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Proteaceous Ornamentals

Banksia, Leucadendron, Leucospermum and Protea

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Photograph on the front cover:

1. Leucospermum ‘Caroline’
2. Protea ‘Pink Ice’
3. Leucadendron ‘Safari Sunset’

By courtesy of
Eric Hunt
www.orchidphotos.org

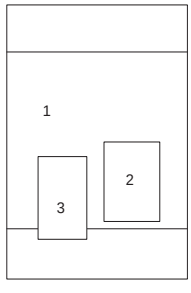

Plate I: Celia Rosser
Banksia Serrata (Saw Banksia) 1972, watercolour and pencil on paper, 55.8 x 76.2 cm
Collection of the artist, Image courtesy of Monash University Museum of Art

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PREFACE

by Richard A. Criley, University of Hawaii

More than 1400 species have been recognized in the ancient Proteaceae family (Rebelo 1995). Their occurrence is mostly distributed between Australia with about 800 species and Africa with about 400 species with the remainder found in South America, the islands east of New Guinea, and a few species in southeast Asia, New Zealand, and Madagascar. They are broadly referred to as proteas, although we identify specific genera by their Latin names. The subfamily Proteoideae, largely found in Africa, has contributed the genera *Protea, Leucadendron,* and *Leucospermum* to floricultural trade, while the Australian Grevilleoideae has contributed *Banksia* and *Grevillea* that have found similar use in floriculture and landscaping. Other genera are still emerging in importance (Criley, 2001). Registration of proteaceous ornamentals by the International Protea Register is web-based: http://www.nda.agric.za/docs/Protea2002/proteaceae_register.htm.

Recognizing the importance of these plants, Dr. Jules Janick, editor of the *Horticultural Reviews* series, enlisted a number of authors to prepare reviews of four genera: Dr. Margaret Sedgley (1998) to cover *Banksia*, Dr. Richard Criley (1998) to cover *Leucospermum*, Drs. J. H. Coetzee and Gail Littlejohn (2001) to cover *Protea* and Drs. Jaacov Ben-Jaacov and Avner Silber (2006) to cover *Leucadendron*. Since the literature about these plants is quite diverse and some is published in less-than-widely-read languages such as Afrikans and Hebrew, these authors have brought to the fore syntheses of the taxonomy, culture, breeding, propagation, nutrition, disease and insect pests, and postharvest practices that would otherwise remain out of the grasp of most readers. Obviously, some of the information on economics and areas of production were out-dated at the time of this re-publication, and additional research has been published.

Although these reviews summarize many sources of literature for these ornamentals, the Protea Working Group of the International Society for Horticultural Science also has generated significant information from seven symposia and one workshop on proteas, with papers published in the *Acta Horticulturae* series.(listed below).Moreover, students of Professor Gerard Jacobs of the University of Stellebosch in South Africa have published theses that have added significantly to our knowledge of physiology and management of the South African *Protea* and *Leucospermum*, while Dr. Sedgley's students at the University of Adelaide have contributed to our knowledge of *Banksia*. Research has been conducted in many of the Mediterranean climates in which proteas survive and thrive, most notably South Africa, Zimbabwe, Israel, New Zealand, Australia, southern California, Hawaii, the Canary Islands, Portugal, and France, but the search for "new" floral crops has lead to evaluations in Chile, Costa Rica, Thailand, and interest in other parts of the world has grown as well.

Through the joint efforts of the International Protea Association and the International Society for Horticultural Science, it has been possible to gather together the reviews on *Banksia, Leucadendron, Leucospermum*, and *Protea* into this volume of *Scripta Horticulturae*. We thank the publishers of *Horticultural Reviews*, John Wiley & Sons, Inc., for permission to bring these valuable sources together into one book. May this volume stimulate additional research and understanding of these fascinating plants!

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Banksia: New Proteaceous Cut Flower Crop*

by: Margaret Sedgley

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I. INTRODUCTION

Banksia species (Plate I) have been cultivated for the international cut flower market for only 20 to 30 years, but there is increasing interest in areas other than the native home, Australia, with production in Israel, South Africa, Hawaii, and California (Ben-Jaacov 1986; Sedgley 1996). Within Australia, *Banksia* is one of the four most widely planted commercial native genera, but production is based on seedling material and between plant variability is high. *Banksia* species for the fresh cut flower market must fulfill strict commercial criteria, which include terminal blooms and long stem length (Fig. 1.1), and further research is needed into all aspects of *Banksia* biology and production. In addition to the fresh cut flower market, *Banksia* stems are traded as dried and dyed blooms, and a wide range of species is used in environmental horticulture, for the attractive inflorescences and foliage, and to attract birds and other wildlife. Although there has been little work conducted so far on the use of banksias as pot plants, recent developments with related genera suggest that such an approach may be productive (Ben-Jaacov et al. 1989). *Banksia* wood and cones are turned or incorporated into ornaments, and the timber of some species has been used for furniture.

Fig. 1.1. Inflorescence of *Banksia* 'Waite crismon', shown together with other flowers.

Other genera from the Proteaceae that are important horticulturally include the Australian *Grevillea, Dryandra, Isopogon, Telopea*, and *Macadamia*, and the South African *Protea, Leucadendron, Leucospermum*, and *Serruria*. Horticultural aspects of *Banksia* production have been reviewed by Sedgley (1996), and recent research reviews on related genera include leaf blackening in cut *Protea* flowers (Jones et al. 1995), while *Leucospermum* will be covered by Criley in this volume. The objective of the present paper is to review research activity that underpins the current development of *Banksia* as a floricultural crop.

II. TAXONOMY

The *Banksia* genus includes 76 taxa, which are currently grouped into two subgenera, three sections, and 13 series (Table 1.1) (George 1981, 1988, 1996, 1997; Maguire et al. 1996). The most widely cultivated species for floriculture belong to the subgenus *Banksia* sections *Banksia* and *Coccinea*, and are characterized by terminal flowering of large showy inflorescences. These include the scarlet Banksia, *B. coccinea*, the pink *B. menziesii* (Fig. 1.2), the green/yellow *B. Baxteri* and *B. speciosa*, and the orange species *B. ashbyi, B. prionotes, B. hookeriana, B. burdettii*, and *B. victoriae. B. ashbyi* is mainly cultivated in Israel, whereas the others are grown in most *Banksia* production areas. Others cultivated to a lesser extent for cut flowers or foliage include the yellow-flowered species *B. grandis, B. sceptrum*, and *B. integrifolia*, the brown *B. solandri* and *B. brownii*, and the orange *B. ericifolia*. Many other species of *Banksia* produce axillary blooms that are obscured by foliage and have short stems, but some terminal flowering forms of otherwise axillary-bearing species, such as the red *B. occidentalis*, have recently been identified and used for cut flower production.

The most important commercial species is *B. coccinea*, and this is also the most problematic taxonomically. It has a number of unique features, and no obvious close relatives in the genus. A recent cladistic analysis of the genus failed to clarify its status (Thiele and Ladiges 1996), and it is hoped that molecular systematics will provide the answer (Maguire et al. 1997d; Mast 1997). It is important to know the taxonomic affinities of the major commercial species, so that attempts at interspecific hybridization can be directed toward the most closely related and hence productive crosses.

Table 1.1. Systematic sequence in *Banksia* (after George 1997).

Subgenus *Banksia*
- Section *Banksia*
  - Series *Salicinae: B. dentata L.f., B. aquilonia* A.S. George, **B. integrifolia L.f., B. plagiocarpo* A.S. George, B. *oblongifolia* Cav., *B. robur* Cavanilles, *B. conferta* A.S. George, **B. paludosa* R.Br., **B. marginata* Cav., *B. canei* J.H. Willis, *B. saxicola* A.S. George.
  - Series *Grandes: *B. grandis* Willd., B. *solandri* R.Br.
  - Series Banksia: *B. serrata L.f., B. aemula* R.Br., *B. ornata F.* Muell. ex Meissn.,**B. bmrteri* R.Br., **B. speciosa* R.Br., **B.* menziesii R.Br., **B. candolleana* Meissn., *B. sceptrum* Meissn.
  - Series *Crocinae: *B. prionotes* Lindley, **B. burdettii* E.G. Baker, **B. hookeriana* Meissn., *B. victoriae* Meissn.
  - Series *Prostratae: B. goodii* R.Br., **B. gardneri* A.S. George, *B. chamaephyton* A,S. George, **B. blechnifolia F.* Muell., **B.* repens Labill., **B. petiolaris F.* Muell.
  - Series *Cyrtostylis: *B. media* R.Br., **B. pmemorsa* Andrews, *B. epica* A.S. George, *B. pilostylis C.* Gardner, **B. attenuata* R.Br., **B. ashbyi* E.G. Baker, *B. benthamiana C.* Gardner, *B.* audax C. Gardner, *B. lullfitzii C.* Gardner, **B. elderiana F.* Muell & Tate, **B. laevigata* Meissn., *B. elegans* Meissn., *B. lindleyana* Meissn.
  - Series *Tetragonae: *B.* lemanniana Meissn., *B. caleyi* R.Br., *B. aculeata* A.S. George.
  - Series *Bauerinae: *B. baueri* R.Br.
  - Series *Quercinae: *B. quercifolia* R.Br., B. *oreophila* A.S. George.
- Section *Coccinea: *B. coccinea* R.Br.
- Section *Oncostylis*
  - Series *Spicigerae: B. spinulosa* A.S. George, **B. ericifolia L.f., B. verticillata* R.Br., *B. seminuda* (A.S. George) B. Rye, *B. littoralis* R.Br., **B. occidentalis* R.Br., **B. brownii* Baxter ex R.Br.
  - Series *Tricuspidae: *B.* tricuspis Meissn.
  - Series *Dryandroideae: B. dryandoides* Baxter ex Sweet.

Series *Abietinae: *B. sphaerocarpa* R.Br., **B.* micrantha A.S. George, *B. grossa* A.S.George, **B. telmatiaea* A.S. George, *B. leptophylla* A.S. George, *B.* lanata A.S. George, *B. scabrella* A.S. George, *B. violacea C.* Gardner, *B. incana* A.S. George, **B. laricina C.* Gardner, **B. pulchella* R.Br., *B. meisneri* Lehmann, **B. nutans* R.Br.
Subgenus *Isostylis: B. ilicifolia* R.Br., *B. oligantha* A.S. George, *B. cuneata A.S. George.

*Species tested for interspecific compatibility.

Fig. 1.2. Inflorescence and foliage of *Banksia menziesii*.

III. BREEDING SYSTEMS

A. Reproductive Structure

Banksia species range from prostrate forms to trees, and all are evergreen woody perennials (Fig. 1.3), some of which regenerate from lignotubers following fire. Many flowers are crowded into showy inflorescences, which are followed by infructescences, often called cones, in which relatively few seeds develop in large woody follicles. The most common flower colors are yellow, orange, green, brown, and red. *Banksia violacea* produces purple flowers, and although the blooms are too small and obscured by foliage to be used in floriculture, it may provide a useful character for plant breeding. Foliage may be fine and needle-like or coarsely serrated. *Banksia* floral structure conforms to the typical proteaceous pattern of large numbers of individual flowers grouped together to form conspicuous inflorescences (Fig. 1.2). In *B. coccinea* and *B. menziesii,* the flowers are produced spirally on the inflorescence, with 13 separate genetic spirals initiating simultaneously (Fuss and Sedgley 1990). The flowers develop in pairs, with each flower subtended by a floral bract and the pair of florets and their floral bracts subtended by a common bract. These bracts are inconspicuous, and the floral display is provided by the colored perianths and styles.

