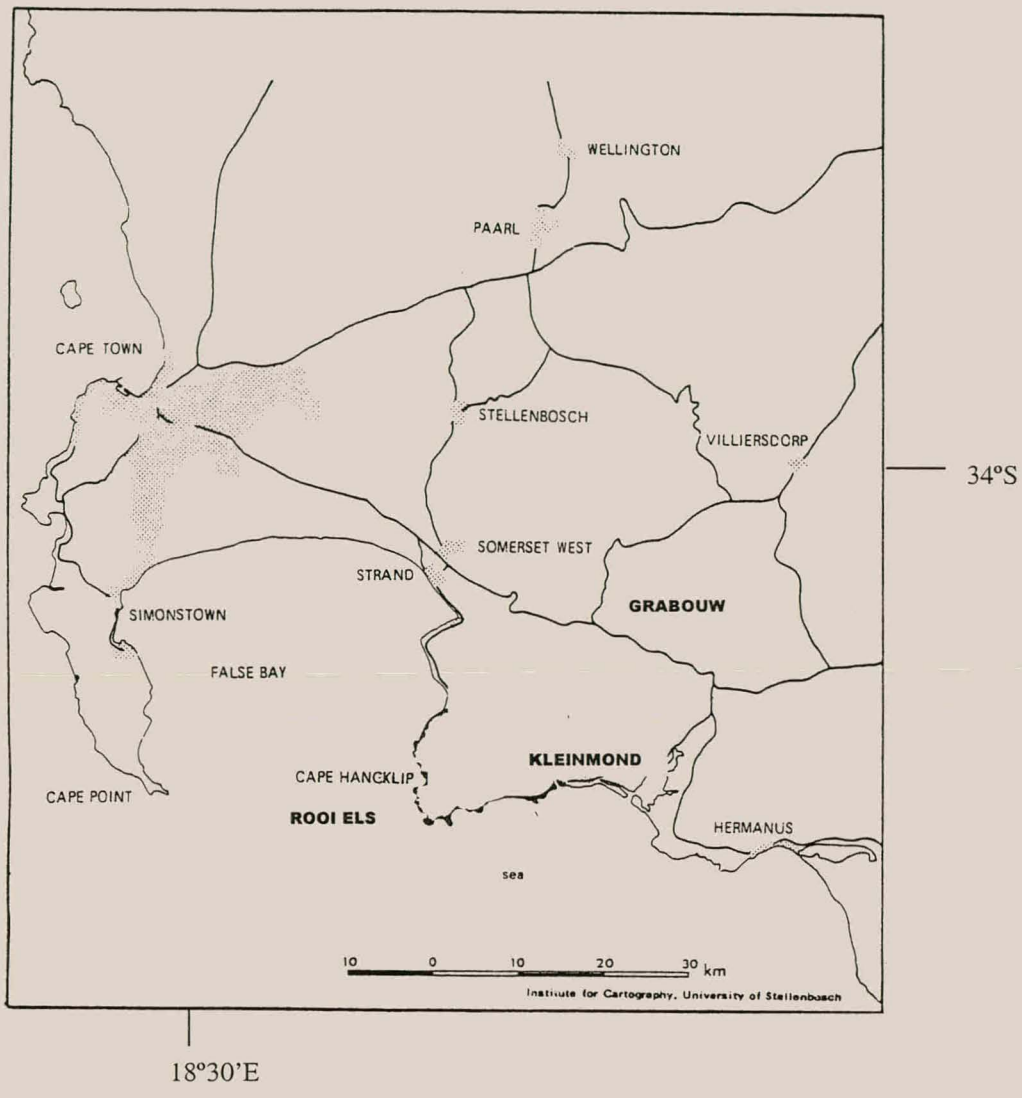


Figure 3.1. The three study localities, Rooi Els (L1), Kleinmond (L2) and Grabouw (L3), in the coastal zone of the Western Cape, South Africa, where harvesting of *Brunia albiflora* take place.

Table 3.1. Plant performance* of three growth categories of *Brunia albiflora* at three localities in the Western Cape.

Locality	Growth category			
	C1	C2	C3	Mean
L1	4.5a	2.0d		3.3
L2	4.5a	1.0e	2.0d	2.5
L3	4.0b	2.0d	3.0c	3.0
Mean	4.3	1.7	2.5	2.9

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils
Letters differing from each other indicate significant differences at p>0.05.
* Expressed as plant volume (Wratten & Fry, 1980).

Table 3.2A. Mean soil chemical properties for three localities in the Western Cape, coastal zone and three growth performance categories of *Brunia albiflora*.

		Horizon	$pH_{(KCl)}$	C	N	C:N	P	Exchangeable cations				Exch acidity	CEC	Saturation percentage			
				%			$mg\ kg^{-1}$	Ca	Mg	K	Na	$cmol_c\ kg^{-1}$		Ca	Mg	K	Na
														%			
Locality	L1	A	3.1	2.2	0.06	39	3	0.20	0.62	0.08	0.45	3.55	4.56	5.21	13.71	1.86	9.19
		E_1	3.5	1.1	0.04	29	3	0.09	0.26	0.04	0.15	2.15	3.24	3.68	8.69	2.01	4.77
		E_2	3.9	1.1	0.03	34	4	0.10	0.24	0.05	0.15	1.61	2.82	5.27	9.63	1.78	6.54
	L2	A	4.0	1.3	0.05	24	5	0.52	0.33	0.25	0.12	2.26	3.81	13.52	8.47	6.58	3.06
		E	4.5	0.8	0.03	34	4	0.25	0.19	0.13	0.08	1.19	2.10	11.43	8.49	6.03	3.94
		B	4.8	1.0	0.03	26	6	0.34	0.33	0.24	0.14	1.92	3.95	9.77	10.05	5.89	3.85
	L3	A	3.7	1.1	0.05	22	6	0.48	0.35	0.11	0.06	2.03	3.14	15.38	11.09	3.38	1.89
		E	4.0	0.6	0.02	27	3	0.18	0.23	0.10	0.03	1.01	1.89	8.19	9.25	4.38	1.62
		B	4.1	0.4	0.02	26	2	0.10	0.29	0.08	0.03	1.05	1.43	5.52	13.97	4.76	2.36
Performance Category	C1	A	3.4	1.3	0.04	32	5	0.20	0.29	0.13	0.18	2.21	3.50	6.43	7.59	3.67	4.14
		E_1, E	3.8	0.9	0.03	29	3	0.10	0.18	0.05	0.10	1.73	2.31	5.55	6.33	3.08	3.45
		E_2, B	4.2	1.4	0.04	38	7	0.22	0.28	0.20	0.15	2.04	4.24	4.55	6.38	4.34	3.62
	C2	A	3.6	1.3	0.05	28	7	0.45	0.39	0.10	0.13	2.31	3.41	12.73	11.59	2.80	4.01
		E_1, E	4.0	0.4	0.02	24	4	0.14	0.13	0.06	0.06	0.99	1.81	8.07	7.75	3.95	3.24
		E_2, B	4.3	0.3	0.02	22	2	0.12	0.12	0.05	0.07	0.75	1.44	7.20	7.93	3.36	4.85
	C3	A	4.3	1.4	0.07	22	2	0.62	0.42	0.29	0.11	2.23	3.97	15.70	10.53	7.19	2.56
		E_1, E	4.6	1.2	0.04	40	3	0.38	0.43	0.21	0.09	1.38	3.03	12.68	14.17	7.08	3.08
		E_2, B	4.5	0.6	0.04	23	2	0.25	0.57	0.15	0.08	1.88	2.37	10.84	24.20	6.21	3.17

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils

Table 3.2B. Mean iron, aluminium and trace element content of soils at three localities in the Western Cape, coastal zone and three growth performance categories of *Brunia albiflora*.

		Horizon	$Fe_{(DCB)}$	$Fe_{(pyro)}$ %	$Al_{(pyro)}$	Trace elements Cu	Zn mg kg^{-1}	Mn
Locality	L1	A	0.012	0.006	0.050	0.081	0.101	0.009
		E_1	0.009	0.001	0.047	0.069	0.067	0.010
		E_2	0.010	0.001	0.123	0.062	0.076	0.049
	L2	A	0.219	0.046	0.072	0.091	0.076	0.079
		E	0.358	0.084	0.023	0.087	0.096	0.012
		B	0.906	0.221	0.027	0.077	0.050	0.038
	L3	A	0.420	0.084	0.109	0.128	0.128	3.917
		E	0.697	0.126	0.542	0.117	0.065	0.241
		B	1.540	0.104	0.197	0.127	0.074	0.270
Performance Category	C1	A	0.043	0.014	0.000	0.130	0.126	3.654
		E_1, E	0.051	0.017	0.002	0.072	0.060	0.211
		E_2, B	0.431	0.135	0.014	0.080	0.068	0.292
	C2	A	0.103	0.024	0.104	0.090	0.105	0.243
		E_1, E	0.124	0.037	0.526	0.079	0.063	0.024
		E_2, B	0.221	0.048	0.274	0.108	0.072	0.034
	C3	A	0.753	0.143	0.167	0.081	0.061	0.157
		E_1, E	1.328	0.235	0.102	0.148	0.125	0.038
		E_2, B	2.700	0.216	0.027	0.087	0.051	0.022

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils
$Fe_{(DCB)}$ – dithionite citrate bicarbonate extractable iron (iron oxides)
$Fe_{(pyro)}$ – pyrophosphate extractable iron
$Al_{(pyro)}$ – pyrophosphate extractable iron

Table 3.3. Texture of soils at three localities in the Western Cape, coastal zone with three growth performance categories.

Locality	Category	Soil Form	Horizon	Texture			stone/ gravel
				clay	silt	sand	
				%			
L1	C1	Fernwood	A	1	3	94	0
			E_1	1	4	92	0
			E_2	1	2	86	0
	C2	Fernwood	A	1	8	89	0
			E_1	0	4	90	0
			E_2	0	3	90	0
L2	C1	Houwhoek	A	2	9	88	1
			E	2	12	82	6
			B	4	5	78	10
	C2	Concordia/ Lamotte +	A	4	13	82	0
		Constantia/Concordia	E	7	13	79	2
			B	7	12	83	42
	C3	Glenrosa/	A	8	13	76	26
		Cartref	E	6	9	83	28
			B	9	14	74	*80
L3	C1	Houwhoek	A	1	8	88	**19
			E	1	13	84	**26
			B	1	8	89	54
	C2	Cartref	A	1	10	87	**10
			E	1	10	88	**39
			B	0	4	94	*70
	C3	Klapmuts	A	10	13	74	12
			E	15	17	63	37
			B	46	39	12	12

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils

* Estimated by profile inspection. Decomposed lithocutanic sandstone
** Large rocks also abundent and not shown in figure.

Table 3.4A. Soil chemical properties of different growth performance categories of *Brunia albiflora*, at three localities in the Western Cape coastal zone.