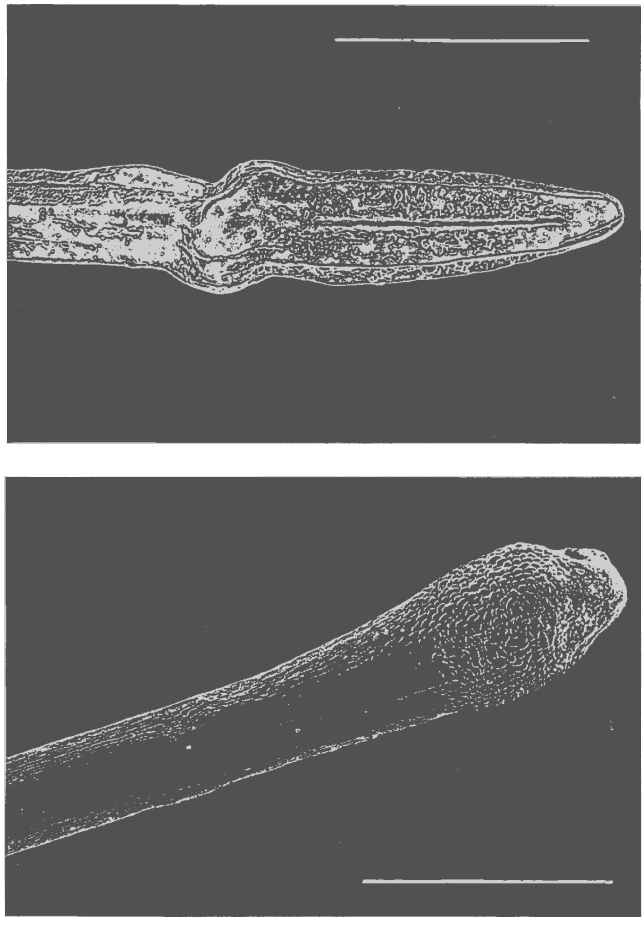
Fig. 1.3. Tree of *Banksia baxteri.*

Each *Banksia* flower has four tepals, with a single bilobed anther attached by a short filament to the distal region of the perianth. The pistil consists of an ovary with two ovules, and a long style with a small pollen-receptive stigmatic area in the apical region. In some species, the style elongates more quickly than the perianth during floral development, and arches beyond the corolla tube by protruding between two perianth members. An unusual feature of the genus is that the *Banksia* floral display is contributed entirely by the perianth and the style. In *B. coccinea,* for example, the inflorescence is gray prior to anthesis from the gray color of the perianths, and red following anthesis from the red color of the styles.

The distal portion of the *Banksia* style is specialised for pollen presentation, and its structure varies between species (Fig. 1.4) (Sedgley et a1.1993). The receptive stigmatic cells are located in a groove toward the tip of the pollen presenter, which in most species is located longitudinally and obliquely terminal, although in a few it is transverse or lateral. In*B. menziesii,* the pollen presenter has a complex internal structure, as observed by light microscopy, with the transmitting tissue enclosed by transfer cells, which may serve to maximize water and nutrient supply to the growing pollen tubes (Clifford and Sedgley 1993). The transfer cells are not present in the rest of the style, and the number of transmitting tissue cells declines over the approximately 2 cm length of the style, with only 11 cells present at the junction with the ovary. The *Banksia* style is a robust wiry structure with lignified sclerenchyma tissue located in the outer cortex. After flowering, the inflorescence develops into a woody infructescence, and successfully fertilised ovaries develop into follicles, each with one or two seeds. In most species the infructescence does not increase in size after flowering, and the mature follicles are much larger than the ovaries at anthesis, resulting in spatial limitations to fertility (Fuss and Sedgley 1991a,b). An exception is *B. grandis* in which the axis, common bracts, and floral bracts enlarge around the follicles and become lignified, such that the mature infructescence can be used for cutting and turning into craft objects. Most species do not release their seeds until after fire (Zammit and Westoby 1987).

B. Breeding Biology

As in many other proteaceous genera, the flower of *Banksia* exhibits protandry, with the anthers dehiscing prior to flower opening to deposit their pollen on the pollen presenter (Sedgley and Fuss 1995). This generally occurs about one day before the flower opens, and following anthesis the pollen is collected by foraging fauna. At this stage the stigma papilla cells are not receptive to pollen, and peak stigma receptivity is attained three days after flower opening. This has been determined by increase in the width of the stigmatic groove and by increase in pollen germination on the stigma in *B. menziesii* (Fuss and Sedgley 1991a), and in *B. coccinea* by increase in stigmatic secretion (Fuss and Sedgley 1991b). In the natural habitat all of the flower's own pollen has been removed by insect, bird, or mammal pollinators by the time the stigma is receptive, and the flower may be cross pollinated by a foraging animal that has visited another plant.



(a)

(b)

Fig. 1.4. Pollen presenter *of (a) Banksia serrata* and *(b) Banksia grandis.* Bar represents 1 mm.

Outcrossing is a feature of the genus (Carthew et al. 1988; Sedgley 1995d; Goldingay and Carthew 1997), and most species of *Banksia* that have been studied produce less seed following self pollination than following cross pollination. The self

incompatibility is only partial, however, as controlled hand pollination of *B. menziesii* resulted in 80% infructescence set following crossing compared with 33% following selfing, and 6 follicles per crossed inflorescence compared with 1.3 after selfing (Fuss and Sedgley 1991c). In *B. coccinea* all pollinated inflorescences set some seed, but the crossed infructescences had 40.7 seeds compared with 27.9 after selfing (Fuss and Sedgley 1991b,c). Further information was obtained from a 5 by 5 diallel experiment, with the results measured by pollen tube growth, observed using fluorescence microscopy (Fuss and Sedgley 1991b). Pollen tubes had reached the base of the style by six days after pollination, but self pollination generally resulted in poorer tube growth. Statistical analysis showed that some plants were more successful parents than others, that some genotype combinations were better than others, and that some crosses were more fertile when conducted in one direction than in the other. These results indicate that *Banksia* has a mixed mating system with complex genetic interactions. Most species are characterised by relatively low seed yields (Ayre and Whelan 1989), and this has been attributed to a wide range of possible causes, including breeding system constraints, pollinator limitation, insect and bird predation, and poor nutrition.

C. Genetic Variability

Outcrossing plants generally show high levels of morphological variability, and this is true of the *Banksia* genus. For example, there are four distinct geographically isolated forms of *B. canei* reported (Salkin and Hallam 1978). More subtle variation is found in most species, including variability in yield, bloom quality and color, time of flowering, and disease tolerance (Fuss and Sedgley 1991a; Sedgley 1995c,d).

In addition to morphological characters, biochemical methods are increasingly used to measure genetic variation. Isozyme analysis has demonstrated high levels of genetic diversity in *B. attenuata, B. menziesii* (Scott 1980), and *B. cuneata* (Coates and Sokolowski 1992), and this has been confirmed in the latter species using RAPD-PCR analysis (Maguire and Sedgley 1997c). A further application of RAPD-PCR is to compare plants in wild populations with those in cultivation. This approach has demonstrated that for *B. coccinea,* variability is lower between cultivated than between natural populations, indicating that the cultivated populations studied are closely related to each other and suggesting that the germplasm in cultivation may not represent the full variability available in the wild (M. A. Rieger and M. Sedgley unpublished). This is not the case for *B. menziesii,* which appears to be well-represented in cultivation. Using RAPD-PCR, it is also possible to identify which natural and cultivated populations are the most closely related, so that wild populations that are already represented in cultivation do not need to be sampled further.

IV. PLANT IMPROVEMENT

Variability is a disadvantage to the grower because it leads to inconsistency in product, but it means that there is ample scope for selection and breeding of new improved cultivars. For *Banksia* the method of preserving desirable characteristics is single plant selection followed by vegetative propagation. The population subjected to selection may be wild populations in the native habitat, open pollinated populations under cultivation, or cultivated populations derived from controlled pollination.

A. Controlled Pollination

Research into the *Banksia* breeding system has been used to develop controlled hand pollination methods (Fuss and Sedgley 1991c). Inflorescences of the seed parent are covered with a bag to exclude pollinating fauna, after the removal of all open flowers. One day later, the bag is opened, pollen is removed from all newly-opened flowers

using a looped synthetic pipe-cleaner, all unopened flowers are removed, and the bag is replaced. Three days later, at peak receptivity of the stigma, pollen is transferred to the stigma, using the pollen-laden pollen presenter from the pollen parent as a paint brush to insert the pollen into the stigmatic groove. The bag is replaced for a few days, to prevent any further pollen transfer, after which it is removed during the remainder of the seed development period, which varies with species from five to sixteen months (Sedgley et al. 1994). Seed set following controlled hand pollination is around 3.5% (Sedgley et al. 1996), and mature seed are collected and germinated for subsequent selection.

Pollen storage and viability testing are important adjuncts to a breeding program. *B. menziesii* pollen was stored at 20, 4, -20, -80, and -196°C, and assessed using a semi-solid medium of 1% agar, 15% sucrose, 0.01% boric acid, 0.03% calcium nitrate, 0.02% magnesium sulphate, 0.01% potassium nitrate, with an incubation temperature of 25°C (Maguire and Sedgley 1997a). Germination after six months remained constant at around 70% in all treatments, except 20°C storage, which gave only 25% germination. Pollen viability was assessed using fluorescein diacetate, but the results did not reflect the loss of germinability at 20°C and correlation with *in vitro* results were variable. There was no effect of floret position on the inflorescence on germination, but pollen viability varied over the flowering period with maximum germination mid-season.

B. Selection

Strict criteria based upon commercial requirements must be applied to the population under selection (Sedgley 1995c,d). These include size, number, quality and color of blooms, stem length, time of flowering, length of the flowering period, vase life, disease tolerance, and ease of vegetative propagation. Quality is a very complex set of characteristics, comprising stem length and straightness, with minimal leaf damage and abnormal florets (Fuss and Sedgley 1991a). Adequate testing of superior selections is required, as some characters, such as bloom color, may alter during the flowering season (Bickford and Sedgley 1994, 1995). In the red, pink, apricot, yellow, and bronze variants of *B. menziesii*, the overall inflorescence color derives from the combination of style and perianth, which may comprise different hues. Where anthocyanin pigments are responsible for the color, intensity may vary with temperature and thus with season and location. Selection for color stable variants is an important aim of *B. menziesii* improvement.

RAPD-PCR can be used to generate fingerprints specific for each new cultivar of *Banksia*, to aid in identification and registration (Maguire et al. 1994; Sedgley 1995a,b). There is also potential to use the method in marker-aided selection, to accelerate progress, as plants do not need to be grown to maturity from seed before they can be assessed horticulturally.

C. Interspecific Compatibility

For most horticultural crops, significant gains in productivity, quality, and novelty have resulted from chance or deliberate interspecific hybridization, and research on *Banksia* has addressed this aspect of reproductive biology. Experimentation has focused on the commercial cut flower species, with interspecific sexual compatibility investigated in *B. prionotes, B. hookeriana, B. menziesii,* and *B. coccinea* (Tables 1.1, 1.2). Some species supported no germination of interspecific pollen, some supported normal pollen tube growth, and others produced pollen tube abnormalities, including thickened walls, bulbous swellings, directionless growth, burst tips, and branched tubes (Sedgley et al. 1994, 1996; Maguire and Sedgley 1997b). Control of pollen tube growth in the pistil was imposed in the pollen presenter and upper style. A number of species combinations showed pollen tube growth to the base of the style, but only the *B. hookeriana* by *B. prionotes* cross has so far resulted in seed set (Table 1.2). Given that

intraspecific seed set of *Banksia* is very low, in the order of 3.5% (Sedgley et al. 1996), it is important to repeat the crosses that showed pollen tube growth to the base of the style, with higher numbers of pollinations.

Table 1.2. Banksia interspecific combinations with pollen tube growth to the base of the style or with viable seed set (Sedgley et al. 1994, 1996; Maguire and Sedgley 1997b).