Loc	Cat	Soil Form	Horizon	$pH_{(KCl)}$	C	N	C:N	P	Exchangeable cations				Exch acidity	CEC	Saturation percentage			
					%			mg kg^{-1}	Ca	Mg	K	Na	$cmol_c$ kg-1		Ca	Mg	K	Na
															%			
L1	C1	Fernwood	A	3.0a	3.0a	0.08a	41a	3c	0.17b	0.85a	0.09a	0.66a	4.93a	6.17a	2.61c	14.04a	1.42a	10.55a
			E_1	3.3c	1.8b	0.06b	33a	2d	0.11c	0.42b	0.04a	0.24b	3.8b	4.18b	2.88c	11.02a	1.03a	5.77d
			E_2	3.9a	1.8b	0.04c	44a	6a	0.12c	0.37b	0.08a	0.20b	2.60c	4.54b	3.16c	9.35a	1.71a	4.47e
	C2	Fernwood	A	3.3c	1.4c	0.04c	36a	3c	0.23a	0.40b	0.07a	0.23b	2.18d	2.96c	7.81a	13.38a	2.31a	7.82c
			E_1	3.7b	0.4d	0.02d	25a	4b	0.07d	0.10c	0.04a	0.07c	0.93e	2.29c	4.47b	6.36a	2.99a	3.76e
			E_2	3.9a	0.4d	0.02d	25a	2d	0.08d	0.11c	0.02a	0.09c	0.63e	1.10d	7.39a	9.91a	1.86a	8.61b
L2	C1	Houwhoek	A	3.6f	1.2b	0.05b	25c	8b	0.25d	0.16d	0.20c	0.11b	2.08b	3.45d	7.40e	4.70d	5.96a	3.24b
			E	4.3d	0.4c	0.02d	25c	3d	0.14e	0.08e	0.08d	0.05d	1.18d	1.46g	8.88e	5.10d	4.98a	3.70a
			B	4.8b	2.2a	0.07a	34b	12a	0.50b	0.42a	0.47a	0.23a	2.98a	7.30a	6.83f	5.80d	6.57a	3.14b
	C2	Concordia/	A	4.1e	1.3b	0.06a	24cd	6c	0.68a	0.45a	0.16c	0.11b	2.33b	3.87a	17.97a	11.73b	4.21a	2.79b
		Lamotte +	E	4.6c	0.6c	0.03c	19e	5c	0.27d	0.21c	0.13d	0.08c	1.25d	2.24f	11.91d	9.22c	5.72a	3.79a
		Constantia/	B	4.9a	0.4c	0.03c	14e	3d	0.25d	0.24c	0.11d	0.10b	1.08d	2.16f	11.67d	11.00b	5.03a	4.64a
		Concordia																
	C3	Glenrosa +	A	4.2e	1.4b	0.06a	24cd	1e	0.63a	0.38b	0.39b	0.13b	2.38b	4.12b	15.19b	8.97c	9.56a	3.15b
		Cartref	E	4.7c	1.4b	0.03c	57a	3d	0.34c	0.28c	0.19c	0.11b	1.15d	2.60e	13.49c	11.13b	7.39a	4.33a
			B	4.7c	0.4c	0.01d	31b	2d	0.26d	0.32b	0.14c	0.09c	1.70c	2.39e	10.80d	13.35a	6.06a	3.77a
L3	C1	Houwhoek	A	3.7d	0.9c	0.04c	22a	4b	0.39c	0.25e	0.08d	0.05c	1.60c	2.21c	17.53a	11.43c	3.43c	2.28b
			E	3.9c	0.3d	0.01d	30a	2d	0.06e	0.04f	0.04f	0.01e	0.63e	1.30d	4.88e	2.88e	3.25c	0.89e
			B	4.0c	0.3d	0.01d	36a	3c	0.03e	0.03f	0.04f	0.03d	0.55f	0.89e	3.64f	4.00e	4.74bc	3.24a
	C2	Cartref	A	3.3e	1.1b	0.05b	23a	12a	0.43b	0.33d	0.06e	0.05c	2.43a	3.40b	12.41b	9.65d	1.89d	1.43d
			E	3.6d	0.4d	0.02d	28a	3c	0.07e	0.07f	0.03f	0.02d	0.80d	0.92e	7.83d	7.67d	3.14c	2.17b
			B	3.9c	0.3d	0.01d	27a	2d	0.02e	0.02f	0.03f	0.01e	0.55f	1.05e	2.55g	2.88e	3.18c	1.29d
	C3	Klapmuts	A	4.3b	1.3a	0.07a	20a	2d	0.61a	0.46c	0.18b	0.08a	2.08b	3.82a	16.21a	12.19c	4.81b	1.96c
			E	4.5a	1.0b	0.04c	22a	3c	0.41b	0.57b	0.22a	0.06b	1.60c	3.46b	11.87bc	17.20b	6.77a	1.82c
			B	4.3b	0.8c	0.06b	14a	1e	0.24d	0.82a	0.15c	0.06b	2.05b	2.35c	10.37c	35.05a	6.36a	2.56b

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils
Letters differing from each other in columns within locality indicate significant differences at p>0.05.

Table 3.4B: Iron, aluminium and trace element content of soil with different growth performance categories of *Brunia albiflora*, at three localities in the Westen Cape coastal zone.

Locality	Category	Soil Form	Horizon	$Fe_{(DCB)}$	$Fe_{(pyro)}$ %	$Al_{(pyro)}$	Trace elements Cu	Zn mg kg^{-1}	Mn
L1	C1	Fernwood	A	0.012a	0.007a	0.000e	0.106a	0.122a	0.014b
			E_1	0.009a	0.002a	0.006e	0.059a	0.075a	0.020b
			E_2	0.009a	0.001a	0.042d	0.063a	0.096a	0.099a
	C2	Fernwood	A	0.012a	0.004a	0.101b	0.057a	0.080a	0.004c
			E_1	0.009a	0.000a	0.087c	0.078a	0.060a	0.000c
			E_2	0.012a	0.001a	0.204a	0.061a	0.056a	0.000c
L2	C1	Houwhoek	A	0.054f	0.016e	0.000d	0.129a	0.104a	0.097a
			E	0.090e	0.035d	0.000d	0.062a	0.048a	0.000a
			B	1.224a	0.389a	0.000d	0.088a	0.045a	0.076a
	C2	Concordia/ Lamotte + Constantia/ Concordia	A	0.225d	0.046d	0.166a	0.074a	0.063a	0.071a
			E	0.306d	0.096c	0.069bc	0.084a	0.064a	0.001a
			B	0.587c	0.128b	0.080b	0.070a	0.052a	0.032a
L3	C3	Glenrosa + Cartref	A	0.378d	0.076c	0.051c	0.070a	0.062a	0.071a
			E	0.678c	0.123b	0.000d	0.115a	0.177a	0.035a
			B	0.908b	0.147b	0.000d	0.075a	0.054a	0.007a
L1	C1	Houwhoek	A	0.062c	0.02d	0.000e	0.154c	0.151b	10.851a
			E	0.055c	0.015d	0.000e	0.096f	0.059e	0.613c
			B	0.061c	0.013d	0.000e	0.089g	0.064e	0.703b
L2	C2	Cartref	A	0.072c	0.023d	0.045d	0.139d	0.173a	0.655bc
			E	0.058c	0.015d	1.421a	0.076h	0.064e	0.070e
			B	0.066c	0.014d	0.537b	0.193a	0.109c	0.070e
L3	C3	Klapmuts	A	1.128c	0.210c	0.283c	0.092f	0.061e	0.244d
			E	1.979b	0.348a	0.204c	0.181b	0.073d	0.041e
			B	4.492a	0.285b	0.055d	0.100e	0.049f	0.038e

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
C1 – plots with good plant performance on grey soils
C2 – plots with poor plant performance on grey soils
C3 – plots with poor plant performance on yellow soils
Letters differing from each other in columns within locality indicate significant differences at $p>0.05$.
$Fe_{(DCB)}$ – dithionite citrate bicarbonate extractable iron (iron oxides)
$Fe_{(pyro)}$ – pyrophosphate extractable iron
$Al_{(pyro)}$ – pyrophosphate extractable iron

Table 3.5. Pearsons correlation coefficients (r, n=16) and levels of significance (*P*) for *Brunia albiflora* performance with soil properties at three localities in the Western Cape coastal zone.

Horizon		$pH_{(KCl)}$	C	N	P	Exchangeable cations K	Ca	Mg	Na	Exch acidity	CEC	Trace elements Cu	Zn	Mn	pyrophosphate Al	Fe	DCB Fe
A	r	-0.40	0.32	0.14	-0.08	-0.17	-0.59	0.10	0.42	0.30	0.24	0.55	0.38	0.32	-0.44	0.15	0.15
	P	*0.13*	*0.22*	*0.62*	*0.76*	*0.52*	***0.02***	*0.71*	***0.10***	*0.26*	*0.37*	***0.03***	*0.15*	*0.22*	***0.09***	*0.59*	*0.59*
E_1, E	r	-0.37	0.25	0.22	-0.38	-0.28	-0.31	0.07	0.28	0.42	0.18	-0.10	-0.16	0.30	-0.29	0.17	0.12
	P	*0.15*	*0.35*	*0.41*	*0.14*	*0.29*	*0.24*	*0.79*	*0.29*	*0.11*	*0.50*	*0.70*	*0.57*	*0.26*	*0.28*	*0.52*	*0.66*
E_2, B	r	-0.24	0.65	0.54	0.62	0.45	0.12	0.20	0.56	0.56	0.61	-0.19	0.05	0.36	-0.30	0.20	0.04
	P	*0.37*	***0.01***	***0.03***	***0.01***	***0.08***	*0.66*	*0.45*	***0.02***	***0.03***	***0.01***	*0.49*	*0.87*	*0.17*	*0.26*	*0.47*	*0.99*

Figures in bold indicate a significant correlation $P \leq 0.10$.

PAPER 4

Nutrient composition of *Brunia albiflora* (Pillans) leaves and nutrient removal by flowering shoots.

Abstract

Nutritional requirements for optimum growth of *Brunia albiflora* (Pillans) need to be determined to enable rational fertiliser applications. Leaves and stems of *B. albiflora* at three localities in the Western Cape, were sampled at two dates. The first sampling date corresponded with anthesis and the second with the resumption of vegetative growth. The aim was to determine which plant component and which sampling date reflected the nutrient status of the plant and to establish nutrient concentrations, which could be used in future as a reference. Leaves were chosen as index tissue as they gave more consistent higher concentrations than stems. Sampling at anthesis was appropriate as it is a period easy to discern and there were no apparent advantages of sampling in April. Leaf concentrations *of B. albiflora* were found to be low in N, P, K, Mg and Zn, compared to that of other woody plants, whereas Ca, Cu and Mn appeared to have similar concentrations. Nutrient removal was calculated by sampling and analysing flowering shoots of well performing plants at three localities in February at anthesis. The removal of macro-elements by cropping a plantation in full production was 38 kg N, 1.5 kg P, 35 kg K, 40 kg Ca and 5 kg Mg per hectare, based on 25 flowering shoots per plant and 5 000 plants per hectare.

Introduction

The sclerophyllous shrub *Brunia albiflora* (Pillans) is increasingly being cultivated for the cut flower industry for its attractive conflorescence. With increasing commercial cultivation it is important to understand the environmental and nutritional requirements of these plants. It has been found that sclerophyllous shrubs, woody plants with rubbery leaves retaining water, are specially adapted to low nutrient environments, in particular phosphorus (Loveless, 1961). Sclerophylly, the evergreen nature, and longevity of leaves of these plants, have been suggested as mechanisms for conserving nutrients (Stock, Van der Heyden & Lewis, 1992). Sclerophyll leaves are also able to photosynthesise for longer periods compared to that of deciduous plants, as leaves are active for a longer period. No leaf analysis data exist for *B. albiflora*. Leaf analysis data are important for the development of diagnostic norms that can be an aid to rational nutrition management.

Commercial fertilisation with certain nutrients may not be necessary for *B. albiflora* because of its specific adaptations. However, adaptation to low nutrient levels does not mean these plants are intolerant to high nutrient levels. Through intensive harvesting every year, considerable amounts of nutrients are removed, which could reduce soil nutrient levels to limiting concentrations. There is a need to eliminate guesswork and develop fertiliser programmes for 'fynbos' on a scientific basis.

Fruit producers have traditionally relied on standardised chemical analyses of plant organs as an indicator of the nutritional status of the plant (Neilson & Neilson, 1997). In South Africa, diagnostic leaf analyses norms have been developed for deciduous fruit (Beyers, 1962) and grapes (Conradie, 1980; 1981). Similar norms for 'fynbos' are still lacking. To determine standards for nutritional levels for optimum growth, easily identifiable index tissues should be sampled in a reproducible way to minimise sampling error (Maier, Barth, Chvyl & Bartetzko, 1995). Sampling time also needs to be standardised because of seasonal variation in nutrient content. The preferred sampling time is when the rate of change of nutrient concentration is minimal but still reflects the nutritional status adequately. For perennial crops, annual leaf and soil sampling are used together to maintain optimum nutrient availability (Neilson & Neilson, 1997). In the absence of fertiliser trials, commercial plantings, which have the desired productivity and quality characteristics, can be used to obtain preliminary interpretation standards for perennial crops (Cresswell, 1989).

The commercial cultivation of *B. albiflora* is a new field, with no cultural guidelines. The aim of this study was to present nutrient analysis data of easily identifiable index tissues of *B. albiflora,* which

could be used in future as a reference. Nutrient removal data by flowering shoots are also reported, which may serve as a basis for fertiliser recommendations, pending the results of fertiliser trials.

Materials and methods

Plant sampling and analytical procedures.

Plant sampling and analyses were carried out on three field experiments and two dates as described in a previous study (Poole, paper 3, p.70). For the establishment of plant norms, leaf analyses from well performing plants (C1 plots) were used. For total nutrient removal by flowering shoots, five randomly selected shoots (± 40 cm) were sampled from well performing plants at each of three localities (Rooi Els (L1), Kleinmond (L2) and Grabouw (L3)) at anthesis (February 1998). Flowering shoots were divided into four fractions, namely: flower cluster, stems and leaves of sylleptic side shoots and main shoots. These fractions were weighed separately for each flowering shoot and a composite sample of each fraction from the five flowering shoots was used for chemical analysis. From this data, nutrient removal by flowering shoots was estimated, assuming that 25 flowering shoots per plant were harvested at each locality.

Statistical methods

Correlation coefficients for soil and plant data were calculated using Pearsons correlation coefficients. Analysis of variance was carried out on all plant and leaf data from C1 plots at the three localities sampled in February and April by means of the Statistical Analysis System (SAS) (SAS Institute Inc., 1990). No statistical analyses were possible on nutrient removal data as composite samples were used.

Results and Discussion

Nutrient content of plant components.

Although sampling throughout the season would have been preferable to determine seasonal trends in nutrient concentration and translocation in plant components, due to limited funds sampling was possible on two dates only. The first sampling date was at an easily identifiable phenological stage, namely anthesis (February). The second date was two months later (April), corresponding with the resumption of vegetative growth. Standardising sampling time is important due to the variation in nutrient concentration over and between seasons. For this reason the time

of sampling should coincide with a phenological stage and not be a categoric calendar date, as the phenology of plants will differ due to locality and climatic variation.

Because of complex interaction patterns found between locality and plant performance category, it was decided to treat categories as replications in order to evaluate for each locality the effect of time of sampling and the plant component sampled. The results are presented in Table 4.1. For all localities, disregarding main effect results in the case of sampling date x component interactions, consistent significant differences between sampling dates were obtained only for N and P. February samples were higher in N, with Mn and Mo showing similar differences and tendencies. Phosphorus was higher in April possibly due to the sink strength of inflorescences for P (Fig. 4.1A).

Again, disregarding main effect results in the case of significant sampling date x component interactions at all localities, N, Mn, B and Mo concentrations were higher and K lower in leaves compared to that of stems. Phosphorus and Na were higher in leaves at Rooi Els (L1) and Kleinmond (L2) with the reverse true for Grabouw (L3).

Regarding time of sampling, anthesis seems to be appropriate as it is an easily identifiable stage. There appears to be little advantage in April sampling in terms of nutrient concentrations. In view of the greater ease of analysing leaves as well as the findings that leaves generally have higher concentrations of important elements like N, P, Mn and B compared to that of stems, leaves appear to be the plant component to be sampled.

Relationships between plant and soil nutrient content

Correlation coefficients and significance levels of nutrient content of leaves and stems sampled in February and April, with nutrient concentrations in soil horizons, are shown in Table 4.2. Nutrient levels in leaves sampled in February (anthesis), generally showed more significant correlations with soil nutrient content than stems did. Nitrogen in leaves sampled in February showed a negative correlation with N in the lower two soil horizons and with organic carbon in the A and E_2 or B horizons. Stems, however, showed an opposite correlation in the case of A horizons but conformed to leaves concerning the E_2 or B horizons. The general negative correlation in the case of N may be due to a physiological dilution effect, as concomitant studies (Poole, paper 3, p.87) showed C and N content of soil to be positively correlated to plant performance (plant volume). Plant nutrient concentrations seem to show more significant correlations with the nutrient saturation of the soil than with the exchangeable cations (Table 4.2). Calcium in leaves sampled in February

showed a positive correlation with the Ca saturation percentage of E_1 horizons. However, stems only showed a negative correlation with A horizons, which corresponded with the negative correlation found for soil Ca with plant performance (Poole, paper 3, p.87). Sodium in leaves and stems were significantly correlated with Na saturation percentage in A and E_2 or B horizons, which confirms the hypothesis that where there is Na in the soil, *B. albiflora* will use it (Poole, paper 3, p.77). This appears to indicate that this plant has a requirement for this element. Pyrophosphate extractable aluminium in A horizons showed a positive correlation with Al in leaves in February. Stems, however, showed a negative correlation in this regard in the case of E and E_2 or B horizons. According to Poole (paper 3, p. 87) plant performance and soil Al were negatively correlated. Copper and Zn in leaves and stems sampled in February showed positive correlations with the Cu and Zn content of E_2 or B horizons and Zn in leaves also showed a positive correlation with Zn content of A horizons.

Correlations between nutrient content in leaves sampled in April and that in soil, differed from those in February in that no significant correlations were found in the case of soil N and organic C. The P content of leaves, however, showed a positive correlation with the P content of the A and E_2 or B horizons and the P content of stems with that of A horizons. Calcium in leaves and stems in April showed a negative correlation with the Ca saturation percentage of A horizons, similar to February results for stems. Sodium in leaves and stems showed the same pattern as in February for A horizons and also showed a positive correlation with the Na saturation percentage of E_1 horizons. Iron in leaves sampled in April was generally positively correlated to iron oxides Fe_{DCB} and Fe_{pyro} in soil, whereas no correlation was found in February. Iron in leaves correlated positively with the iron content of A and E_1 horizons as did stems, with the additional positive correlation of stems with iron oxides $Fe_{(DCB)}$ of the E_2 or B horizon. Aluminium in leaves and stems sampled in April showed a positive correlation with Al in A horizons.

Leaf and stem analysis do not appear to be very sensitive to differences in plant performance, as very few elements showed significant correlations with plant growth performance (Table 4.3). Only Ca in the leaves sampled in February reflected the negative relationships between availability of this element in topsoils and plant performance. Negative relationships were also found for Al and Fe in leaves and for Fe and N in stems during April concerning plant performance and element content. This did not conform to the content of these elements in the soil (Poole, paper 3, p.87).

Nutrient concentration in leaves and stems

From the results previously discussed, leaves from side shoots just under the inflorescence were chosen as index tissue for plant analyses. Nutrient content of the plants in general were low and is possibly due to the plant not storing any nutrients but taking them up when needed. This appears to be in accordance with results obtained concerning carbohydrates in *B. albiflora*. Here it was found that plants are more dependent on current photosynthates than stored carbohydrates (Poole, paper 2, p.47). The nutrient content of plants with good growth performance (C1 plots) were used as a guidelines for future use. Table 4.4 gives the leaf concentrations of nutrients of such plants in February and April.

Nitrogen concentration in leaves was highest at Grabouw (L3) in February and lowest at Rooi Els (L1), probably because of fertilisation practices. Phosporus in leaves also showed this pattern at both dates. Potassium in leaves was highest at Grabouw (L3) and Kleinmond (L2), also reflecting the effect of the fertiliser at these two localities. Calcium and Na in leaves were highest in leaves at Rooi Els (L1) possibly due to the influence of the sea spray (Poole, paper 3, p.73). Magnesium in leaves was the same at Rooi Els (L1) and Grabouw (L3) and higher than that of Kleinmond (L2) in February and higher at Rooi Els (L1) than at Kleinmond (L2) in April.

Nitrogen, K, Ca, Mn and B concentrations in leaves of *B. albiflora* were higher than those found in *Protea* cv. Pink Ice (Maier *et al.*, 1995) and *Leucadendron* cv. Safari Sunset (Cecil, Barth, Maier, Chvyl, & Bartetzko, 1995). Phosphorus and Zn concentrations in leaves were similar to those found in Proteaceae. Phosphorus concentrations in *B. albiflora* tissue were extremely low when compared to those of vines, which are considered as conservative P feeders, with concentrations of 0.14-0.55 % during fruit set (Conradie, 1981). This is possibly a result of the adaptation of these plants to low P environments (Loveless, 1961). *B. albiflora* may also not store P, taking it up only when required. Magnesium and Na concentrations in leaves of *B. albiflora* were the same as for *Leucadendron* cv. Safari Sunset (Cecil *et al.*, 1995) but higher than that of *Protea* cv. Pink Ice (Maier *et al.*, 1995). Sodium is an element requiring further research in fertilisation trials as it may have an important function in these plants. Iron concentrations in leaves sampled at Rooi Els (L1) and Grabouw (L3) in February were very high compared to other plants. The maximum in vine leaves is cited as 170-180 $mg.kg^{-1}$ (Conradie, 1981). It has also been observed that good plant performance of *B. albiflora* appears to occur on iron rich, podzolic soils (Poole, paper 3, p.77). Molybdenum concentrations in leaves of *B. albiflora* were higher than those found in *Pinus radiata* (Bengston, Brendemuehl, Pritchett & Smith, 1968) and other woody plants (Taiz & Zeiger, 1991).

Elements which appeared to be lower than those found in deciduous and other woody plants were: N, P, K, Mg and Zn, whereas Ca, Cu and Mn appeared to have similar concentrations than in other woody plants (Taiz & Zeiger, 1991; Table 4.3).

The only macro-element showing a significant difference in the date of sampling was P, which was higher in leaves in April compared to February. The lower concentration in leaves in February was possibly due to the higher sink strength of the flowers in February (Kozlowski, 1992) (Fig. 4.1A). The trace elements Fe, Al and Mo were significantly higher in leaves in February, with only Cu showing higher leaf concentrations in April.

Nutrient composition of and removal by flowering shoots.

Because samples were pooled for this study, analysis of variance was not possible in the case of calculations of nutrient removal by flowering shoots. Standard errors were used as indication of differences between element content of plant parts (Fig. 4.1A & B). Nitrogen was equally proportioned between leaves and flowers. Phosphorus, K and Cu accumulated in the flower at harvesting, which is possibly the reason for P and Cu being lower in leaves sampled in February (Table 4.4). Magnesium, Fe, Al, and B were highest in the leaves of flowering stems. Magnesium and B uptake and allocation patterns appeared to be similar (Fig. 4.1A & B). Aluminium and Fe also had similar patterns of nutrient distribution, with Al concentrations much higher than that of Fe. This is unusual, as Al is not regarded as an essential element for plants. Zinc and Ca had significantly higher concentrations in stems than in other plant parts. Main shoots did not appear to store much nutrients and were significantly lower in K, Mg, Al, Fe and Cu, compared to the other plant parts (Fig. 4.1A & B).

The apparent higher N, P and K concentrations in flowering shoots at Grabouw (L3) (Table 4.5) were expected as this locality received N, P, and K fertigation. The fertiliser application at Grabouw (L3) was higher than that at Kleinmond (L2). The heavier flowering shoots at Grabouw (L3) could possibly be due to selection at the other two localities, caused by the first commercial picking before sampling took place. It appears that higher amounts of N and P were removed from Grabouw (L3) due to higher concentrations of N and P in flowering shoots and a larger mass of flowering shoots. The apparent higher K removal at Kleinmond (L2) and Grabouw (L3) can partly be ascribed to fertilising with this element. Magnesium concentration appeared to be higher in flowering shoots at Rooi Els (L1). This was unexpected as Mg was included in the fertiliser program at Grabouw (L3) and Kleinmond (L2). The higher Mg content at Rooi Els (L1) may have

been caused by sea spray, as also indicated by the apparent higher Na content. The effect of sea spray should be best reflected by Na and Mg concentration in the plant (Lull, 1964). Plants at Rooi Els (L1) appear to have higher Na and Mg concentrations (Table 4.4 & 4.5). Magnesium and Ca removal was apparently higher at Grabouw (L3) due to the higher mass of flowering shoots.

Concentrations of elements in flowering shoots of *B. albiflora* were slightly higher than those reported for Protea species, except for P, which was similar or lower (Claassens, 1986; Maier *et al.*, 1995). Nutrient removal by flowering shoots at Rooi Els (L1) followed the same pattern as found for *Protea* cv. Pink Ice (Maier *et al.*, 1995), except that in the case of *B. albiflora* Mn removal was higher than Fe removal and B removal was higher than Zn removal. Data also corresponded with that for *Leucadendron* cv. Silvan Red (Cecil *et al.*, 1995), except that in the case of *B. albiflora,* K removal was of the same order as for N, whereas in 'Silvan Red' it was approximately half that of N.