Female parent	Male parent	Pollen tube growth	Viable seed set
B. menziesii	*B. baxteri*	Yes	No
	B. speciosa	Yes	No
	B. candolleana	Yes	No
	B. prionotes	Yes	No
	B. burdettii	Yes	No
	B. tricuspis	Yes	No
B. prionotes	*B. baxteri*	Yes	No
	B. speciosa	Yes	No
	B. elderiana	Yes	No
	B. coccinea	Yes	No
	B. brownii	Yes	No
	B. tricuspis	Yes	No
B. hookeriana	*B. prionotes*	Yes	Yes
B. coccinea	*B. ericifolia*	Yes	No
	B. micrantha	Yes	No
	B. sphaerocarpa	Yes	No

Natural interspecific hybrids have occurred, both in the wild and under cultivation (Taylor and Hopper 1988), including crosses between *B. hookeriana* and *B. prionotes*. One such putative hybrid with horticultural merit, registered as the cultivar 'Waite Orange' (Sedgley 1991), was studied using morphological, sexual, and biochemical characters (Sedgley et al. 1994, 1996). Hybrid status of 'Waite Orange' was confirmed using morphological characters, and controlled pollination showed that the hybrid was fertile following controlled selfing and backcrossing to both parental species, as well as following open pollination, but that seed set was lower than for the parental species. In addition, interspecific hybridization between *B. hookeriana* and *B. prionotes* was investigated via pollen tube growth, seed set, and morphological measurements. Pollen tube growth to the ovary was observed following self and cross intraspecific pollination of both species and following interspecific hybridization to *B. hookeriana* as the seed parent, but not in the reciprocal cross. All crosses resulted in seed set, except for self pollination of *B. prionotes* and interspecific pollination to *B. prionotes* as the seed parent. Mortality of hybrid seedlings was high. RAPD analysis of hybrid seedlings from two families showed the presence of paternal *B. prionotes* bands in all 11 seedlings tested. Leaf length or width of nine hybrid seedlings that survived to the ten leaf stage was intermediate between that of intraspecific seedlings of both parents at the same age. It was concluded that hybridization between *B. hookeriana* and *B. prionotes* is unilateral, with interspecific seed set of *B. hookeriana* comparable to that following intraspecific pollination. Isozyme and AP-PCR analysis confirmed that the two parent species were closely related.

D. Cultivars

Banksia species are relatively new to the cut flower industry, and there has been little emphasis placed on cultivar development. There are seven named cultivars of *Banksia* for amenity use, but only three for cut flower production, and all are propagated vegetatively to perpetuate their superior varietal characteristics. The ten named cultivars were derived from open pollinated populations under cultivation, and none so far has resulted from controlled hybridization.

Of the seven cultivars for environmental horticulture, three are prostrate forms. 'Celia Rosser' is derived from an open-pollinated seedling of B. canei. It has deeply lobed leaves, a prostrate growth habit, and yellow inflorescences. 'Austraflora Pygmy Possum' is a coastal low-growing form of *B. serrata*, and 'Roller Coaster' is a prostrate variant of *B. integrifolia*. The other four cultivars have the more usual upright habit of *Banksia* species. 'Limelight' is a sport of *B. ericifolia* with lime green foliage, 'Giant Candles' is an interspecific hybrid between *B. ericifolia* and *B. spinulosa* var. *spinulosa* that arose in cultivation, 'Lemon Glow' is a yellow-flowered form of *B. spinulosa* var. *cunninghamii*, and 'Birthday Candles' is a dwarf form of *B. spinulosa* var. *spinulosa*. All of these varieties are for garden use, with 'Birthday Candles' for pot and garden cultivation.

There are three terminal-flowering cultivars for cut flower production. 'Waite Orange' (Fig. 1.1) is a natural interspecific hybrid between *B. hookeriana* and *B. prionotes*, that flowers between the peak period of the two parental species and so extends the season for production of orange *Banksia* blooms (Sedgley 1991, 1995c,d). 'Waite Crimson' is a mid-season dark red selection of *B. coccinea* (Sedgley 1995a), and 'Waite Flame' is an early season orange-red selection, also of *B. coccinea* (Sedgley 1995b).

V. PHYSIOLOGY

A. Flowering

Floral intitation of the species *B. coccinea, B. menziesii, B. hookeriana,* and *B. baxteri* occurs between October and December, the southern hemisphere late spring and early summer (Fuss et al. 1992; Rohl et al. 1994). Although floral initiation occurs at roughly the same time of year in all four species, flowering does not, and the main difference between them is in the rate of development of the initiated inflorescences. This is very important commercially, as it means that pruning must be carried out prior to October, even in the late-flowering species such as *B. coccinea*, or the grower risks removing initiated blooms for the next year's harvest (Sedgley and Fuss 1992). Only the thickest shoots will initiate an inflorescence, and the likelihood of a shoot producing a bloom is correlated with shoot age and shoot size. The age of a shoot is determined from the number of bud scar rings, with two-year-old shoots having a ring of bud scale scars at the base, and another ring half way along the shoot. Most blooms are produced on shoots that are two years old, with only a minority produced on one- or three-year-old shoots. Thus, each shoot must be allowed to develop for two years before a bloom can be expected, and some shoots never produce blooms. These are thin and weak compared with those that do, and there is a minimum shoot diameter, measured at the bud scar ring at the base of the current flush growth, which must be achieved for a shoot to flower. The critical diameter is 4.5 mm for *B. coccinea,* 6 mm for *B. menziesii,* 8 mm for *B. hookeriana,* and 11 mm for *B. baxteri,* and the information has been used to develop a pruning strategy for *Banksia* (Sedgley and Fuss 1992). High light intensity is also important for successful flowering of *Banksia,* with pruning to prevent shading an important consideration.

Floral initiation in the southern hemisphere late spring or early summer indicates that the environmental cues of increasing temperature and daylength may be important. This has been confirmed by experiments in which plants of *B. coccinea* and *B.*

hookeriana were grown in environmental growth chambers, with full control of temperature and daylength (Rieger and Sedgley 1996). Four sets of conditions were imposed, with 8 and 16 h daylength, each with two temperature regimes of 15/10°C (day/night) and 25/20°C. For *B. coccinea,* most floral initiation occurred at 16 h 25/20°C and 16 h 15/10°C, with less initiation at 8 h 15/10°C and none at 8 h 25/20°C. This indicates that long daylength may be the environmental trigger for flowering in this species. For *B. hookeriana,* both the 16 and 8 h 25/20°C treatments stimulated flowering, with no floral initiation at 15/10°C with either 16 or 8 h daylength. This indicates that for *B. hookeriana* temperature has the major control over floral initiation.

Manipulation of *Banksia* flowering, to induce early or late flowering or to extend the production season, is not currently practised, but these research results introduce the possibility for extension of the flowering period of *B. coccinea.* By using supplementary lights to increase the natural daylength during winter, it may be possible to induce the plants to initiate earlier, and so possibly to flower earlier. Extension of the flowering period by inducing late initiation is more of a problem, as the plants would need short days at a time when natural daylength is increasing. While this is difficult in the field, it may be possible under protection. Manipulation of temperature, as required for *B. hookeriana,* could also be achieved under cover.

The *Banksia* bloom is an inflorescence comprising many hundreds of individual flowers; if initiation is incomplete, it can result in uneven or truncated blooms. Low temperature effects appear to be particularly common, correlating with abnormal blooms of *B. coccinea* (Fuss and Sedgley 1991a) and *B. menziesii* (Fuss et al. 1992). Careful site selection and provision of windbreaks or shelter are the most effective means of controlling the problem.

B. Propagation

Banksia seeds are encased by woody follicles in cone-like infructescences. The follicles of most species are adapted to open only after fire (Elliot and Jones 1992), although there are exceptions to this rule, including *B. marginata* and *B. integrifolia* (Wardrop 1983). Heat generated during a wildfire melts adhesive material sealing the follicle, and the effect can be simulated in a fire or oven. A period of rain after the wildfire is important in some species, and this can be simulated by submerging the infructescences in cold water for between one and three days, followed by sun drying (Elliot and Jones 1992). In contrast to some other genera of Proteaceae, the seeds of *Banksia* species require no germination pre-treatment. They are generally large and rich in nutrients (Pate et al. 1986), and so tend to have high germination success rates. The temperature optimum for germination varies with species, from 18-23°C for *B. integrifolia* to 28-32°C for *B, aemula* (Heslehurst 1979), with 10-25°C the best range for *B. coccinea* (Bennell and Barth 1986a). For germination of *B. coccinea, B. aculeata,* and *B. ornata,* l5°C is the optimum temperature, with 70% germination of *B. aculeata* seed at 25°C as compared with 100% at *15°C.* Germination rate is slow, with first emergence after about three weeks, but taking up to three months for complete germination. Following germination, seedling growth is fastest at 25°C.

Propagation of *Banksia* species by rooted cuttings is variable (Bennell and Barth 1986a), and is based on semi-hardwood material collected following the spring growth flush, during the cooler months of the year. Some species will produce roots with no auxin treatment (George 1984), although better results are achieved with 3,500 ppm indolebutyric acid (IBA) for most species. The highest strike rates for *B. coccinea* were achieved with 8,000 to 12,000 ppm IBA (Bennell and Barth 1986a), and although some cuttings produced roots at all concentrations tested, root development was better with IBA than without. Genotype also influences rooting, with variation from 0 to 80% success for different individuals of *B. hookeriana* and *B. prionotes* (Sedgley 1995c,d).

Success with micropropagation has resulted in culture establishment of *B. coccinea, B. ericifolia, B. lemanniana, B. marginata, B. menziesii, B. ornata, B. prionotes, B. serrata,*

and *B. spinulosa* var. *collina* from nodal segments and shoot tips (K. M. Tynan, E. S. Scott, and M. Sedgley unpublished). Murashige and Skoog medium with benzyladenine resulted in slow growth and multiplication rates, with shoot formation on cultures of *B. coccinea* and *B. spinu]osa* var. *collina.* Roots were induced on excised shoots of *B. coccinea* using filter paper bridges over liquid medium, but there has been little success so far in hardening off rooted explants.

There has been little consistent success with grafting and budding of *Banksia* species. Rootstocks used for experimentation are generally seedlings of *B. integrifolia, B. spinulosa,* and *B. marginata* that are tolerant of heavy soils and of the root rot fungus *Phytophthora cinnamomi* Rands (McCredie et al. 1985a). Bennell and Barth (1986b) used a wedge graft for field-grown scions of *B. coccinea* and *B. menziesii,* which had been girdled four weeks prior to grafting. The overall success rate for both species was between 30 and 40% at 20 weeks, but a further complication is that grafts may survive for a number of years, with the union failing under conditions of stress (Elliot and Jones 1992). At present the success rate does not justify commercial use of grafting for *Banksia,* and further research is needed into graft compatibility.

C. Water and Nutrient Uptake

Most species of *Banksia* are native to the Mediterranean climate areas of south-western Australia, with some from south-eastern Australia and one tropical species that extends into New Guinea and the Aru Islands (George 1987). All species grow best in light sandy soils of acid pH, and the south-western Australian species are particularly intolerant of heavy soils. Most are adapted to a hot, arid summer prone to bushfires, and have developed strategies to cope with these conditions (Cowling and Lamont 1986). They are adapted to poor soils of low nutritional status, particularly phosphorus, and develop proteoid roots for increased nutrient absorption (Lamont 1986; Low and Lamont 1986). Proteoid roots are specialisations for solubilization of soil phosphates (Grierson and Attiwill, 1989*),* and to increase the root surface area for absorption. In the native habitat they are major exporters to other parts of the plant of phosphate, potassium, and amino acids during the wet winter season (Jeschke and Pate 1995).

The *Banksia* root system is dimorphic, with proteoid root-bearing shallow lateral roots in the top 15 cm, and a single tap or sinker root extending down to 7 m, or to the water table if located higher than this depth (Low and Lamont 1990; Dodd and Bell 1993; Pate et al. 1995). Proteoid roots die during the arid summer, and regenerate during the wet winter of the native habitat, while shoot growth patterns are the reverse, with extension during summer. The amount of water required by *Banksia* plants of different ages has not been determined, but water stress can be a limitation to seedling establishment in the wild (Burgman and Lamont 1992; Enright and Lamont 1992). Investigation of xylem and phloem sap of *B. prionotes* indicates that lateral root xylem sap is more concentrated in virtually all solutes than that of sinker roots, even during the dry summer following senescence of the proteoid roots (Jeschke and Pate 1995). Gradients in xylem sap concentration suggest lateral abstraction and storage of incoming phosphate in basal stem parts during winter with subsequent release to the xylem in summer for the growing period. Phloem sap is more concentrated than xylem sap in nutrient ions and amino acids.