In full production, an estimated 125 000 flowering stems per hectare can be harvested. Using this norm of 25 flowering shoots per plant and 5 000 plants per hectare, the average nutrient content for localities, removal of macro-elements was calculated to be 38 kg N, 1.5 kg P, 35 kg K, 40 kg Ca and 5 kg Mg per hectare. From this data it is obvious that considerable amounts of nutrients are removed with the harvest. These nutrients need to be replenished, especially in view of the fact that *B. albiflora* is normally grown on highly leached, acid, sandy soils (Poole, paper 3, p.73).

Conclusion

Plants need adequate nutrients throughout their growing period to produce good quality products. Knowledge of adequate nutritional levels of the plant is therefore required, which can be reflected by index tissues analyses. Leaf analyses need to be looked at in conjunction with soil properties as crop productivity is a function of the natural fertility of the soil plus nutrients added as fertiliser, organic residues and other sources, physical and biological properties, climate, management and other inherent factors involved.

There is a need to standardise on index tissues and time of sampling in order to make meaningful comparisons of data. Sampling should correspond with a phenological stage and not a calender date, as stages will vary annually depending on locality and climatic conditions. It appears that the nutrient content of *B. albiflora* does not reflect the growth performance within the context of time of sampling and plant component used in this study. As an interim measure it can be proposed that

leaves from side shoots just under the flower be used as index tissue as they are the youngest mature shoots on the plant and are considered to be the most sensitive indicators of the nutritional status of the plant. Sampling at anthesis, approximately in February, would be the most convenient time to sample as this is an easily identifiable phenological stage as well as a period when the plant is considered to have an increased demand for nutrients.

This study has generated data on the concentrations of certain nutrients in leaves of *B. albiflora* plants as well as indications of the amounts of nutrients removed through harvesting, which can amount to appreciable losses over time. As the demand for these flowers increases, there will be a greater demand for better quality and the extra inputs in terms of fertiliser should be advantageous. This can only be verified by means of fertiliser trials. As an interim measure, the amounts of nutrients removed by the harvest can serve as a basis for a rational fertiliser program, supported by tissue analyses to verify responses.

Fertilisation trials with different nutrient additions need to be carried out in order to establish sensitivities to toxicity and shortages and to determine critical nutrient levels in index tissues. Of particular importance is the role of Al and Na. The relationship between nutrient concentration and yield response also requires further research. It is important that diagnosis be aimed at correcting nutrient problems and preventing the development of problems in the future.

Literature cited

Bengtson, G.W., Brendemuehl, R.H., Pritchett, W.L. & Smith, W.H. 1968. Forest fertilization theory and practice, pp. 108-167. Tennessee Valley Authority National Fertilizer Development Center, Muscle Shoals, Alabama 35660.

Beyers, E. 1962. Diagnostic leaf analysis for deciduous fruit. *S.Afr.J.Agric.Sci.* **5**: 315-329.

Cecil, J.S., Barth, G. E., Maier, N.A., Chvyl, W.L. & Bartetzko, M.N. 1995. Leaf chemical composition and nutrient removal by stems of Leucadendron cvv. Silvan Red and Safari Sunset. *Aust. J. Expt. Agric.* **35**: 547-555.

Claassens, A.S. 1986. Some aspects of the nutrition of proteas. *Acta Hort.* **185**: 171-179.

Conradie, W.J. 1980. Seasonal uptake of nutrients by Chenin blanc in sand culture: I Nitrogen. *S.Afr.J.Enol.Vitic.* **1(1)**: 59-64.

Conradie, W.J. 1981. Seasonal uptake of nutrients by *Chenin blanc* in sand culture: II Phosphorus, potassium, calcium and magnesium. *S.Afr.J.Enol.Vitic.* **2(1)**: 7-13.

Cresswell, G. C. 1989. Development of leaf sampling technique and leaf standards for kiwifruit in New South Wales. *Aust. J. Expt. Agric.* **29**: 411-417.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. *Bot. Rev.* **58**: 109-185.

Loveless, A.R. 1961. A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. *Annals of Botany* **25**: 168-184.

Lull, H.W. 1964. Ecological and silvicultural aspects. **In**: Chow, T.V. (ed.), Handbook of applied hydrology. pp. 6-7 McGraw-Hill book company, New York.

Maier, N.A., Barth, G.E., Chvyl, W.L. & Bartetzko, M.N. 1995. Effect of sampling time and leaf position on leaf nutrient composition of Protea 'Pink Ice'. *Aust. J. Expt. Agric.* **35**: 275-283.

Neilson, G.H & Neilson, D. 1997. Orchard nutrition to maximise crop quality and minimise environmental degradation. *Acta Hort.* **448**: 365-373.

SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2, Cary, NC.

Stock, W.D., Van der Heyden, F. & Lewis, O.A.M. 1992. Plant structure and function. **In**: Cowling, R. (ed.), The ecology of fynbos, nutrients, fire and diversity. pp. 226-239. Oxford University Press.

Taiz, L. & Zeiger, E. 1991. Mineral nutrition,. **In**: Brady E.B. *et al.* (eds), Plant physiology pp. 100-119. The Benjamin/Cummings Publishing Company, Inc. Redwood City, California.

Table 4.1. Nutrient composition of components of *Brunia albiflora* sampled at two dates and three localities in the Western Cape coastal zone.

Locality	Sampling Date	Plant Component	N	P	Ca	*Mg	K	Na	*Al	*Fe	Mn	*Zn	*Cu	B	Mo
			%						mg kg^{-1}							
L1	February	Leaves	0.80a	0.019c	0.99d	0.16a	0.68a	0.28a	324b	243a	184a	8a	3d	43a	1a
		Stems	0.36a	0.019c	1.23b	0.08c	0.89a	0.20a	359a	156a	42c	8a	8c	12c	1a
	April	Leaves	0.53a	0.031a	1.14c	0.18a	0.66a	0.20a	214c	138a	127b	11a	20b	43a	0b
		Stems	0.37a	0.027b	1.36a	0.11b	1.00a	0.20a	198c	124a	32c	9a	32a	16b	1a
L2	February	Leaves	0.93a	0.019c	1.07a	0.13a	0.74c	0.22a	378a	221a	153a	7c	3c	34a	2a
		Stems	0.42a	0.017c	1.03a	0.07c	0.95b	0.16a	279c	128d	50c	11a	7b	10c	1b
	April	Leaves	0.65a	0.030a	0.90a	0.13a	0.75c	0.20a	271c	156c	124b	8b	10a	32a	1b
		Stems	0.47a	0.026b	1.00a	0.10b	1.03a	0.22a	313b	191b	47c	6c	10a	16b	1b
L3	February	Leaves	1.01a	0.032c	0.98a	0.14a	0.80c	0.15a	441a	278a	907a	14a	6d	26a	3a
		Stems	0.43c	0.030c	0.92a	0.09c	1.01b	0.13b	246c	125c	331a	16a	7c	15c	1b
	April	Leaves	0.77b	0.039b	0.67c	0.12b	0.69d	0.07d	273b	191b	765a	13a	13a	19b	1b
		Stems	0.45c	0.051a	0.83b	0.12b	1.11a	0.10c	308b	184b	259a	12a	10b	13d	1b
Locality	Sampling date														
L1	February		0.58a	0.019b	1.11b	0.12b	0.78b	0.24a	342a	200a	113a	8b	6b	27b	0.9a
	April		0.45b	0.029a	1.25a	0.14a	0.83a	0.20b	206b	131b	79b	10a	26a	29a	0.8a
L2	February		0.67a	0.018b	1.05a	0.10b	0.85a	0.19a	329a	174a	102a	9a	5b	22b	1.5a
	April		0.56b	0.028a	0.95b	0.11a	0.89a	0.21a	292b	174a	85b	7b	10a	24a	0.6b
L3	February		0.72a	0.031b	0.95a	0.11b	0.90a	0.14a	344a	201a	619a	15a	6b	21a	1.8a
	April		0.61b	0.045a	0.75b	0.12a	0.90a	0.09b	290b	187b	512a	13b	11a	16b	0.7b
Locality		Plant Component													
L1		Leaves	0.67a	0.025a	1.06b	0.17a	0.67b	0.24a	269a	191a	155a	9a	12b	43a	1.0a
		Stems	0.37b	0.023b	1.30a	0.09b	0.94a	0.20b	279a	140b	37b	8a	20a	14b	0.8b
L2		Leaves	0.79a	0.025a	0.99a	0.13a	0.74b	0.21a	324a	188a	139a	7a	6b	33a	1.4a
		Stems	0.44b	0.022b	1.02a	0.09b	0.99a	0.19b	296b	160b	48b	8a	8a	13b	0.7b
L3		Leaves	0.89a	0.036b	0.82a	0.13a	0.74b	0.11b	357a	234a	836a	14a	9a	23a	1.6a
		Stems	0.44b	0.040a	0.87a	0.11b	1.06a	0.12a	277b	155b	295b	14a	8a	14b	0.9b

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
* significant interaction between sampling date and plant component sampled within locality
Letters differing from each other in columns within locality indicate significant differences at p>0.05

Table 4.2. Pearsons correlation coefficients (r, n=16) and levels of significance (*P*) for plant nutrient content of *Brunia albiflora* with soil nutrient content for two sampling dates and three localities in the Western Cape coastal zone.

Sampling Date	Plant component	Soil Horizon		N	*N/C	P	Exchangeable cations Ca	Mg	K	Na	Saturation percentage Ca	Mg	K	Na	$Fe_{(DCB)}$	$Fe_{(pyro)}$	$Al_{(pyro)}$	Trace elements Cu	Zn	Mn
February	Leaves	A	r	-0.31	-0.56	0.28	0.42	-0.24	0.20	0.48	0.07	0.59	0.22	0.61	0.36	0.36	0.67	0.33	0.72	-0.01
			P	*0.24*	***0.03***	*0.30*	*0.11*	*0.38*	*0.45*	***0.06***	*0.81*	***0.02***	*0.41*	***0.01***	*0.17*	*0.17*	***0.00***	*0.20*	***0.00***	*0.98*
		E	r	-0.49	-0.25	-0.31	0.53	-0.11	0.49	0.56	0.47	0.00	0.38	0.47	0.32	0.31	-0.15	-0.12	-0.11	-0.25
			P	***0.06***	*0.34*	*0.24*	***0.04***	*0.69*	***0.05***	***0.02***	***0.06***	*0.99*	*0.15*	***0.07***	*0.22*	*0.24*	*0.57*	*0.66*	*0.68*	*0.34*
		E_2, B	r	-0.58	-0.69	-0.25	0.13	-0.35	0.34	0.18	0.60	-0.20	0.41	0.69	0.25	-0.17	-0.12	0.69	0.63	-0.37
			P	***0.02***	***0.00***	*0.34*	*0.63*	*0.19*	*0.20*	*0.49*	***0.01***	*0.45*	*0.12*	***0.00***	*0.35*	*0.53*	*0.67*	***0.00***	***0.00***	*0.16*
	Stems	A	r	-0.24	0.48	-0.25	-0.24	-0.08	-0.17	0.40	-0.49	0.07	-0.13	0.49	0.31	0.31	0.21	0.38	0.41	-0.04
			P	*0.38*	***0.06***	*0.36*	*0.37*	*0.78*	*0.53*	*0.13*	***0.05***	*0.79*	*0.62*	***0.05***	*0.24*	*0.24*	*0.44*	*0.15*	*0.12*	*0.87*
		E	r	-0.40	-0.30	-0.42	-0.02	-0.16	-0.19	0.43	-0.16	-0.16	-0.28	0.34	0.27	0.32	-0.74	-0.21	-0.05	0.18
			P	*0.12*	*0.27*	*0.11*	*0.93*	*0.55*	*0.47*	***0.10***	*0.56*	*0.56*	*0.29*	*0.20*	*0.31*	*0.22*	***0.00***	*0.43*	*0.84*	*0.50*
		E_2, B	r	-0.37	-0.62	-0.25	0.09	0.08	0.21	0.14	0.08	-0.09	0.30	0.45	0.22	-0.02	-0.45	0.56	0.66	0.14
			P	*0.16*	***0.01***	*0.35*	*0.74*	*0.76*	*0.44*	*0.60*	*0.76*	*0.75*	*0.26*	***0.08***	*0.42*	*0.93*	***0.08***	***0.02***	***0.01***	*0.60*
April	Leaves	A	r	0.14	-0.10	0.59	-0.23	-0.66	-0.33	0.63	-0.50	0.40	0.42	0.59	0.54	0.53	0.60	0.12	0.57	0.00
			P	*0.59*	*0.72*	***0.02***	*0.39*	***0.01***	*0.21*	***0.01***	***0.05***	*0.12*	***0.10***	***0.02***	***0.03***	***0.03***	***0.01***	*0.65*	***0.02***	*0.99*
		E	r	0.18	0.23	-0.11	0.05	-0.53	0.04	0.75	-0.12	-0.22	0.55	0.76	0.47	0.51	-0.14	-0.28	-0.14	-0.23
			P	*0.51*	*0.39*	*0.68*	*0.86*	***0.04***	*0.89*	***0.00***	*0.66*	*0.42*	***0.03***	***0.00***	***0.07***	***0.04***	*0.61*	*0.30*	*0.61*	*0.39*
		E_2, B	r	0.24	0.00	0.45	0.14	-0.33	0.34	0.60	0.26	-0.41	0.40	0.38	0.35	-0.08	-0.07	0.17	0.71	-0.38
			P	*0.37*	*0.99*	***0.08***	*0.60*	*0.22*	*0.20*	***0.01***	*0.34*	*0.12*	*0.13*	*0.15*	*0.18*	*0.76*	*0.80*	*0.53*	***0.00***	*0.14*
	Stems	A	r	-0.12	-0.23	0.64	-0.22	-0.08	-0.26	0.55	-0.45	-0.02	-0.15	0.45	0.61	0.61	0.60	-0.07	0.55	0.05
			P	*0.66*	*0.38*	***0.01***	***0.04***	*0.77*	*0.33*	***0.03***	***0.08***	*0.94*	*0.57*	***0.08***	***0.01***	***0.01***	***0.01***	*0.80*	*0.27*	*0.85*
		E	r	0.00	-0.13	-0.22	0.12	-0.37	0.11	0.62	-0.14	-0.50	0.21	0.65	0.59	0.62	-0.01	-0.01	-0.10	-0.28
			P	*0.99*	*0.63*	*0.42*	*0.65*	*0.15*	*0.69*	***0.01***	*0.61*	*0.05*	*0.43*	***0.01***	***0.02***	***0.01***	*0.97*	*0.97*	*0.72*	*0.30*
		E_2, B	r	-0.19	-0.42	0.16	0.15	-0.40	0.12	0.57	0.29	-0.43	0.13	0.21	0.54	0.42	-0.07	0.04	0.50	-0.41
			P	*0.48*	*0.11*	*0.55*	*0.57*	*0.12*	*0.66*	***0.02***	*0.27*	***0.10***	*0.62*	*0.42*	***0.03***	*0.11*	*0.79*	*0.89*	***0.05***	*0.12*