Under cultivation, phosphorus toxicity can be a problem for *Banksia* species, with symptoms reported in cut flower plantings with soil levels of greater than 40 ppm. In a detailed study, interactive effects between phosphorus and iron have been reported in *B. ericifolia* subsp. *ericifolia* grown in soilless potting medium (Handreck 1991). As the phosphorus level was increased, iron deficiency symptoms increased, indicating preferential translocation of phosphorus over iron. The ideal ratio of phosphorus to iron in the medium was around 20, in media containing less than 3 mg/L phosphorus and 1.5 g/L iron. An important feature of *Banksia* biology is that high levels of nutrients are concentrated in the seeds to give seedlings an advantage in the poor native soils of

Australia (Groves et al. 1986; Pate et al. 1986).

D. Postharvest Physiology

Relatively little research has been conducted on preservative or pulsing solutions for fresh *Banksia* cut blooms, but sucrose pulsing generally does not enhance quality or longevity, and concentrations above 2% are detrimental. Work with *B. coccinea* found no effect of sucrose pulsing, with blooms having a vase life of 15 days in water plus 0.01% chlorine (Delaporte et al. 1997). Hydroxy quinoline sulphate is detrimental, as it causes reduction in vase life and accelerated opening of the florets. Cold dry storage is possible at 2°C and 100% relative humidity in darkness for 14 days, after which there is a 10-day vase life.

Research aimed at postharvest insect removal has tested a range of measures (Seaton and Joyce 1992, 1993). Conventional disinfestation methods involving chemical control have no phytotoxic effects on *B. hookeriana* blooms, but there is a need to develop alternative methods for safety reasons. Gamma irradiation is unsuitable because it damages *Banksia* blooms (Seaton and Joyce 1992), as do volatiles such as acetaldehyde, although to a lesser extent. Low temperature and high carbon dioxide treatments show promise for *Banksia* stems, as all test insects are killed by 10 to 14 days storage at 1°C, with a reduction to seven days if 45-60% CO_2 is combined with the low temperature treatment (Seaton and Joyce 1993). *B. hookeriana* has an acceptable vase life following treatment of up to 28 days at 1°C. Hot water dips are less successful, with *Banksia* blooms damaged by all treatments that kill insects.

Lower-quality blooms unsuitable as fresh stems are often dried. For natural drying the blooms are hung, and the process can be accelerated by solar heating, hot air dryers, dehumidifiers, microwaving, freezing, and dehydration using silica gel. The colors of both flowers and leaves fade under these conditions, and sulfuring to preserve color is achieved either by burning elemental sulfur or by using sulfur dioxide gas in an enclosed area. The orange *Banksia* species and *B. menziesii* respond well to sulfuring. Stems can be bleached using hypochlorite, chlorite, peroxide, or hydrosufite (Dubois and Joyce 1992), or preserved by placing in 10% glycerine for 24 h before drying. This latter treatment gives a shiny gloss to the dried product, which retains flexibility. It is not suitable for cut blooms, as these damage easily when treated with glycerine.

Dyed *Banksia* blooms are popular for some markets. Blooms of pale colored species such as *B. baxteri, B. speciosa,* and the unopened buff colored flowers of the orange species are dipped into aniline or water-soluble dyes. These impart a wide range of bright, vibrant colors, including blue, purple, orange, red, and green, or combinations. Uptake dyes produce more subtle colors but are not much used.

VI. PRODUCTION

A. Culture

Banksia species are cultivated almost exclusively without protection and planted directly into soil. There has been little attempt at protected cultivation, although *B. menziesii* can be grown experimentally in nutrient solution (Avidan et al. 1983 cited by Ben-Jaacov et al. 1989). Between-plant spacings vary from 2 m for the more compact species such as *B. coccinea* to 3.5 m for the more spreading *B. speciosa* and *B. prionotes,* with between-row spacings of between 3 and 6.5 m (Sedgley 1996). Windbreaks, weed removal, and rabbit protection are often used, and a mulch of a freely-draining medium such as gravel or coarse sand aids in protection of the roots from extremes of temperature. Drippers or microjets are the most efficient for irrigation, and tensiometer studies indicate that in Australia irrigation of 4 litres per plant per day is advisable in all except the winter months. Application of nitrogen, potassium, and iron are important, but high levels of phosphorus are generally avoided, with slow-release

low-phosphorus fertilizer used in most nurseries. Healthy growth has been recorded with 0.5 g urea plus 0.5 g potassium chloride applied per plant through the irrigation system every six weeks, with 1 g ammonium nitrate and 1 g potassium sulfate per week during the active growth and flowering period. Iron chelate is also applied when chlorosis is a problem.

B. Diseases and Pests

The most important disease of *Banksia* species, both in the wild and under cultivation, is root rot caused by the pathogen *Phytophthora cinnamomi.* The disease is soil borne, and is readily transmitted on feet, vehicles, tools, and by water. In the nursery, the disease causes damping off of seedlings. In the field, poor growth is followed by drying and wilting of the foliage, because by the time above-ground symptoms are visible, the root system has been heavily colonised. In addition to dead roots, there is often collar rot at ground level. It has been recorded that a number of other *Phytophthora* species infect *Banksia* plants, particularly in nurseries. These include *P. dreshsleri* Tucker, *P. nicotianae* Waterhouse, *P. cactorum* Schrot., and *P. citricola* Sawada (Hardy and Sivasithamparam 1988; Tynan et al. 1995).

Control of *Phytophthora is* very difficult. Introduction of the disease to a new nursery or planting should be avoided, as it is impossible to eradicate the disease once it is established, and it can survive in soil without a host for many years. The development of *Phytophthora*-tolerant cultivars may be possible (Tynan et al. 1995), as there is both between and within species variability (Cho 1981, 1983; McCredie et al. 1985a,b). Tolerance screening requires an effective non-destructive method (Dixon et al. 1984), and an excised root assay appears to be the most reliable (Tynan et al. 1995). Another promising approach is the use of antagonistic biological control agents; the bacterium *Pseudomonas cepacia* Burkh. has been used to suppress the effects of the disease in the nursery (Turnbull et al. 1992). Grafting of susceptible types onto tolerant species has been suggested as an alternative control measure for the field (McCredie et al. 1985a), but grafting success to date has not reached commercial levels. Chemicals can be used to combat *Phytophthora,* but eradication of the fungus from infected land is difficult, and there may be phytotoxic effects.

Banksia species are attacked by relatively few pests, and most are insects that cause damage to the blooms or seeds (Scott 1982; Zammit and Hood 1986; Wallace and O'Dowd 1989; Woods 1988; Vaughton 1990). Tunnelling moth larvae *(Arotrophora* spp.) are the most common of the *Banksia* flower caterpillars, both under cultivation and in the wild. The adult moth lays eggs on immature blooms and the larvae move into the center of the inflorescence stem and kill large numbers of flowers by feeding on the soft tissue. The larvae pupate in the flower stem, and control is difficult because they are protected within the inflorescence rachis. Larvae of a number of Lepidopteran genera may cause damage by feeding on flowers, including *Cryptophasa sp., Peraglyphis idiogenes* Common, and *Xyloryctis* spp. The Coleopteran *Myositta* has been reported on *B. menziesii* flowers in the wild, and leaf damage can be caused by the chewing snout beetle, *Catosarcus* sp. In contrast to the small number of flower predators, a wide range of insect genera has been recorded feeding on seeds within the *Banksia* infructescence. These include Lepidopterans of the genera *Arotrophora, Chalarotona, Scieropepla, Xyloryeta, Xyloryctis, Brachmia,* and *Carposina,* the Coleopterans *Alphitopis nivea* Pascoe, *Cechides amoenus* Pascoe, and *Myositta* spp, and unidentified Coleopteran weevils.

Banksia seeds form part of the natural diet of parrots and cockatoos, and cones are often predated in cultivated plantings and in the wild (Vaughton 1990; Witkowski et al. 1991). Predators include the crimson rosella, *Platycereus elegans* Gmelin, and the yellow-tailed black cockatoo, *Calyptorhynchus funereus* Shaw. Open blooms are often removed from the plant, as well as cones with developing seeds.

VII. CONCLUSIONS

Banksia species are already established as cut flower crops, and are amongst the most readily identifiable of Australian native plants (Plate I). They are accepted on international markets and demand currently exceeds supply. This situation will not continue indefinitely, and while lesser quality may be acceptable in a sellers' market, this will not be the case as supply increases. Considerably more research is needed into all aspects of *Banksia* production so that stems can compete with the high standard expected of established cut flower crops such as rose and carnation.

In addition to making good commercial sense, there are strong environmental reasons why further research into *Banksia* biology is essential. Until the early 1980s, most *Banksia* stems for the cut flower market were bush picked from the native habitat, particularly in south-western Australia (Pegrum 1988), and *Banksia* is still the second largest bush picked genus in Australia. This has resulted in major damage to natural ecosystems via disturbance, introduction of disease, and depletion of seed reserves. Soil and plant destruction is caused by access vehicles, and soil-borne diseases are spread on tires and footwear. The root rot fungus *Phytophthora cinnamomi* attacks a wide range of native genera, including *Banksia,* and is very readily distributed (Shearer et al. 1991). The aerial canker diseases *Diplodina* sp., *Zythiostroma* spp., and *Botryosphaeria ribis* Gossenb. & Dugger are spread via infected secateurs, and have been the cause of more recent concern. *Diplodina* cankers girdle branches and eventually kill the plant, the disease being most prevalent in stands aged over 12 years. Removal of blooms depletes the seed bank and has implications for continued regeneration. Legislation is now in place to prevent bush picking of *B. coccinea* and *B. baxteri* from crown land, and this has resulted in an increase in *Banksia* plantings for cut flower production.

The visual appeal of *Banksia* blooms is unquestioned, but there are other features that will ensure continued popularity, including long shelf life and variety of color and form. Continued research input into production problems is needed to ensure stability of the international industry in a new but increasingly popular cut flower commodity.

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2

Leucospermum: Botany and Horticulture*

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I. INTRODUCTION

The Proteaceae embrace 82 genera, of which the most important cut flower genera are *Protea, Leucospermum, Leucadendron, Banksia* (Sedgley 1998), and *Grevillea* (Joyce et al. 1997), all of which also have species used as cut foliages (Parvin 1991a) and landscape material. The nut crop, *Macadamia,* is one of the other prized members of the Proteaceae. In this review, the noun *protea (proteaceous* when used as an adjective) is used in a general sense for the cut flower members of the family, while a genus name is used where it was clearly identified in a citation.

Venkata Rao (1971) noted, perhaps incorrectly, that the family Proteaceae contains very few plants of economic importance but that most are rich nectar producers and of value to apiarists. Indeed, it is the copious nectar production in some ornithophilous species of *Protea* that may lead to the black leaf disorder of the cut flower (Dai and Paull 1995; Jones et al. 1995). Many proteaceous species are adapted to pollination by birds, and the large solitary inflorescences of these have also attracted the interest of humans because of their ornamental qualities.

Brits et al. (1983) reviewed the development of proteas as cultivated crops in South Africa. In his introduction to the first newsletter of the International Protea Association, G. J. Brits (1984) noted that many South African flowering plants were developed as horticultural crops in Europe, but despite early attempts to cultivate proteas in Europe their specialized horticultural requirements prevented them from incurring a similar fate. The distribution of the Proteaceae is linked to the occurrence of acid soils that are extremely deficient in plant nutrients. This linkage continues to frustrate horticulturists who are used to nurturing their plants with fertilizers.