Figures in bold indicate a significant correlation P ≤ 0.10.
* Organic carbon (C) in soil correlated with N in plant tissues.

Table 4.3. Pearsons correlation coefficients (r, n=16) and levels of significance (*P*) for *Brunia albiflora* performance with element content of leaves and stems, for two sampling dates and three localities in the Western Cape coastal zone.

Sampling Date	Plant Component		N	P	Ca	Mg	K	Na	Al	Fe	Mn	Zn	Cu	B	Mo
Feb	Leaves	r	-0.26	0.17	-0.58	-0.15	0.35	-0.26	0.00	0.11	-0.27	-0.09	0.16	-0.37	-0.40
		P	*0.33*	*0.53*	***0.02***	*0.58*	*0.19*	*0.33*	*1.00*	*0.70*	*0.32*	*0.74*	*0.56*	*0.16*	*0.13*
	Stems	r	-0.40	0.33	-0.13	0.13	0.17	-0.18	0.12	-0.22	-0.25	0.11	0.13	-0.04	-0.27
		P	*0.12*	*0.21*	*0.64*	*0.62*	*0.52*	*0.50*	*0.65*	*0.42*	*0.35*	*0.67*	*0.64*	*0.89*	*0.30*
April	Leaves	r	0.30	0.41	-0.06	0.42	0.09	-0.02	-0.55	-0.52	-0.27	0.12	0.25	-0.26	-0.15
		P	*0.25*	*0.11*	*0.81*	*0.11*	*0.73*	*0.95*	***0.03***	***0.04***	*0.30*	*0.65*	*0.34*	*0.32*	*0.58*
	Stems	r	-0.53	0.25	-0.02	0.36	0.21	-0.03	-0.38	-0.47	-0.27	-0.18	0.42	-0.01	0.04
		P	***0.04***	*0.35*	*0.94*	*0.18*	*0.44*	*0.90*	*0.15*	***0.07***	*0.32*	*0.50*	*0.11*	*0.97*	*0.88*

Figures in bold indicate a significant correlation $P \leq 0.10$.

Table 4.4. Mean concentration of nutrients in leaves of well performing plants of *Brunia albiflora* at three localities in the Western Cape coastal zone at two sampling dates.

	February (anthesis)				April				
Nutrient	L1	L2	L3	Mean Sampling Date	L1	L2	L3	Mean Sampling Date	Significance between Sampling Date
			(%)				(%)		
N	0.62c	0.75b	1.21a	0.86	0.62a	0.72a	0.71a	0.68	ns
P	0.019c	0.022b	0.037a	0.026	337c	369b	430a	0.038	*
K	0.71b	0.82a	0.77a	0.77	0.62b	0.78a	0.74a	0.71	ns
Ca	0.95a	0.86b	0.70c	0.84	1.23a	0.80b	0.60c	0.88	ns
Mg	0.15a	0.11b	0.15a	0.14	0.20a	0.12b	0.15ab	0.16	ns
Na	0.30a	0.11c	0.18b	0.20	0.25a	0.15b	0.08c	0.16	ns
			($mg\ kg^{-1}$)				($mg\ kg^{-1}$)		
Fe	260a	175b	314a	256	112b	114b	185a	137	*
Al	343b	330b	401a	358	182b	188b	271a	214	*
Cu	3.7b	3.3b	4.2a	3.7	26.0a	6.8c	14.1b	15.6	*
Zn	8b	5c	16a	10	11a	8b	13a	11	ns
Mn	240b	26c	330a	199	95b	37c	284a	139	ns
B	40a	25b	24b	30	42a	20b	17c	26	ns
Mo	1.20b	0.88c	3.14a	1.74	0.58a	0.62a	0.63a	0.61	*

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
Numbers followed by the same letters in rows within the same sampling period do not differ significantly at $p>0.05$
ns = non significant at $p>0.05$
* = significant at $p>0.05$

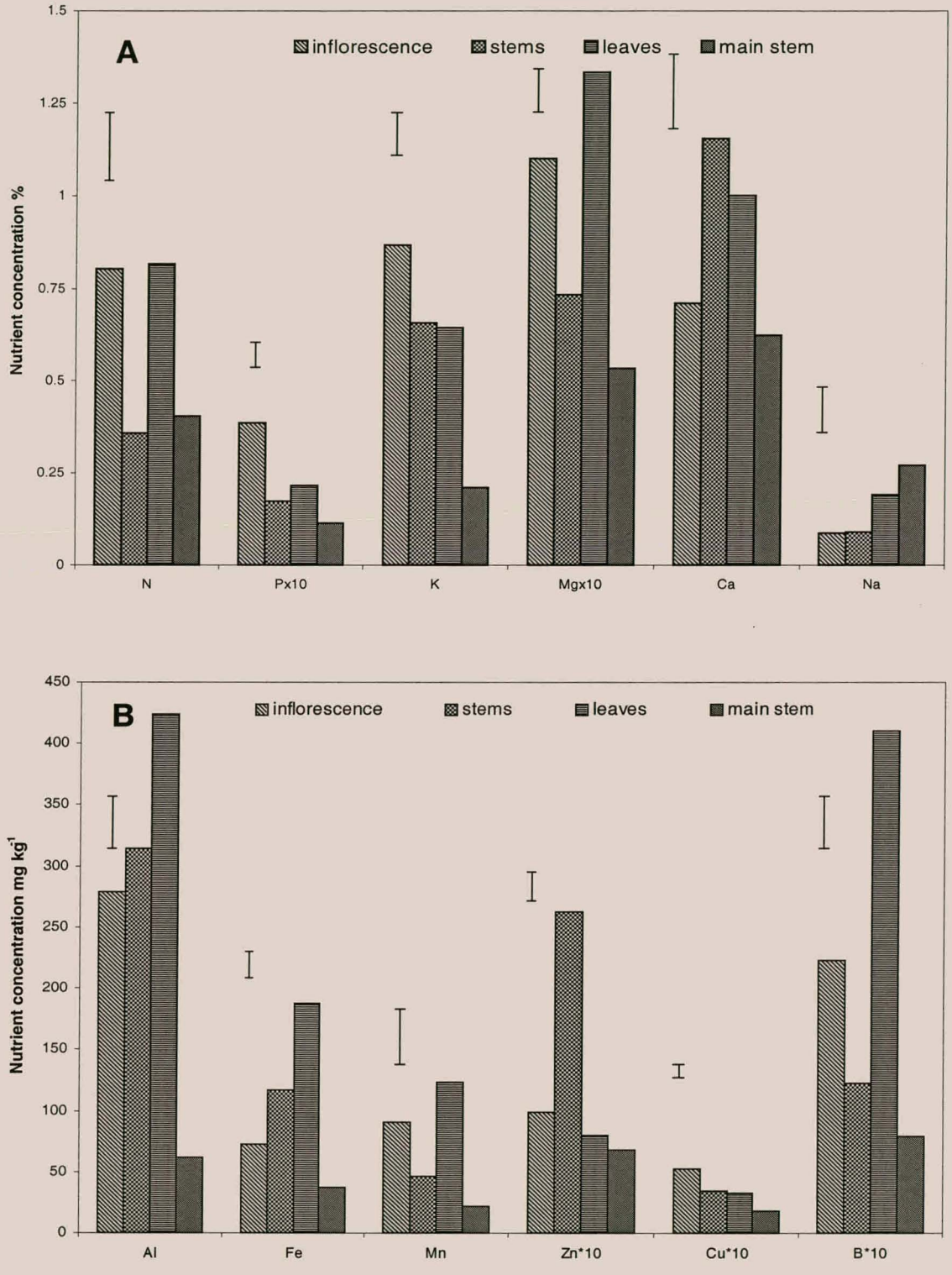


Figure 4.1 A & B. Nutrient content of four components of flowering shoots of *Brunia albiflora* sampled at anthesis (February 1998). Values are an average for three localilties in the Western Cape coastal zone. Vertical bars indicate LSD for p>0.05.

Table 4.5. Mean total nutrient content and removal in flowering shoots of *Brunia albiflora*, Western Cape coastal zone

	Concentration in dry mass				Removal per plant*			
	L1	L2	L3	Mean Locality	L1	L2	L3	Mean Locality
	(%)				(g)			
N	0.58	0.60	0.91	0.70	3.3	5.5	14.1	7.6
P	0.02	0.02	0.04	0.03	0.1	0.2	0.7	0.3
K	0.46	0.67	0.79	0.64	2.6	6.1	12.3	7.0
Ca	0.80	0.97	0.67	0.81	4.5	8.9	10.4	7.9
Mg	0.12	0.10	0.09	0.10	0.7	0.9	1.4	1.0
Na	0.17	0.15	0.14	0.15	1.0	1.3	2.2	1.5
	(mg kg^{-1})				(mg)			
Fe	104	87	120	104	59	80	187	109
Al	279	246	325	283	158	225	504	296
Cu	4	3	5	4	2	2	7	4
Mn	109	32	112	84	62	29	174	88
Zn	8	6	15	10	5	6	23	11
B	25	28	21	25	14	25	32	24
Mo	0.9	1.0	1.0	1.0	0.5	0.9	1.6	1.0
					Dry mass (gram)**			
		Total per stem 40cm			23	36	62	40
		Inflorescence			11	13	26	17
		Side shoots			1	2	3	12
		Leaves			6	12	20	13
		Main stem			4	8	12	8

L1 – Rooi Els
L2 – Kleinmond
L3 – Grabouw
* = 25 flowering shoots per plant
** = large variation in dry mass at three localities due to selection caused by first commercial picking before sampling

APPENDIX A

LOCALITY	Rooi Els , L1, Plot 1
SOIL FORM	Fernwood
CLASSIFICATION	Fw 2110
TERRAIN	Footslope
SLOPE	Straight
ASPECT	West
ALTITUDE	5 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-300	Non-homogenous white sand 2.5 Y 8/1 and black organic matter 10 YR 2/1. Water table at 60mm below surface in winter.
E	300-600	Non-homogenous grey sand 10 YR 6/1 and very dark grey organic matter 10 YR 3/1. Water table at 470mm below surface in summer
E	600-900	Non-homogenous grey sand 10 YR 5/1 and very dark grey organic matter10 YR 3/1, more integrated.

LAB NO DEPTH (MM) HORIZON	1.1.1 0-300 A	1.1.2 300-600 E	1.1.3 600-900 E
Particle size (mm) distribution (%)			
Gravel > 2 mm	0	0	0
Coarse sand 2-0.500 mm	11	13	22
Medium sand 0.5-0.200 mm	55	54	47
Fine sand 0.2-0.020 mm	34	33	31
Silt 0.02-0.002 mm	5	3	2
Clay <0.002 mm	1.0	1.0	1.0
Textural class	sand	sand	sand
Exchangeable cations ($cmol_c\ kg^{-1}$)			
Na	0.85	0.31	0.23
K	0.10	0.04	0.12
Ca	0.22	0.10	0.07
Mg	0.96	0.43	0.24
Sum Cations	2.14	0.88	0.67
Exchangeable acidity pH 7	5.35	3.90	3.50
CEC	7.50	5.44	5.60
Base saturation pH 7 (%)	29	16	12
pH H2O pasta	3.9	4.2	4.9
pH KCl	3.0	3.3	3.9
Resistance (ohm)	356	1020	1930
P citric ($mg.kg^{-1}$)	4.0	3.6	9.7
C (%)	3.5	2.3	1.3
C-pyro (%)	1.65	0.75	1.2
N (%)	0.09	0.07	0.05
C:N	37	34	26
Fe DCB (%)	0.01	0.01	0.01
Fe pyro (%)	0.01	0.00	0.00
Al pyro (%)	0.000	0.010	0.080
Cu ($mg.kg^{-1}$)	0.144	0.072	0.050
Zn ($mg.kg^{-1}$)	0.151	0.087	0.083
Mn ($mg.kg^{-1}$)	0.020	0.009	0.028

LOCALITY	Rooi Els , L1, Plot 2
SOIL FORM	Fernwood
CLASSIFICATION	Fw 2110
TERRAIN	Footslope
SLOPE	Straight
ASPECT	West
ALTITUDE	5 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-300	Non-homogenous colour, light grey 2.5 Y 7/1 and organic material very dark grey 10 YR 3/1. Water table within 30mm of surface in winter
E	300-600	Less organic material visible, grey 10 YR 5/1. Water table within 410mm of surface in winter
E	600-900	Grey 10 YR 5/1

LAB NO	1.2.1	1.2.2	1.2.3
DEPTH (MM)	0-300	300-600	600-900
HORIZON	A	E	E
Particle size (mm) distribution (%)			
Gravel > 2 mm	0	0	0
Coarse sand 2-0.500 mm	21	13	20
Medium sand 0.5-0.200 mm	53	54	52
Fine sand 0.2-0.020 mm	26	33	28
Silt 0.02-0.002 mm	1	6	3
Clay <0.002 mm	1.0	0.6	0.4
Textural class	sand	sand	sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.47	0.17	0.17
K	0.07	0.04	0.04
Ca	0.11	0.12	0.18
Mg	0.74	0.41	0.50
Sum Cations	1.39	0.74	0.89
Exchangeable acidity pH 7	4.50	2.85	1.70
CEC	4.84	2.92	3.49
Base saturation pH 7 (%)	29	25	25
pH H2O pasta	3.9	4.2	4.9
pH KCl	2.9	3.3	3.9
Resistance (ohm)	652	1387	2016
P citric ($mg.kg^{-1}$)	2.5	0.9	1.3
C (%)	2.6	1.4	2.2
C-pyro (%)	0.6	0.5	1.8
N (%)	0.06	0.04	0.04
C:N	46	32	61
Fe DCB (%)	0.01	0.01	0.01
Fe pyro (%)	0.00	0.00	0.00
Al pyro (%)	0.000	0.000	0.002
Cu ($mg.kg^{-1}$)	0.067	0.046	0.076
Zn ($mg.kg^{-1}$)	0.093	0.062	0.109
Mn ($mg.kg^{-1}$)	0.008	0.031	0.169

LOCALITY	Rooi Els , L1, Plot 3
SOIL FORM	Fernwood
CLASSIFICATION	Fw 1110
TERRAIN	Footslope
SLOPE	Straight
ASPECT	West
ALTITUDE	5 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-300	Light grey 10 YR 7/1. Water table within 80mm of surface in winter
E	300-600	Light grey 10 YR 7/1
E	600-900	Light grey 10 YR 7/1. Water table within 800mm of surface in summer

LAB NO	1.3.1	1.3.2	1.3.3
DEPTH (MM)	0-300	300-600	600-900
HORIZON	A	E	E
Particle size (mm) distribution (%)			
Gravel > 2 mm	0	0	0
Coarse sand 2-0.500 mm	9	15	16
Medium sand 0.5-0.200 mm	22	54	55
Fine sand 0.2-0.020 mm	69	31	29
Silt 0.02-0.002 mm	13	4	2
Clay <0.002 mm	0.8	0.4	0.2
Textural class	sand	sand	sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.24	0.09	0.09
K	0.04	0.02	0.01
Ca	0.23	0.08	0.06
Mg	0.44	0.12	0.11
Sum Cations	0.96	0.31	0.28
Exchangeable acidity pH 7	2.70	1.30	0.75
CEC	3.07	3.65	1.15
Base saturation pH 7 (%)	31	8	24
pH H2O pasta	4.2	4.6	4.6
pH KCl	3.1	3.6	3.8
Resistance (ohm)	1503	4180	3417
P citric ($mg.kg^{-1}$)	1.6	6.3	2.9
C (%)	1.7	0.4	0.4
C-pyro (%)	0.3	0.2	0.1
N (%)	0.04	0.02	0.02
C:N	42	20	22
Fe DCB (%)	0.01	0.01	0.01
Fe pyro (%)	0.01	0.00	0.00
Al pyro (%)	0.131	0.129	0.290
Cu ($mg.kg^{-1}$)	0.069	0.078	0.036
Zn ($mg.kg^{-1}$)	0.105	0.054	0.052
Mn ($mg.kg^{-1}$)	0.007	0.000	0.000

LOCALITY	Rooi Els , L1, Plot 4
SOIL FORM	Fernwood
CLASSIFICATION	Fw 1110
TERRAIN	Footslope
SLOPE	Straight
ASPECT	West
ALTITUDE	5 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description		
A	0-300	Light grey 10 YR 7/1 with visible organic material. Water table at 70mm below surface in winter		
E	300-600	Light grey 10 YR 7/1.		
E	600-900	Grey 10 YR 6/1. Water table at 800mm below surface in summer		
LAB NO		1.4.1	1.4.2	1.4.3
DEPTH (MM)		0-300	300-600	600-900
HORIZON		A	E	E
Particle size (mm) distribution (%)				
Gravel	> 2 mm	0	0	0
Coarse sand	2-0.500 mm	14	18	20
Medium sand	0.5-0.200 mm	53	59	58
Fine sand	0.2-0.020 mm	33	23	22
Silt	0.02-0.002 mm	3	3	4
Clay	<0.002 mm	0.7	0.3	0.3
Textural class		sand	sand	sand
Exchangeable cations ($cmol_c.kg^{-1}$)				
Na		0.22	0.05	0.10
K		0.09	0.05	0.03
Ca		0.23	0.06	0.10
Mg		0.35	0.09	0.11
Sum Cations		0.89	0.25	0.33
Exchangeable acidity pH 7		1.65	0.55	0.50
CEC		2.85	0.92	1.05
Base saturation pH 7 (%)		31	27	31
pH H2O pasta		4.2	4.7	4.8
pH KCl		3.5	3.9	4.0
Resistance (ohm)		1159	4459	5562
P citric ($mg.kg^{-1}$)		3.8	1.6	2.0
C (%)		1.2	0.3	0.3
C-pyro (%)		0.6	0.2	0.2
N (%)		0.01	0.05	0.03
C:N		30	30	28
Fe DCB (%)		0.01	0.01	0.01
Fe pyro (%)		0.00	0.00	0.00
Al pyro (%)		0.071	0.045	0.118
Cu ($mg.kg^{-1}$)		0.044	0.078	0.086
Zn ($mg.kg^{-1}$)		0.055	0.065	0.059
Mn ($mg.kg^{-1}$)		0.000	0.000	0.000

APPENDIX B

LOCALITY	Kleinmond, L2, Plot 1
SOIL FORM	Houwhoek
CLASSIFICATION	Hh 2100
TERRAIN	Upper midslope
SLOPE	7% Straight/slightly convex
ASPECT	West facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-100	Grey 2.5Y B 5/1 (moist), fine sand, many fine roots, mainly fine. Abrupt, wavy transition.
E	100-200	Light grey 2.5 Y B 7/1 (moist), pure sand, single grained, many roots, abrupt, wavy transition.
B1	200-600	2.5YR 2.5/2 Ortstein present in horizon (degenerating)
B2	600+	Saprolite 7.5 YR 5/6

LAB NO	2.1.1	2.1.2	2.1.3
DEPTH (MM)	0-100	100-200	200-600
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	3	7	70
Coarse sand 2-0.500 mm	18	21	35
Medium sand 0.5-0.200 mm	21	20	12
Fine sand 0.2-0.020 mm	61	59	41
Silt 0.02-0.002 mm	9	18	5
Clay <0.002 mm	0.9	0.9	3.8
Textural class	loamy sand	loamy sand	loamy sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.13	0.08	0.30
K	0.17	0.03	0.61
Ca	0.17	0.07	0.37
Mg	0.13	0.06	0.44
Sum Cations	0.60	0.25	1.72
Exchangeable acidity pH 7	1.75	0.95	2.90
CEC	3.66	1.32	7.06
Base saturation pH 7 (%)	17	19	24
pH H2O pasta	4.1	4.2	5.1
pH KCl	3.5	4.1	4.8
Resistance (ohm)	1915	3083	
P citric ($mg.kg^{-1}$)	5.2	2.7	13.3
C (%)	0.9	0.3	1.9
C-pyro (%)	0.6	0.2	1.9
N (%)	0.05	0.03	0.07
C:N	21	31	32
Fe DCB (%)	0.03	0.03	0.99
Fe pyro (%)	0.00	0.01	0.35
Al pyro (%)	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.155	0.083	0.058
Zn ($mg.kg^{-1}$)	0.117	0.064	0.040
Mn ($mg.kg^{-1}$)	0.133	0	0.081

LOCALITY	Kleinmond, L2, Plot 2
SOIL FORM	Houwhoek
CLASSIFICATION	Hh 2100
TERRAIN	Midslope
SLOPE	9% Straight
ASPECT	West facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-100	Dark grey 2.5 Y 4/1 (moist), fine sand, many fine roots, mainly fine. Clear transition.
E	100-200	Dark greyish brown 10 YR 4/2
B1	200-600	Dark yellowish brown 10YR3/4 , few fine roots, abrupt transition
B2	600-700	Ortstein (hardness locally degrading) 2.5 YR 2.5/2
B3	700+	Ferruginised sandstone tending to hard plinthite 7.5 YR 5/6