Proteas were first cultivated seriously in the early 1900s at the National Botanic Gardens at Kirstenbosch in the Cape Province of South Africa, but they had been gathered from mountain veld even earlier and marketed in Cape Town, where an appreciation and acceptance of these cut flowers developed. Following public concern about the pressure that wild flower harvesting was having on the habitat, in 1920 the Kirstenbosch Botanical Gardens encouraged the founding of the "Society for the Protection of Wild Flowers," whose early emphasis was the planting of veld flowers to protect the native flora, a "planting brigade rather than a plucking brigade" according to their original brochure (Brits 1984; Rourke 1980). The progression of proteas in their development as a commercial crop is illustrated in Table 2.1. The use of plantings of selected clonal material is still expanding, while the last stage, use of clonal materials from genetic manipulation, has not begun.

The first South African publication on the cultivation of proteas appeared in 1921 (Matthews 1921). This historic, but almost forgotten, article was the forerunner of the vast popular literature available today. Some cultural guides of more recent standing include publications by Vogts (1958, 1960, 1962, 1979, 1980, 1982), Watson and Parvin (1970), Furuta (1983), Harre (1988b, 1995), Matthews (1993), and McLennan (1993). The foundations for commercial protea cultivation in the Western Cape of South Africa were established during the 1940s to the 1970s by Frank C. Batchelor, who conducted the first breeding efforts, collected natural hybrids and established vegetatively propagated plants, set standards of quality, marketed cultivated proteas overseas, founded the forerunner of South African Protea Producers and Exporters Association (SAPPEX), and identified production research needs. During the 1950s, Marie Vogts gathered the known information about proteas and published it (Vogts 1958). She also identified areas needing more research (Vogts 1960) and played a key role in limiting the damage to wild populations by publishing cultural methods (Vogts 1962, 1979; Vogts et al. 1972).

By the 1960s, a small number of managed "flower orchards" were producing flowers of better quality than most of those gathered from the wild, and the introduction of refrigeration facilities in the 1980s improved keeping quality prior to long-distance shipment. Flower importers in the northern hemisphere wanted

continuous supplies of the same species throughout the year, whereas most of the proteas being shipped were highly seasonal. A partial solution to this problem has been to gather early- and late-flowering variants to lengthen the season. More recently, the Fynbos Unit of the South African Agricultural Research Council has been breeding in the important genera of proteas to develop a longer flowering period (Brits 1978, 1992a, 1992b; Littlejohn et al. 1995; van Vuuren 1995).

Table 2.1. Development of proteas as commercial cut flowers from harvesting in the wild to selection and development of clonal materials. Adapted from: Matthews and Matthews 1994.

Stage	Characteristics	Quantity & quality
1. Harvesting from naturally occurring proteas in the wild	No control of production, weather-dependent, no disease control, high picking costs	Quality and quantity unreliable
2. Plantations raised from seed	Efficient layout, disease control possible, use of irrigation, high replacement rate	Improved reliability and quality, but flower forms variable
3. Plantations from vegetatively propagated material	Stock improved by selection from best seedling materials	Improved reliability and quality, quantities a function of plant numbers
4. Plantations of selected clonal material	Selection from breeding programs for: flower and leaf life, stem length, disease resistance, packing and shipping qualities, flowering time, productivity	Reliable supplies, premium flower quality, uniform product, high productivity
5. Clonal materials from genetic manipulation and propagation by tissue culture	Rapid response to market requirements for color, vaselife, stem length. Rapid response to disease problems	Premium quality flowers that exactly meet market needs, uniform product, high productivity, and highly competitive with other flower crops

During the 20th International Horticultural Congress (1978) in Sydney, Australia, growers and researchers from South Africa, Hawaii, Israel, New Zealand, and Australia proposed the concept of an international organization to disseminate the information being generated in different parts of the world. The International Protea Association (IPA) was established in 1981 in Melbourne, Australia, by delegates to the first IPA Conference. The IPA initially represented the interests of growers and shippers, while the researchers formed the International Protea Working Group (IPWG) during 1984 meetings in Stellenbosch, South Africa, under the auspices of the Ornamental Section of the International Society for Horticultural Science. Recognizing a need to keep records on new cultivars as they were developed and released, the IPA supported establishment of the International Registration Authority for Proteas in Stellenbosch, South Africa (joan@pgb3.agric.za). It has recently published (Int. Reg. Auth. 1997) the fourth edition of the International Protea Register.

Biennial meetings of the IPA and occasional concurrent meetings of the IPWG

and IPA have been productive venues for the exchange of information between scientists and the commercial growers. Each produced its own publication for many years before they were merged in 1994, with the *Protea News* of IPWG now being published as part of the *Journal of the International Protea Association.* Four volumes of *Acta Horticulturae* (185, 254, 316, 387, and 453) present some of the most readily available information on proteas, but the newsletters and journals of the two organizations are largely unavailable outside the membership base. This review includes a generous sampling of information shared in these resources.

The principal protea production areas initially were South Africa, California and Hawaii in the USA, Australia, and New Zealand. Israel's floriculture industry joined them in the mid-1970s following a visit and talks by California's leading protea grower, Howard Asper. Since then, interest in the production of proteas has spread to many other countries, and nascent production for export is underway in Spain (Canary Islands), Zimbabwe, France, Mexico, San Salvador, and Chile.

Worldwide, there may be about 900 protea growers. Verifiable figures of the numbers of growers of *Leucospermum* are not possible to obtain, and even the figures on numbers of growers of Proteaceae are, at best, estimates. South Africa counts over 300 producers affiliated with SAPPEX, while Australia has over 150 affiliated with the Australian Flora and Protea Growers Association. The sources for both figures estimate that perhaps twice as many smaller growers are not affiliated. Elsewhere, estimates are 40 growers for New Zealand, 30 for Hawaii, 90 for California, and 55 for Israel.

In 1983, at the founding of the IPA, it was estimated that a little over 800 ha were planted to cultivated proteas, while in the early 1990s, the area was 5 times greater (Parvin 1991b). South Africa registered the greatest increase in cultivated area as a result of pressures to reduce harvesting from the wild. A recent report (Malan 1997) estimated that 173,000 *Leucospermum* species and hybrid plants were established on 66 ha in intensive cultivation as of 1996 and a harvest of 1.3 million stems was projected for 1997-98. In 1992, Zimbabwe was estimated to have about 240 ha of protea plantings (Harre 1992). Australia's native plant industry began to expand in the 1980s, reaching about 63 ha of cultivated *Leucospermum* in 1993 out of more than 945 ha devoted to native and introduced proteas (Turnbull 1997). Israel had about 20 ha of proteas (1.5 ha in *Leucospermum) in* 1992 (Meltzer 1992), with only 85,000 *Leucospermum* stems sold at auction in 1995-96 (J. Ben-Jaacov, personal communication). The cultivated area for all proteas in Hawaii in 1996 was 66 ha (Hawaii Agr. Stat. Serv. 1997) and in California 192 ha (Karen Robb, personal communication).

Figures for the economic value of *Leucospermum* are hidden in the overall category of proteas, although figures from the Dutch auctions showed a per stem price for imported *Leucospermums* ranging from 0.75 to 0.70 (US$) in 1994-95. The per stem price for *L. patersonii* at auction in Israel was 76 cents in 1995-96 and 103 cents in the first three-quarters of the 1996-97 season (J. Ben-Jaacov, personal communication). In the USA, proteas are combined into the category of "other cut flowers" except for Hawaii, where the return to protea growers was $1.2 million in 1996 and in San Diego County of California where farm gate value (1996) was $3.57 million (Karen Robb, personal communication). A mid-90s figure for the farm gate value of *Leucospermum* in Australia was about one million dollars from 20 ha (David Matthews, personal communication). A figure of $12 million was estimated for the worldwide value of cut proteas in the late 1980s, and this may represent less than 1/2% of the world's annual expenditure for flowers (Parvin 1991b). The proportion of this figure that *Leucospermum* represents is undetermined, although reports suggest it is about 10% (Forsyth 1992).

II. BOTANY

A. Origin and Ecology

Before Australia, Antarctica, South America, and Africa drifted apart, they shared a zoological and botanical ancestry. Africa parted from the ancestral landmass about 120 million years ago, whereas South America and Australia separated about 70 million years ago. Sir Joseph Hooker (cited in Venkata Rao 1971) observed in 1860, that

> the many bonds of affinity between the three southern floras, the Antarctic, Australian and African, indicate they have been members of one great vegetation which may once have covered as large a southern area as Europe now does the northern. The geographical changes that have resulted in its dismemberment into isolated groups scattered over a southern ocean must have been great indeed.

The Proteaceae presently occur across the three temperate southern hemisphere continents (Australia, Africa, South America) that formerly were connected as Gondwanaland (Gondwana). The success of the dispersed members of the family has been attributed to inherent genetic plasticity (Dixon 1987). The concentration of Proteaceae in Australia (45 genera, 800+ species) argues for their origin there but endemism also exists in the African Proteaceae (16 genera, Rourke 1997), and no genera are common between the continents. South Africa presents great diversification in the subfamily Proteoideae (Vogts 1982). Proteaceous fossils dating from the early Tertiary period have been found in Victoria (Australia) as well as in Antarctica. The South American genera are evolutionarily closer to the eastern Australia taxa. Venkata Rao (1971) suggested that Proteaceae evolved in the mountainous rainforest conditions of eastern Australia in the Cretaceous period before spreading out into the lowlands and adapting to more xerophytic conditions. Western Australia and Africa are, in his view, secondary centers of diversification. The Proteaceae are largely distributed on soils of low nutrient content, often with acidic pH values.

B. Morphology

Leucospermum species are evergreen woody perennials with growth habits that range from small trees to spreading shrubs to prostrate ground covers. Some species produce a thickened lignotuber at ground level which contribute to vegetative regeneration of the plant following fires. The root systems are profusely branched with clusters of rootlets of limited growth appearing on the main roots. These are known as proteoid roots (Purnell 1960; Lamont 1986). Venkata Rao (1971) and Lamont (1986) state that proteoid roots are not mycorrhizal but may require a biological stimulus for their development. The leaves are simple, smooth to hairy, with entire to toothed margins. The inflorescences are manyflowered and resemble compositaceous clusters with short, thick receptacles subtended by involucral bracts. The flowers are simple with three basic whorls, the perianth, androecium, and gynoecium. The flowers are 4-merous, hermaphroditic, and perigynous (Venkata Rao 1971). Although the flowers are structurally regular, three posterior tepals are fused and the anterior one remains free so that the perianth is bilabiate. The style emerges through this discontinuity, and the tepals reflex to show reds, oranges, and yellows. Stamens are adnate to the tepals with the anther fused to the tepal midrib. Pollen grains are triporate and are shed before the stigma is receptive. The pistil has a long, curved style with a lateral stigma subtended by a pollen collecting apparatus.

Rourke (1972) and Jacobs (1985) describe the inflorescence as a capitulum that develops from an axillary rather than a terminal bud, but that appears to arise distally. Inflorescences may be solitary, as in *L. cordifolium, L. lineare,* and *L. vestitum,* or in clusters (conflorescences), as in *L. oleifolium, L. tottum,* and *L. mundii.* The individual florets consist of a perianth formed by four fused perianth segments, one of

which separates from the other three as the flower opens. The perianth curls back to display a prominent style; the striking appearance of the whole inflorescence of open flowers resembles a pincushion-thus one of the common names is pincushion protea. The styles, perianth, and involucral bracts may be white, yellow, pink, orange, or red and the combinations are responsible for the popularity of the pincushion proteas as cut flowers.

The fruit of the *Leucospermum* is an indehiscent achene with a gelatinous pericarp (functionally, an elaiosome) and a tough seed coat consisting of several layers of sclerified cells. A reinterpretation of the pericarp-testa interface suggests that a crystalliferous layer found at this boundary is part of the testa outer integument rather than the pericarp (Manning and Brits, 1993). The embryology of Proteaceae has received considerable study by Venkata Rao (1971). The ovule is solitary and orthotropous and develops into a large (c. 8 mm), rounded seed, non-endospermic with mainly oily and proteinaceous food reserve. The species name, *Leucospermum,* which means "white seed," refers to the elaiosomes, which dry out to become pale and papery in herbarium specimens, but which are fatty, juicy coverings attractive to native ant species that drag the seed to shallow underground nests in the fynbos habitat. This may enable dispersal and germination (Brits 1987).