LAB NO	2.2.1	2.2.2	2.2.3	2.2.4
DEPTH (MM)	0-100	100-200	200-600	600-700
HORIZON	A	E	B1	B2
Particle size (mm) distribution (%)				
Gravel > 2 mm	0	4	0	0
Coarse sand 2-0.500 mm	9	16	36	23
Medium sand 0.5-0.200 mm	22	18	13	26
Fine sand 0.2-0.020 mm	68	66	51	51
Silt 0.02-0.002 mm	8	6	4	6
Clay <0.002 mm	2	3	5	6
Textural class	loamy sand	loamy sand	loamy sand	loamy sand
Exchangeable cations ($cmol_c.kg^{-1}$)				
Na	0.09	0.02	0.16	0.10
K	0.23	0.12	0.33	0.12
Ca	0.33	0.20	0.64	0.30
Mg	0.19	0.09	0.41	0.10
Sum Cations	0.84	0.43	1.53	0.61
Exchangeable acidity pH 7	2.40	1.40	3.05	2.00
CEC	3.23	1.60	7.54	1.60
Base saturation pH 7 (%)	26	27	20	38
pH H2O pasta	4.0	5.1	5.4	5.3
pH KCl	3.7	4.6	4.8	5.1
Resistance (ohm)	1128	3054		
P citric ($mg.kg^{-1}$)	10.8	4.3	9.9	4.9
C (%)	1.4	0.6	2.5	1.5
C-pyro (%)	0.6	0.4	2.8	1.5
N (%)	0.05	0.03	0.07	0.04
C:N	29	19	36	59
Fe DCB (%)	0.08	0.15	1.46	1.37
Fe pyro (%)	0.03	0.06	0.43	0.20
Al pyro (%)	0.000	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.103	0.041	0.117	0.068
Zn ($mg.kg^{-1}$)	0.090	0.031	0.050	0.069
Mn ($mg.kg^{-1}$)	0.061	0.000	0.071	0.053

LOCALITY	Kleinmond, L2, Plot 3
SOIL FORM	Concordia with a transition to Lamotte
CLASSIFICATION	Cc 2000/Lt 2100
TERRAIN	Midslope
SLOPE	8% straight
ASPECT	West-facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-150	Very dark grey 7.5 YR 3/1, fine sand, many roots, mainly fine, gradual transition
E	150-250	Dark grey 2.5 YR 4/1, fine sand, gradual transition, many fine roots
B1	250-450	Yellowish brown 10 YR 5/4, fine sand, abrupt transition, few roots
B2	450-700	Ferrihumic nodules, 10 YR 3/3 dark brown, very hard in yellowish brown 10 YR 5/6 (moist) course sand with very many course fragments

LAB NO	2.3.1	2.3.2	2.3.3	2.3.4
DEPTH (MM)	0-150	150-250	250-450	450-700
HORIZON	A	E	B1	B2
Particle size (mm) distribution (%)				
Gravel > 2 mm	0	3	43	60
Coarse sand 2-0.500 mm	15	15	49	2
Medium sand 0.5-0.200 mm	30	16	9	6
Fine sand 0.2-0.020 mm	56	58	42	92
Silt 0.02-0.002 mm	10	18	13	15
Clay <0.002 mm	5	6	6	9
Textural class	loamy sand	sandy loam	loamy sand	sandy loam
Exchangeable cations ($cmol_c.kg^{-1}$)				
Na	0.11	0.10	0.10	0.17
K	0.13	0.11	0.10	0.18
Ca	0.58	0.21	0.21	0.15
Mg	0.48	0.22	0.22	0.23
Sum Cations	1.29	0.64	0.63	0.73
Exchangeable acidity pH 7	2.60	1.35	1.10	1.05
CEC	4.19	2.24	2.05	1.67
Base saturation pH 7 (%)	31	29	31	44
pH H2O pasta	4.8	5.2	5.6	5.6
pH KCl	4.0	4.5	4.9	4.3
Resistance (ohm)	2414	3564	4433	4343
P citric ($mg.kg^{-1}$)	6.7	6.7	1.6	2.0
C (%)	1.5	0.7	0.5	0.3
C-pyro (%)	1.1	0.6	0.1	0.4
N (%)	0.06	0.03	0.03	0.03
C:N	24	23	18	24
Fe DCB (%)	0.17	0.34	0.61	0.18
Fe pyro (%)	0.05	0.11	0.14	0.05
Al pyro (%)	0.223	0.083	0.089	0.127
Cu ($mg.kg^{-1}$)	0.092	0.103	0.075	0.150
Zn ($mg.kg^{-1}$)	0.078	0.055	0.059	0.062
Mn ($mg.kg^{-1}$)	0.07	0.001	0.044	0.000

LOCALITY	Kleinmond, L2, Plot 4
SOIL FORM	Constantia with a transition to Concordia
CLASSIFICATION	Ct 2200/Cc 2000
TERRAIN	Midslope
SLOPE	10% Straight
ASPECT	West-facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-150	Very dark greyish brown 10 YR 3/2 (moist), fine sand, single grain, loose, gradual transition, many roots
E	150-250	Yellowish brown 10 YR 5/4, sandy loam, friable single grain, clear transition, many roots
B	250+	Brownish yellow 10 YR 6/8 with pale white mottles, few roots, loamy sand, many course fragments, gravel rock and stones, friable

LAB NO DEPTH (MM) HORIZON	2.4..1 0-150 A	2.4.2 150-250 E	2.4.3 250-600 B1	2.4.4 600+ B2
Particle size (mm) distribution (%)				
Gravel > 2 mm	0	2	75	80
Coarse sand 2-0.500 mm	9	11	35	3
Medium sand 0.5-0.200 mm	23	18	16	40
Fine sand 0.2-0.020 mm	68	71	49	56
Silt 0.02-0.002 mm	17	7	11	8
Clay <0.002 mm	4	7	9	7
Textural class	sandy loam	loamy sand	loamy sand	loamy sand
Exchangeable cations ($cmol_c.kg^{-1}$)				
Na	0.10	0.07	0.09	0.11
K	0.19	0.14	0.12	0.07
Ca	0.79	0.32	0.30	0.17
Mg	0.43	0.19	0.26	0.26
Sum Cations	1.51	0.73	0.76	0.61
Exchangeable acidity pH 7	2.05	1.15	1.05	0.75
CEC	3.55	2.23	2.26	1.74
Base saturation pH 7 (%)	43	33	34	35
pH H2O pasta	5.5	5.6	5.8	5.5
pH KCl	4.2	4.7	5.0	4.8
Resistance (ohm)	2202	3720	5305	5406
P citric ($mg.kg^{-1}$)	5.6	3.4	4.0	5.6
C (%)	1.2	0.5	0.2	0.3
C-pyro (%)	0.9	0.6	0.7	0.2
N (%)	0.05	0.03	0.02	0.02
C:N	24	13	11	24
Fe DCB (%)	0.28	0.27	0.56	0.42
Fe pyro (%)	0.04	0.09	0.12	0.07
Al pyro (%)	0.109	0.055	0.070	0.177
Cu ($mg.kg^{-1}$)	0.055	0.065	0.064	0.032
Zn ($mg.kg^{-1}$)	0.048	0.073	0.044	0.023
Mn ($mg.kg^{-1}$)	0.071	0.000	0.020	0.000

LOCALITY	Kleinmond, L2, Plot 5
SOIL FORM	Glenrosa
CLASSIFICATION	Gs 2111
TERRAIN	Midslope
SLOPE	9% Straight
ASPECT	West facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-150	Dark brown 7.5 YR 3/2 (moist), fine sand, abrupt, smooth transition, many roots.
B	150-900	Yellowish brown 10 YR 5/6 (moist), sandy loam, course fragments common gravel and stones, abrupt smooth transition
C	900+	Brownish yellow 10 YR 6/8 (moist), weathering sandstone

LAB NO	2.5.1	2.5.2	2.5.3C	2.4.4
DEPTH (MM)	0-150	150-600	600-900	900+
HORIZON	A	B	B2	C
Particle size (mm) distribution (%)				
Gravel > 2 mm	25	37	83	90
Coarse sand 2-0.500 mm	12	12	20	3
Medium sand 0.5-0.200 mm	29	24	32	46
Fine sand 0.2-0.020 mm	59	64	49	51
Silt 0.02-0.002 mm	11	13	11	16
Clay <0.002 mm	8	8	7	7
Textural class	sandy loam	sandy loam	sandy loam	sandy loam
Exchangeable cations ($cmol_c kg^{-1}$)				
Na	0.11	0.08	0.09	0.11
K	0.44	0.22	0.17	0.09
Ca	0.47	0.30	0.26	0.23
Mg	0.26	0.19	0.24	0.32
Sum Cations	1.29	0.79	0.76	0.75
Exchangeable acidity pH 7	2.55	1.35	0.95	0.70
CEC	3.87	2.85	2.25	2.65
Base saturation pH 7 (%)	33	45	34	28
pH H2O pasta	4.9	5.3	5.5	5.6
pH KCl	4.1	4.6	4.7	4.8
Resistance (ohm)	1819	2465	2861	3921
P citric ($mg.kg^{-1}$)	1.8	5.2	2.2	1.3
C (%)	1.5	1.3	0.5	0.4
C-pyro (%)	0.8	0.6	0.5	0.3
N (%)	0.06	0.02	0.02	0.01
C:N	24	66	24	30
Fe DCB (%)	0.34	0.62	0.62	0.70
Fe pyro (%)	0.07	0.12	0.10	0.08
Al pyro (%)	0.101	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.065	0.12	0.063	0.052
Zn ($mg.kg^{-1}$)	0.067	0.048	0.061	0.039
Mn ($mg.kg^{-1}$)	0.089	0.020	0.013	0.000

LOCALITY	Kleinmond, L2, Plot 6
SOIL FORM	Cartref
CLASSIFICATION	Cf 2100
TERRAIN	Midslope
SLOPE	9% Straight
ASPECT	West facing
ALTITUDE	20 m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-150	Dark greyish brown 10 YR 4/2 (moist), fine sand, loose, abrupt transition, many fine roots
E	150-250	Brown 10 YR 4/3
B1	250+	Yellowish brown 10 YR 5/6 (moist), very many course fragments mainly gravel and angular course stones

LAB NO	2.6.1	2.6.2	2.6.3
DEPTH (MM)	0-150	150-250	250+
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	28	20	80
Coarse sand 2-0.500 mm	19	77	7
Medium sand 0.5-0.200 mm	23	6	33
Fine sand 0.2-0.020 mm	58	18	60
Silt 0.02-0.002 mm	16	5	17
Clay <0.002 mm	8	5	12
Textural class	sandy loam	loamy sand	sandy loam
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.15	0.13	0.09
K	0.34	0.16	0.11
Ca	0.80	0.39	0.26
Mg	0.49	0.37	0.40
Sum Cations	1.77	1.06	0.86
Exchangeable acidity pH 7	2.20	0.95	2.45
CEC	4.37	2.35	2.53
Base saturation pH 7 (%)	40	28	34
pH H2O pasta	5.1	5.5	5.6
pH KCl	4.3	4.8	4.7
Resistance (ohm)	1343	2465	2583
P citric ($mg.kg^{-1}$)	0.2	1.6	2.2
C (%)	1.4	1.4	0.4
C-pyro (%)	0.6	0.3	0.3
N (%)	0.06	0.03	0.01
C:N	24	48	38
Fe DCB (%)	0.42	0.74	1.20
Fe pyro (%)	0.08	0.12	0.19
Al pyro (%)	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.074	0.11	0.087
Zn ($mg.kg^{-1}$)	0.057	0.306	0.047
Mn ($mg.kg^{-1}$)	0.052	0.050	0.000

APPENDIX C

LOCALITY	Grabouw, L3, Plot 1
SOIL FORM	Houwhoek
CLASSIFICATION	Hh 1100
TERRAIN	Midslope
SLOPE	11% Straight
ASPECT	West, North-west facing
ALTITUDE	415m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-300	Gray, 10 YR 5/1, medium sand, very few coarse fragments, roots present.
E	300-600	Brown, 10 YR 5/3 (moist), medium sand, many coarse stones present.
B	600+	Light brownish gray, 10 YR 6/2 (moist), with darker tongues, 10 YR 5/4, coarse sand with coarse gravel and angular coarse stones.