C. Taxonomy

The Proteaceae consists of more than 1700 species in 82 genera, all of which occur in the southern hemisphere. The genus *Leucospermum* consists of 48 species (Table 2.2, Plate 2) confined to southern Africa (Rourke 1972). Only a few species have been utilized as cut flowers *(L. cordifolium, L. patersonii, L. lineare, L. conocarpodendron, L. vestitum),* but natural and manmade interspecific hybrids exist as clonal selections that are grown commercially (Jacobs 1985). Other species are being examined for their potential to contribute disease resistance, foliage traits, and extended flowering seasons.

Chromatographic analyses of 267 species and subspecies of all genera in the Proteaceae have contributed to an understanding of the evolutionary relationships within this family (Perold 1984, 1987). The phenolic compounds, leucodrin and its hydioxylated analogue, leudrin, and the diastereoisomer conocarpin and its ring-opened methyl ester, reflexin, have been used to distinguish between *Leucadendron* and *Leucospermum.* Perold (1988) further demonstrated that the presence or absence of these phenolic compounds could be used in the characterization of *Leucospermum* hybrids. Both leucodrin and conocarpin are absent in *L. cordifolium, L. lineare,* and *L. tottum,* while leucodrin occurs in *L. patersonii* and its hybrids and conocarpin occurs in *L. glabrum* and its hybrids.

Table 2.2. *Leucospermum* species and derivation of the species name (Rourke 1972, SAPPEX 1990, Rebelo 1995).

Species	Authority	Derivation of name
arenarium	Rycroft	Of sandy places
bo usii	Gandoger	After H. Bolus
calligerum	(Gandoger) Gandoger & Schinz	Bearing beauty
catherinae	Compton	After Mrs. Catherine van der Byl and its catherine wheel appearance
conocarpodendron	(L.) Buek	Cone-fruit-tree
cordatum	Phillips	Heart-shaped
cordifolium	(Salisb. Ex Knight) Fourcade	Heart-shaped leaf

cuneiforme	(Burm. F.) Rourke	Wedge-shaped
erubescens	Rourke	Reddening
formosum	(Andr.) Sweet	Beautiful
fulgens	Rourke	Shiny
gerrardii	Stapf	After W. T. Gerrard
glabrum	Phillips	Hairless
gracile	(Salisb. Ex knight) Rourke	Slender
grandiflorum	(Salisdb.) R. Br.	Large/noble flower
guenzii	Meisn.	After W. Guenzius
hamatum	Rourke	Crooked
harpagonatum	Rourke	Sickle-shaped
heterophyllum	(Thunb.) Rourke	Various-leaved
hypophyllocarpodendron	(L.) Druce	Under-leaf-fruit-tree
innovans	Rourke	Novelty
lineare	R. Br.	Linear
muirii	Phillips	After J. Muir
mundii	Meisn	After J. L. L. Mund
oleifolium	(Berg.) R. Br.	Olive-leaf
parile	(Salisb. Ex Knight) Sweet	Equal (similar to other species)
patersonii	Phillips	After H. W. Paterson ?
pedunculatum	Klotzsch in Krauss	Having a stalk
pluridens	Rourke	Many-teeth
praecox	Rourke	Flowering early
pmemorsum	(Meisn.) Phillips	With end bitten off
profugum	Rourke	Fleeing outwards
prostratum	(Thunb.) Stapf	Lying on the ground
reflexum	Buek ex Meisn.	Bent backwards
rodolentum	(Salisb. Ex Knight) Stapf	Smelling like a rose
royenifolium	(Salisb. Ex Knight) Rourke	Wild-coffee (Royena)-leaf
saxatile	(Salisb. Ex Knight) Rourke	Of the rocks
saxosum	S. Moore	Occurring among rocks
secundifolium	Rourke	Unidirectional leaves
spathulatum	R. Br.	Spoon-shaped
tomentosum	(Thunb.) R. Br.	Woolly
tottum	(L.) R. Br.	Native to the Cape (Hottentot)
truncatum	(Buek ex Mesin.) Rourke	Cut off at tip
truncatulum	(Salisb. Ex Knight) Rourke	Small, cut off at tip
utriculosum	Rourke	Having a bladder
vestitum	(Lam.) Rourke	Clothed
winterii	Rourke	After J. Winter
wittebergense	Compton	of the Wittenberg mountains

A number of synonyms and botanical varieties have been collected under the above species by Rourke (1972).

D. Floral Physiology

1. Flowering.

Knowledge on flower initiation and development in *Leucospermum* was summarized in The Handbook of Flowering III (Jacobs 1985). He proposed that *Leucospermum* was a day-neutral plant in which flower initiation was evoked in response to high light intensity in conjunction with intraplant factors such as cessation of shoot growth and release of axillary buds from correlation inhibition. Jacobs et al. (1986) later separated flower growth and development into four stages: pre-floret (inflorescence bud initiation phase), floret initiation (floret primordium initiation phase), floret differentiation, and inflorescence enlargement. Plants grow vegetatively in spring and summer, with floret initiation commencing after shoot extension growth has ceased in fall. The pre-floret phase is characterized by slow growth and the development of bracts without florets in their axils. These bracts make up the involucre that covers the peduncle. In later-formed bracts, florets develop (the timeframe being mid-to-late fall), until cessation of floret initiation during the shortest days of winter (see also Criley et a1.1990). Inflorescences develop slowly through the winter months, then more rapidly as the days become longer and light intensity increases. Depending upon cultivar, flowering occurs in late winter through early spring or even into summer.

For a period after cessation of shoot extension, pinching can induce vegetative growth from the upper axillary buds, indicating, according to Jacobs (1980, 1983), that the plants have not yet entered an induced state. By late fall, an induced state is achieved in a distal axillary bud, and other axillary buds are inhibited. Induction is relatively strong for the more distal buds and decreases basipetally. The developing inflorescence correlatively inhibits axillary buds below it (Jacobs 1980, 1983; Malan et a1. 1994a,b). Any of the top 6 to 10 lateral buds on a decapitated plant are capable of developing as an inflorescence. The 6 to 10 buds below the developing inflorescence develop to about 5 mm in diameter as secondary inflorescence buds composed primarily of bract-like leaves and perianth initials, but they do not develop further unless the primary inflorescence is removed. Removal of the primary inflorescence bud during inductive short days leads to inflorescence initiation in 1 or 2 lateral buds, with a weaker effect the later in the season (Malan 1986). The developmental period of the secondary inflorescence buds becomes shorter the later in the spring that the primary inflorescence is removed due to more rapid accumulation of heat units in the ensuing spring and summer (Jacobs and Honeyborne 1979), however, the ability of a secondary bud to develop a flower declines the later the removal of the primary inflorescence (Jacobs and Honeyborne 1978; Malan et al. 1994b).

The induced state is maintained for about 2 months (in the Cape Province of South Africa) and the plant gradually returns to the noninduced vegetative state by early spring. Secondary inflorescence buds will abscise when the plant returns to a vegetative growth phase. Buds below the secondary inflorescence buds do not develop and remain correlatively inhibited, but they will grow out vegetatively if the shoot is cut back. A key concept is that the buds entering the bract initiation phase must achieve a certain size (characterized as 20 mg DW) or they do not continue to develop (Malan 1986).

Jacobs' (1985) concept that inflorescence initiation was not a response to photoperiod, as it does not occur during the long days (LD) of summer and the induced state is lost during short days (SD) of winter, changed as evidence mounted for a new interpretation. Jacobs' laboratory studied a number of factors, including timing of inflorescence initiation; influence of growth regulators, shading, and photoperiod; effects of defoliation, decapitation, and other manipulations of the shoots to determine how they influenced flowering.

Jacobs et al. (1986) reported that long days delayed onset of the induced state and that flower initiation in *Leucospermum* required high light intensities during vegetative growth followed by SD. The induced state is lost more rapidly under shade

than full sunlight or when the plant is sprayed with GA or ethephon (Napier 1985). Napier's studies showed that a decrease in leaf starch was associated with the diminished capacity to form flowers. Later work (Malan and Jacobs 1987, 1990) demonstrated that LD (3.7 μmol × s^{-1} × m^{-2} provided from incandescent lamps throughout the night period) could prevent flower initiation on upper axillary buds on shoots decapitated at various times from summer through winter, while similarly handled shoots under natural daylengths initiated and developed inflorescences. Night break lighting (2 to 6 hr depending on length of dark period) was also effective in preventing flowering (Malan and Jacobs 1990).

Since the transition from vegetative to induced state occurred at the same time every year, Malan and Jacobs (1987, 1990) suggested that photoperiod might play a key role in the induction of *Leucospermum.* The low level of light energy needed to prevent initiation also argued for the participation of photoperiod in the process. Jacobs and Minnaar's (1980) observations of simultaneous reproductive development also supported the idea of a photoperiod switch. Malan and Jacobs (1990) stated that 'Red Sunset' was a qualitative SD plant that required at least 42 SD inductive cycles (>12 hr dark) for normal flowering. Such conditions prevail at Stellenbosch, South Africa (33°, 54'S) from April to September. Inflorescence development can occur between May and September; however bud responsiveness is weaker after June.

Leaf removal and shading prevented flower initiation in the interspecific hybrid 'Red Sunset' *(L. cordifolium* × *L. lineare)* (Jacobs 1980). Heavy shading applied during summer reduced the number of stems forming an inflorescence (Jacobs 1983), but long stems were less responsive to the inhibition of flowering at low light intensities.

The question may be posed, "Must a shoot reach a certain size or achieve a threshold leaf area, or simply cease elongation to begin to accumulate carbohydrates in order to be receptive to an inductive short day?" The appearance of an inflorescence on short stems of recent origin following a late pinch argues against shoot age or a threshold leaf area as necessary for induction (Jacobs 1980, 1983). Jacobs and Minnaar (1980) reported that production of bracts with florets in their axils commenced simultaneously on all shoots regardless of variations in the time of shoot growth cessation. Cessation of shoot growth on old plants occurred in mid-summer, while shoot growth extended into fall on young plants (Jacobs 1985). Jacobs (1985) noted that early cessation of shoot growth could also be induced by water stress for plants growing under dry land conditions. Malan and Jacobs (1987) stated that buds that had developed a number of bract-like leaves would develop as vegetative shoots if the plants were stimulated into shoot extension growth by rainfall after growth cessation and concluded that shoot growth cessation is not a reliable indicator that the plants had reached an induced state for reproductive development. Cessation of shoot elongation certainly seems implicated, but the question of whether it is a necessary condition is not clear.

The correlative inhibition of primary inflorescence bud upon secondary inflorescence buds was thought due to its IAA production and export (Malan et al. 1994a). Diffusable plant growth substances from primary inflorescence buds were collected in agar receiver blocks and analyzed by radioimmunoassay and by HPLC. IAA content and its export from the primary inflorescence bud did not differ significantly from that of inhibited buds nearby, but the developmental patterns favored the primary inflorescence. Since all buds exported IAA, they concluded that it was not the IAA concentration of a single organ or its inherent ability to export IAA that is responsible for inhibition, but the total amount of IAA moving down the shoot that determined the extent of inhibition. During floret initiation and differentiation, auxin production and export were low, but at the end of the floret initiation stage, IAA and ABA peaked, while GA was present until floret initiation was complete, and cytokinins were high in the pre-floret stage and first half of the initiation stage, but declined during later stages of development (Malan et a1. 1994b,c). GA export peaked just before lateral axillary buds

lost their responsiveness to inductive short days. Since exogenous application of GA also reduced the responsiveness of axillary buds to short days (Napier and Jacobs 1989), Malan et al. (1994b) proposed that GA export from the primary inflorescence bud was responsible for the correlative inhibition of the axillary buds. The GAs could be either GA, or GA, or both, as both were detected by the antiserum and had similar polarities and HPLC retention times.