LAB NO	3.3.1	3.3.2	3.3.3
DEPTH (MM)	0-300	300-600	600+
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	11	39	39
Coarse sand 2-0.500 mm	40	40	62
Medium sand 0.5-0.200 mm	38	41	26
Fine sand 0.2-0.020 mm	22	19	11
Silt 0.02-0.002 mm	11	11	4
Clay <0.002 mm	1.5	0.9	0.4
Textural class	Loamy sand	Loamy sand	Sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.06	0.02	0.04
K	0.08	0.03	0.08
Ca	0.39	0.03	0.03
Mg	0.27	0.03	0.03
Sum Cations	0.79	0.10	0.17
Exchangeable acidity pH 7	1.65	0.65	0.65
CEC	2.22	1.29	0.96
Base saturation pH 7 (%)	36	8	18
pH H2O pasta	4.9	4.6	4.6
pH KCl	3.7	3.8	3.9
Resistance (ohm)	3168	10900	12970
P citric ($mg.kg^{-1}$)	4.9	1.3	4.9
C (%)	1.0	0.3	0.3
C-pyro (%)	0.5	0.2	0.1
N (%)	0.04	0.01	0.01
C:N	23	31	44
Fe DCB (%)	0.06	0.07	0.06
Fe pyro (%)	0.02	0.02	0.01
Al pyro (%)	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.143	0.127	0.097
Zn ($mg.kg^{-1}$)	0.149	0.072	0.074
Mn ($mg.kg^{-1}$)	12.29	0.435	0.367

LOCALITY	Grabouw, L3, Plot 2
SOIL FORM	Houwhoek
CLASSIFICATION	Hh 1100
TERRAIN	Midslope
SLOPE	11% Straight
ASPECT	West, North-west facing
ALTITUDE	415m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-250	Very dark grey, 7.5 YR 3/1 (moist), medium sand, loose, roots common
E	250-400	Brown, 10 YR 5/3 (moist), few coarse stones, broken transition
B	400-600	Light grey, 10 YR 7/2 (moist) with darker tongues, 10 YR 6/3 associated with root channels, coarse sand with coarse gravel and coarse angular stones, gradual transition

LAB NO	3.4.1	3.4.2	3.4.3
DEPTH (MM)	0-250	250-400	400-600
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	10	39	45
Coarse sand 2-0.500 mm	39	36	55
Medium sand 0.5-0.200 mm	39	41	31
Fine sand 0.2-0.020 mm	22	23	14
Silt 0.02-0.002 mm	9	8	4
Clay <0.002 mm	1.5	1.2	0.2
Textural class	Sand	sand	sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.04	0.00	0.02
K	0.08	0.06	0.01
Ca	0.39	0.10	0.03
Mg	0.24	0.05	0.04
Sum Cations	0.75	0.21	0.11
Exchangeable acidity pH 7	1.55	0.60	0.45
CEC	2.21	1.31	0.81
Base saturation pH 7 (%)	34	16	14
pH H2O pasta	4.6	4.8	4.7
pH KCl	3.7	3.9	4.0
Resistance (ohm)	4809	17530	10560
P citric ($mg.kg^{-1}$)	2.9	2.5	1.1
C (%)	0.9	0.3	0.2
C-pyro (%)	0.2	0.3	0.4
N (%)	0.04	0.01	0.01
C:N	22	30	28
Fe DCB (%)	0.06	0.04	0.06
Fe pyro (%)	0.02	0.02	0.01
Al pyro (%)	0.000	0.000	0.000
Cu ($mg.kg^{-1}$)	0.165	0.064	0.08
Zn ($mg.kg^{-1}$)	0.153	0.045	0.054
Mn ($mg.kg^{-1}$)	9.412	0.791	1.038

LOCALITY	Grabouw, L3, Plot 3
SOIL FORM	Cartref
CLASSIFICATION	Cf 1100
TERRAIN	Midslope
SLOPE	8% Convex
ASPECT	West North-West facing
ALTITUDE	415m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-300	Dark grey 7.5 YR 4/1 (moist), medium grained sand, loose, gradual transition
E	300-600	10 YR 7/2, many coarse fragments mainly angular stones, abrupt tonguing transition
B	600+	Many coarse fragments, angular coarse stones.

LAB NO	3.1.1	3.1.2	3.1.3
DEPTH (MM)	0-300	300-600	600+
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	23	39	60
Coarse sand 2-0.500 mm	41	40	37
Medium sand 0.5-0.200 mm	35	39	43
Fine sand 0.2-0.020 mm	24	21	20
Silt 0.02-0.002 mm	9	14	8
Clay <0.002 mm	1.0	1.0	1.0
Textural class	Loamy sand	loamy sand	sand
Exchangeable cations ($cmol_c\ kg^{-1}$)			
Na	0.04	0.02	0.00
K	0.06	0.02	0.05
Ca	0.32	0.05	0.03
Mg	0.26	0.05	0.02
Sum Cations	0.68	0.14	0.10
Exchangeable acidity pH 7	2.35	0.70	0.50
CEC	3.15	0.81	1.56
Base saturation pH 7 (%)	22	17	6
pH H2O pasta	4.1	4.2	4.5
pH KCl	3.3	3.6	4.0
Resistance (ohm)	5594	12010	16920
P citric ($mg.kg^{-1}$)	11.0	2.0	0.7
C (%)	1.1	0.3	0.3
C-pyro (%)	0.3	0.3	0.1
N (%)	0.04	0.02	0.01
C:N	28	17	26
Fe DCB (%)	0.07	0.05	0.08
Fe pyro (%)	0.02	0.01	0.01
Al pyro (%)	0.000	1.090	0.107
Cu ($mg.kg^{-1}$)	0.097	0.072	0.185
Zn ($mg.kg^{-1}$)	0.148	0.062	0.101
Mn ($mg.kg^{-1}$)	0.598	0.083	0.083

LOCALITY	Grabouw, L3, Plot 4
SOIL FORM	Cartref
CLASSIFICATION	Cf 1100
TERRAIN	Midslope
SLOPE	8% Straight
ASPECT	West, North-West facing
ALTITUDE	415m
PARENT MATERIAL	Sandstone

Horizon	Depth (mm)	Description
A	0-200	Very dark grey, 7.5 YR 3/1 (moist), medium sand with many roots, few coarse fragments of angular gravel.
E	200-400	Light brownish grey, 10 YR 6/2
B	400+	Light yellowish brown, 10 YR 6/4, with many angular coarse gravel and boulders

LAB NO	3.2.1	3.2.2	3.2.3
DEPTH (MM)	0-200	200-400	400+
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	15	12	49
Coarse sand 2-0.500 mm	51	39	39
Medium sand 0.5-0.200 mm	30	38	42
Fine sand 0.2-0.020 mm	19	23	19
Silt 0.02-0.002 mm	7	12	9
Clay <0.002 mm	1.0	0.7	0.8
Textural class	Sand	loamy sand	loamy sand
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.06	0.02	0.01
K	0.07	0.04	0.02
Ca	0.54	0.09	0.02
Mg	0.40	0.09	0.03
Sum Cations	1.06	0.25	0.07
Exchangeable acidity pH 7	2.50	0.90	0.60
CEC	3.65	1.03	0.55
Base saturation pH 7 (%)	29	24	13
pH H2O pasta	4.3	4.4	4.5
pH KCl	3.4	3.5	3.8
Resistance (ohm)	4841	10240	22480
P citric ($mg.kg^{-1}$)	12.1	4.7	3.6
C (%)	1.1	0.4	0.3
C-pyro (%)	0.2	0.4	0.2
N (%)	0.06	0.01	0.01
C:N	19	39	29
Fe DCB (%)	0.08	0.07	0.05
Fe pyro (%)	0.02	0.02	0.01
Al pyro (%)	0.089	1.751	0.967
Cu ($mg.kg^{-1}$)	0.18	0.079	0.2
Zn ($mg.kg^{-1}$)	0.198	0.066	0.116
Mn ($mg.kg^{-1}$)	0.712	0.057	0.057

LOCALITY	Grabouw, L3, Plot 5
SOIL FORM	Klapmuts
CLASSIFICATION	Km 2110
TERRAIN	Lower midslope
SLOPE	8% Straight
ASPECT	West, North-West facing
ALTITUDE	415m
PARENT MATERIAL	Shale

Horizon	Depth (mm)	Description
A	0-200	Dark yellowish brown 10 YR 4/4 (moist), with apedal soil structure, loose consistence in dry and moist state, roots common.
E	200-500	Brownish yellow 10 YR 6/8 (moist), weak angular blocky soil structure, consistence soft when dry and slightly firm when moist, few very fine pores, few coarse gravel, abrupt tonguing transition, few roots.
B1	500+	Brownish yellow 10 YR 6/8 (moist), consistence slightly hard when dry and firm when moist, very sticky and slightly plastic, very few gravel rock fragments of mixed shapes.

LAB NO	3.5.1	3.5.2	3.5.3
DEPTH (MM)	0-200	200-500	500+
HORIZON	A	E	B
Particle size (mm) distribution (%)			
Gravel > 2 mm	9	24	15
Coarse sand 2-0.500 mm	40	40	33
Medium sand 0.5-0.200 mm	35	33	30
Fine sand 0.2-0.020 mm	25	27	36
Silt 0.02-0.002 mm	13	17	26
Clay <0.002 mm	11	19	44
Textural class	sandy loam	sandy clay loam	clay
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.07	0.07	0.08
K	0.18	0.25	0.18
Ca	0.60	0.51	0.20
Mg	0.43	0.64	0.99
Sum Cations	1.28	1.46	1.44
Exchangeable acidity pH 7	2.05	1.65	1.25
CEC	3.35	4.41	2.31
Base saturation pH 7 (%)	38	33	62
pH H2O pasta	5.3	5.6	5.7
pH KCl	4.3	4.5	4.7
Resistance (ohm)	4248	5685	3939
P citric ($mg.kg^{-1}$)	1.8	1.6	0.4
C (%)	1.3	1.1	0.8
C-pyro (%)	0.6	0.5	0.2
N (%)	0.06	0.05	0.05
C:N	21	24	15
Fe DCB (%)	1.15	2.27	4.81
Fe pyro (%)	0.20	0.34	0.23
Al pyro (%)	0.291	0.408	0.109
Cu ($mg.kg^{-1}$)	0.086	0.245	0.082
Zn ($mg.kg^{-1}$)	0.049	0.079	0.046
Mn ($mg.kg^{-1}$)	0.231	0.027	0.061

LOCALITY	Grabouw, L3, Plot 6
SOIL FORM	Klapmuts
CLASSIFICATION	Km 2110
TERRAIN	Lower midslope
SLOPE	8% Straight
ASPECT	West, North-west facing
ALTITUDE	415m
PARENT MATERIAL	Shale

Horizon	Depth (mm)	Description
A	0-150	Brown, 10 YR 4/3 (moist), medium sand, loose, few fine pores, roots common
E	150-350	Dark yellowish brown, 10 YR 4/4 (moist), weak, angular blocky soil structure, soft consistence when dry, friable when moist, few coarse gravel present, abrupt tonguing transition
B1	350-670	Brownish yellow 10 YR 6/6 (moist), fine sand, few red mottles, slightly hard when dry, firm when wet, very sticky and plastic, very few gravel rock fragments Brownish yellow 10 YR 6/8 (moist), high clay content

LAB NO DEPTH (MM) HORIZON	3.6.1 0-150 A	3.6.2 150-350 E	3.6.3 350-670 B
Particle size (mm) distribution (%)			
Gravel > 2 mm	16	51	10
Coarse sand 2-0.500 mm	51	44	27
Medium sand 0.5-0.200 mm	26	29	38
Fine sand 0.2-0.020 mm	23	27	35
Silt 0.02-0.002 mm	13	16	32
Clay <0.002 mm	10.2	11.4	46.9
Textural class	sandy loam	sandy loam	silty clay
Exchangeable cations ($cmol_c.kg^{-1}$)			
Na	0.08	0.05	0.04
K	0.18	0.20	0.12
Ca	0.62	0.31	0.29
Mg	0.49	0.50	0.65
Sum Cations	1.38	1.06	1.10
Exchangeable acidity pH 7	2.10	1.55	2.85
CEC	4.30	2.51	2.38
Base saturation pH 7 (%)	32	42	46
pH H2O pasta	5.3	5.6	5.4
pH KCl	4.3	4.5	3.9
Resistance (ohm)	3918	7409	4499
P citric ($mg.kg^{-1}$)	3.1	3.6	1.8
C (%)	1.4	0.9	0.8
C-pyro (%)	0.3	0.3	0.4
N (%)	0.07	0.04	0.06
C:N	19	20	13
Fe DCB (%)	1.10	1.69	4.17
Fe pyro (%)	0.22	0.36	0.34
Al pyro (%)	0.275	0.399	0.100
Cu ($mg.kg^{-1}$)	0.098	0.116	0.117
Zn ($mg.kg^{-1}$)	0.072	0.066	0.051
Mn ($mg.kg^{-1}$)	0.256	0.054	0.014