Malan et al. (1994c) determined that benzyladenine (BA) applied to decapitated shoots prior to floret development in the secondary inflorescence buds increased the dry mass of the inflorescence and number of florets per inflorescence. The results were similar to those of Napier et al. (1986a). Extra bracts were initiated on the peduncle, but precocious floret development (in these bracts) did not occur and the loss of responsiveness to short days in winter time was not affected by the cytokinin compared to untreated buds. Malan et al. (1994c) concluded that BA did not interact with the gibberellins that were apparently inhibiting lateral bud responsiveness to short days.

To sum up the role of growth regulating substances in floral development, it appears that auxin does not play a major role in inhibiting bud responsiveness to short days. Gibberellins from more distal buds, especially the primary inflorescence bud, may play the role of correlative inhibitors of lower buds on the shoot. The more developed the inflorescence bud, the more strongly the lateral buds are inhibited in responding to inductive SD, presumably because of high GA levels (Malan et al. 1994b). Cytokinins are involved in quantitative roles such as increasing the meristem diameter, number of bracts and florets, and number of inflorescences per stem.

In *L. patersonii,* LD were required for floret induction, but SD accelerated floret initiation (Wallerstein 1989; Wallerstein and Nissim 1988). The LD effect quantitatively influenced the number of axillary buds that initiated inflorescences. The most distal axillary buds were the most sensitive. Stem thickening was concurrent with the cessation of stem elongation under SD, but if the axillary meristems failed to develop into inflorescence buds, stem thickening ceased.

2. Pollination Biology.

Species of Proteaceae are frequently pollinated by various honey-seeking birds, bats, and small animals. The flowers are grouped in capitula consisting of 30-300 florets. The florets shed pollen over a period of 7 to 14 days, generally before the pistil of the same flower is receptive (protandry). Fresh pollen remains viable for up to six days when stored at room temperature and up to six weeks when stored at 5°C (Brits and van den Berg 1991). The small stigmatic groove (30-300 µm long) opens within 24 hours and attains maximum receptivity two to five days after anthesis, as shown in Fig. 2.1 (Brits and van den Berg 1991).

Pollen viability can be tested by germinating in 12% sucrose plus 100 mg boron/L (Fig. 2.2) (Brits 1992a). Shchori et al. (1992) reported that better germination was achieved using Taylor's medium in a hanging drop.

Ito et al. (1978, 1990) have described their pollination technique. Since pollen is shed before the stigma is receptive, emerging styles (hooked stage) are gently released from the perianth, and the stigmas are examined for the presence of pollen. The anthers are removed from flowers that do not show pollen on the stigma. Pollen from fully open flowers of selected male parents is applied to the slotted tip of the stigmatic area two days after emasculation and again two days later. The emasculated and pollinated flower is covered to prevent contamination and labeled to identify the cross.

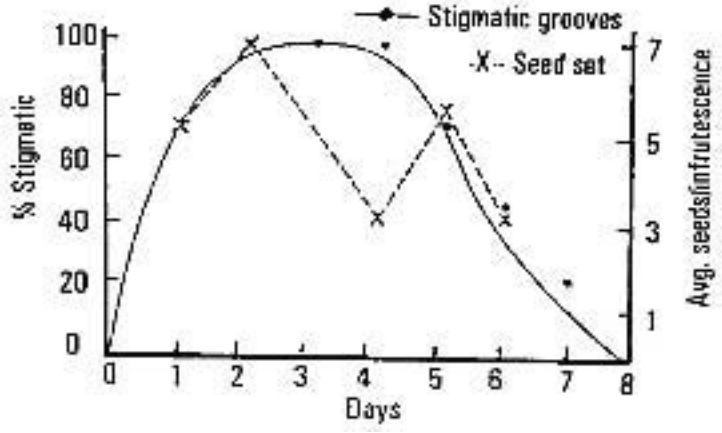

Fig. 2.1 Average percentage of stigmatic grooves open and number of seed set following artificial pollination on successive days after anthesis in Leucospermum cordifolium. Source: Brits and van den Berg 1991.

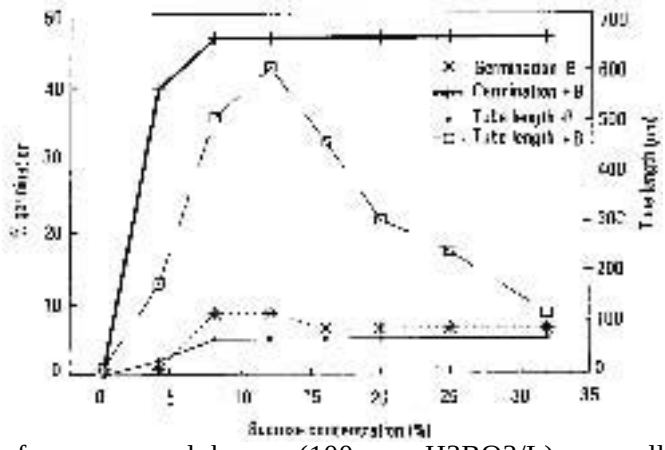

Fig. 2.2 Effect of sucrose and boron (100 mg H3BO3/L) on pollen germination percentage and pollen tube growth in *L. cordifolium*. Source: Brits 1992a.

E. Genetics

Chromosome numbers are constant within the genus at 2*n* = 24, *x*= 12 (Rourke 1972; Van der Merwe 1985). A wide range of interspecific hybrids have been collected and introduced to cultivation (Brits and van den Berg 1991). In addition, directed crosses are being made among species in efforts to produce later flowering, improve color and shape, and introduce tolerance to *Phytophthora cinnamomi* (Brits 1992a). Brits (1992a) noted that self-incompatibility is present to a moderate degree in *Leucospermum* and that interspecific crosses are often highly heterotic. Cross pollination is apparently favored; as only 3 to 4% of selfed flowers set seed as compared to 6 to 8% for cross-pollination (Brits 1992a). Horn (1962) reported even lower percentages of seed set among open pollinated

flower heads. Thus, a strong degree of self-incompatibility and interspecies incompatibilities were proposed (Brits and van den Berg 1991). Resources allocation, insufficient pollinators, and predation are possible alternative explanations for low seed yields.

III. HORTICULTURE

The most widely grown *Leucospermum* species are floriferous, spreading shrubs on which relatively short-stemmed inflorescences are borne in the spring. Horticulturists have had to develop management practices to improve stem length and straightness for their use as cut flowers. Their potential as flowering potted plants was recognized when budded cuttings flowered after rooting; stock plants are being manipulated to achieve stronger branches for this use.

A. Propagation

1. Seed.

Poor seed (or more properly, achene) germination in *Leucospermum* has posed problems for both horticulturists and plant breeders. Much of the early research to overcome this problem has been conducted in the laboratories of Johannes van Staden of the Department of Botany, University of Natal. In preliminary studies (Brown and Van Staden 1973; Van Staden and Brown 1973), removal of the pericarp and seed coat increased germination, as did increasing the oxygen concentration around intact seed. The outer layer of the achene (the pericarp proper) becomes gelatinous upon imbibition and is presumed to interfere with gaseous exchange.

Based on a report (Van Staden and Brown 1977) that oxygen promoted embryo cytokinin levels, Brits and Van Niekerk (1976) used hydrogen peroxide to improve germination. However, the effect was applicable only to proteaceous species with nut-like achenes, as 13 out of 15 serotinous species did not respond to the hydrogen peroxide treatment (Brits 1986b). Brits (1986c) noted that achenes harvested slightly prematurely germinated better than naturally matured achenes and suggested that dormancy was due to restricted oxygen uptake attained during the final stages of seed maturation, and that dormancy probably resides in the outer layer(s) of the seed coat.

The hydrogen peroxide treatment was not always successful, which led Brown et al. (1986) to examine a range of other treatments successful on seed of other plants. Following imbibition, the pericarp was removed, and the seeds were incubated under alternating temperatures of 10°C for 8 h and 20°C for 16 h with light (11 W/m) provided during the high temperature period from cool white fluorescent lamps. Emergence of the radicle was used as the criterion of germination. Germination was on moist filter papers to which various growth regulators were added. Some growth regulators were supplied as soaks prior to placing the achenes on moist filter paper. Germination improved from 11% for controls to 44-50% with GA_3 concentrations of 25 to 500 mg/L. With the commercial product, Promalin (mixture of GA_4, GA_7, and benzyladenine), a 24 h soak improved germination from 10% for the control to 26 to 46% for Promalin concentrations of 50 to 400 mg/L. Achenes germinated on filter paper to which a range of ethephon concentrations had been added also slightly improved germination over that of the control, while incubating achenes in an atmosphere of ethylene gas similarly improved germination. In the same series of experiments, hydrogen peroxide (10% v/v) soaks improved germination to 24%, compared to 12% for controls. They concluded that the gibberellins are the most active group of hormones in stimulating germination of *Leucospermum* achenes and suggested that GA in combination with other treatments needed investigation.

Brits (1986a,c) placed a fluctuating diurnal temperature requirement for germination in an ecological context. An optimum high of 24°C and low of 9°C as

determined from controlled experiments -promoted germination. In burnt mesic conditions of their natural habitat, *Leucospermum* seeds germinated during the winter when water was most likely to be available, rather than in the warm, dry summer. The daily surface temperatures of this sun-warmed soil in winter paralleled those of the controlled experiment, while temperature conditions of unburnt, or lightly or heavily shaded, soils did not meet the temperature requirements for germination. Brits concluded that *Leucospermum* was closely adapted to its environment with regard to germination temperature requirements. He also recorded temperatures at depths of 30 to 45 mm, where seeds buried by ants were found. Daily temperature fluctuations during early winter were of the same order as the known temperature requirements of *L. cordifolium* seeds.

The ecological approach to germination was also evident in a more recent report that desiccation, such as that due to fire, breaks the exotesta, and the endotesta as well when wetted, to permit oxygen diffusion and hydration of the embryo (Brits et al. 1993). Brits et al. (1997) propose that *Leucospermum* has at least one adaptive strategy for each stress or disturbance factor operating in nature: ant dispersal, desiccation-scarification by fire, alternating temperature requirement, and ecologically related temperature requirements. Phasic changes of gibberellins and cytokinins are also believed to control germination through an inductive threshold, mobilization of lipid and protein reserves, cotyledon expansion, and radicle growth (Brits et al. 1995).

Although complicated schema involving sulfuric acid scarification, Promalin (a gibberellin + benzyladenine preparation), pure oxygen, and alternating temperatures work to improve germination to 95% in the laboratory and are effective on a number of species (Brits 1990d), Brits (1991) proposed a simple treatment for commercial seedling production. Dry achenes are soaked in a 1% solution of hydrogen peroxide for 24 hours, the gelatinous pericarp is removed, and the achenes are sown in open seedbeds in autumn when daily temperatures vary from the optimum low at night to the optimum high by day. Satisfactory germination percentages (not reported, but presumed from other reports by the same author to be about 60%) were the result. This procedure was used successfully for *L. cuneiforme* and *L. tottum* by Rodriguez-Perez (1993).

While most propagators agree on the importance of fresh seed for high germination percentages, commercial germination practices for proteaceous seed has been subject to many variations. Parvin (1974) recommended 3 parts of finely screened cinders to 1 part peatmoss as a germination medium with 21°C bottom heat, and "plenty of moisture" leaching through 15 cm of medium. Harre (1986) reported his best successes came from sowing seed in a 1 loam: 1 pumice mixture or 5 loam: 2 coarse sand: 3 pumice during the falling temperatures of autumn, treating with captan to reduce fungal attack, and awaiting germination. The hard-shelled seeds of *Leucospermum* are slow and erratic to germinate, taking 3 to 15 months. Harre soaked seed in 60°C hot water for 30 mins prior to sowing, but did not clearly state whether this practice improved germination. Perry (1987) suggested a hot water soak to minimize seedborne diseases followed by dusting with a fungicidal powder. Once seedlings have reached the first true leaf stage, they are hardened off for potting. Harre also advocated ”wrenching”, a technique whereby the seedlings are disturbed a week before transplanting to induce lateral root formation.

The diversity of successful practices does not lend itself to a single recommendation. Brits' hydrogen peroxide treatment has broad applicability while Harre's practical nurseryman's approach (Harre 1988b) suffices for media, containers, transplanting, and environmental considerations. While uneven germination may be the reason that growers prefer to transplant rather than direct seed to tubes or pots, improvements in seed quality should speed the use of direct seeding in containers suitable for transplanting.

2. Cuttage.

Leucospermum cutting propagation offers few challenges because most plant material roots readily. Brits (1986d) compared terminal and sub-terminal cuttings and found that recently matured terminals taken in autumn rooted best. Harre (1988a)

rooted leaf (or possibly a leaf-bud) cuttings of many protea species, but noted that they did not produce plants. His observations suggest, however, that leafbud cuttings might be examined as a means of rapid increase for new cultivars. However, in other trials, rooting and shoot elongation of leaf-bud cuttings were poor, and up to 32 weeks was required for transplantable cuttings (Rodriguez-Perez 1992).

While *Leucospermum* cuttings can be rooted at almost any physiological stage of development, a preferred cutting is the recently matured new growth, known as a semi-hardwood cutting (Malan 1992). This type of material is gathered in autumn after shoot growth terminates. Harre (1988a) recommended removing the tip about a week before taking the cutting because rooting was improved, and vegetative growth resumed readily following rooting. Manipulation of cuttings on the stock plants before harvest as well as after the collection of cuttings was suggested as a means to improve rooting (Harre 1989). Cuttings (type and maturity not specified) of *L. cordifolium* 'Riverlea' were harvested fully turgid in early morning and held under mist for varying periods before being treated with 2000 ppm IBA and placed under automatic mist (cycle not given). Delays of 3 and 5 days before sticking the cuttings yielded rooting in excess of 90%, while a delay of 7 days reduced rooting to 77%. The cuttings were deemed well enough rooted that hardening could begin after 44 days and potting up after 50 days.

Another aspect to manipulating the future cutting was developed for the production of potted *Leucospermum* plants (Brits et al. 1992). Well-branched cuttings induced by spraying a primary elongating shoot with 960 mg/L ethephon rooted easily in 6 to 8 weeks. Yoshimoto (1982) proposed that air-layering of branched cuttings was another technique that could be used to produce larger plants for pots or for field planting.

As a result of practical experiments, Harre suggested that rooting under 35-50% shade is superior to lower light intensities; that a well-aerated medium leads to superior root quality (his examples included better rooting in cracked tubes and tubes with holes and when cuttings were placed down the side of a tube); and that initial propagation under automated intermittent mist, then shifting onto capillary watering beds as roots initiate, provided excellent results (Harre 1988a, 1989). Cuttings from well-nurtured stock plants 2 to 5 years old are his preferred propagules. He also recommends pinching and cutting back the stock plants to yield more cuttings of a uniform diameter and quality.

Rooting Compounds. While *Leucospermum* cuttings often root without the aid of auxins, most nurseries use auxin treatment to enhance rooting. Rousseau's early report (1968) suggested IBA solutions of 0.2 to 0.4% were adequate and mixtures of IBA/NAA in the same range gave about the same results. McKenzie (1973) used a.quick dip in 0.3% IBA, noting the results were better than with Seradix No. 2 powder. A range of 0.2-0.3% IBA was recommended by Parvin (1974), while Parvin (1982) later reported improved rooting of two South African *Leucospermum* hybrids over untreated controls when liquid IBA-NAA (2:1) formulations were used, and total auxin concentrations were in the range of 1300 (1:10 dilution) to 2500 (1:5 dilution) parts per million. A talc dust of 0.8% IBA (as Hormex #8) yielded somewhat lower rooting percentages than did the liquid formulations, while Yoshimoto (1982) recommended 0.65% IBA in talc powder. Jacobs and Steenkamp (1976) reported on the results of a series of IBA treatments (from 0 to 8000 ppm) and recommended 4000 ppm as either a quick dip solution or talc dust for *L. cordifolium* semi-hardwood cuttings. Asper (1984) routinely used 5000 ppm IBA as a dip treatment to induce rooting.

Propagation Medium and Bottom Heat. Rousseau (1968) used a sandpeat mixture for rooting, while Yoshimoto (1982) found a 1 peat: 2 perlite medium produced the best results. Interestingly, Harre (1988a,b) avoids peatmoss in his post-rooting medium and instead includes scoria, sand, or pumice with soil. He suggests that proteoid roots, which develop in the peat-based medium, do not contribute to the establishment of liners when they are transplanted to the field. A lengthy exchange of opinions

concerning the use of peat or bark suggested there was no good biological basis for avoiding peat, as many proteaceous plants were grown well in media containing peat (Blake 1987). For example, McKenzie (1973) used a 1 peat: l sand medium for propagation and 2 soil: l peat: l sand as a potting mix. Jacobs and Steenkamp (1976) evaluated several rooting media for *L. cordifolium* and recommended a 2:1 or 1:1 mixture of peat and polystyrene grains over mixtures of 2:1, 1:1, or 1:2 peat and sand, because the former clung to the new roots better than did the heavier sand-based medium.

Brits (1986d) reported that bottom heat (23 ± 0.8°G) greatly improved rooting over no bottom heat (12 ± 2°C) under mist, and that the use of IBA-based rooting compounds improved rooting at the cooler temperature but not at the warmer. Cultivar differences were important, with 75% rooting for 'Caroline' and only 30% for 'Hybrid T 75 11 24'. Sub-terminal cuttings did not root as well as terminal cuttings of the same cultivar given bottom heat, but were nearly equal to or outperformed terminal cuttings without bottom heat. Brits also observed that misting at long intervals, and allowing the leaves to dry off between on cycles did not influence cutting mortality, perhaps because the xerophytic character of *Leucospermum* may impart some tolerance to drier rooting conditions. These results suggest the potential to develop simpler, cheaper, and healthier rooting technology than conventional frequent-misting systems (Brits 1986d).

3. Grafting.

Grafting is often viewed as a solution to problems of root system adaptation to low or high pH soils, salinity, or soil-borne diseases. Grafting on lime-tolerant rootstocks has been recommended as an approach to problems of protea production on soils of neutral to slightly basic pH (Brits 1984b). A lime-tolerant species such as *L. patersonii* was recommended. Moffat and Turnbull (1993) evaluated rootstocks resistant to *Phytophthora cinnamomi,* and although none were found in the genus *Leucospermum,* they found a variety of grafting techniques that worked well on either rooted cuttings or on cuttings to be rooted under mist (cutting grafts).

The standard grafting technique is wedge-grafting of leafy semi-hardwood scions onto seedling rootstocks (Rousseau 1966; Vogts et al. 1976), but the requirement of a mist system during wound healing increased costs and stimulated a look at other techniques. Approach grafts are also successful but more time-consuming to execute, and required more aftercare.

During 1976 to 1980, G. J. Brits of the Vegetable and Ornamental Plant Research Institute (Riversonderend, South Africa) conducted 40 grafting and budding experiments to determine rootstock production methods, grafting and budding techniques, potential understocks, and to evaluate the effectiveness of grafting (Brits 1990b, 1990c). Rooted cuttings of *Leucospermum* were superior to seedling rootstocks because of necessary thickness requirements, uniformity, and clonal selection possibilities. The wedge graft, using a 2-bud scion with 0.5 cm^2 leaf blade subtending each bud, yielded 80 to 95% take on rooted cuttings, while chip budding onto unrooted cuttings yielded a 93% success rate. Prior to planting out in the field, the scion should be allowed to produce at least 5-cm-long shoots in the nursery. As to time of year, Brits expressed a preference for early autumn, although he noted that grafts made in the spring had the benefit of producing growth during the same growing season.

The use of cutting grafts, where the graft union develops while the cutting roots, is also recommended (Brits 1990b). Cutting grafts were evaluated using four *Leucospermum* cultivars (Ackerman et a1. 1995). In the second year after planting established liners into the field, the grafted plants significantly out-yielded the same cultivars on their own roots. Ackerman and his colleagues concluded that there was significant advantage to using resistant rootstocks selected for their suitability to the local soil types. Brits (1995b) reported that budding onto a cutting and rooting it was more economical than grafting.

The choice of rootstock was important, because 'Vlam' roots with difficulty while hybrid rootstocks could be selected with 100% capacity to root (Brits 1990b). Brits (1990c) evaluated 19 *Leucospermum* species with rootstock potential and found great

variability in capacities to root as cuttings, support vigorous scion growth when used as rootstocks, and produce a shoot of graftable diameter (Table 2.3). None of the species exhibited great tolerance to *Phytophthora cinnamomi,* although a hybrid of *L. formosum* × *L. tottum* designated as 'T75 11 02,' and another of *L. conocarpodendron* ssp. *viridum* × *L. cuneiforme,* designated 'T75 11 24', performed well in one field experiment.

Selection of rootstock plays a significant role in improving adaptability and yield of *Leucospermum.* Van der Merwe (1985, and references cited therein) produced a number of intergeneric grafts, and suggested close genetic relationships as a result of compatibilities he found. One important result was that *Serruria* may be grafted onto *Leucospermum conocarpodendron* and grown in sites where *Serruria* on its own roots would not survive. Malan (1990) compared an interspecific hybrid *(L. tottum* × *L. formosum)* and 'Sue Ellen' understocks for cuttings wedge-grafted with scions of 'Sue Ellen' (a hybrid of *L. cordifolium* × *L. lineare).* While graft union rates were only 12.2% and 23.8% for 'Sue Ellen' on itself and the hybrid, respectively, due to the inexperience of the laborers, rooting was faster for the hybrid understock cuttings and growth of the scion shoots was better than for the 'Sue Ellen' understock cuttings. Malan also noted that new growth of 'Sue Ellen' scions was less affected by *Phytophthora cinnamomi* root rot when grafted on the hybrid than on its own roots. Brits (1995b) reported that budding onto 'Spider' cuttings in the fall, followed, by LD during winter, produced market-ready plants six months later. Moffat and Turnbull (1994) recommended additional investigation of *L. saxosum* as a potential rootstock with low susceptibility to *Phytophthora.* Root rot resistant understocks have the potential to increase plantings of *Leucospermum* where *Phytophthora* root rot is a problem.

4. Tissue Culture.

Leucospermum cordifolium callus culture without organogenesis was reported by Van Staden and Bornman (1976). Ben-Jaacov and Jacobs (1986) reported success in bud sprouting from semi-hardwood shoot segments of 'Red Sunset', an interspecific hybrid of *L. cordifolium* × *L. lineare,* on filter paper bridges immersed in liquid Anderson medium with 2 ppm BA. Kunisaki (1989, 1990) achieved proliferation from axillary bud explants in half-strength MS inorganic salts, 2% sucrose and 0.2 mg BA per liter. Round, green proliferating bodies were induced to form shoots after transfer to filter paper bridges. After 4 to 6 leaves developed, the propagules with their shoots were transferred to agar medium, then, at 5 to 10 mm in height, they were separated from the propagules and grown on to greater length. Rooting was achieved by soaking the basal 2 to 4 mm stem in 50 or 100 mg IBA/L solutions for 4 days (later modified to a 10-min dip in 150 mg IBA/L). The microcuttings were rooted in an agar-based half-strength MS medium with activated charcoal and 2% sucrose. Kunisaki (1990) reported greater success with a modified composition of the agar rooting medium, but also noted that rooting could be achieved in sterile perlite. A "feeder leaf" technique was employed successfully by Rugge et al. (1990), in which a leaf blade on an explant was inserted into the culture medium. Axillary bud sprouting above the feeder leaf was substantially improved over the bud subtended by the feeder leaf or buds proximal to the feeder leaf in this technique.

Table 2.3. General characteristics of 19 Leucospermum species with rootstock potential for species of the section Brevifilamentum Rourke, determined from horticultural data or deduced from ecological data. Source: Rourke 1972.

	Horticultural Data					Ecological Tolerance				
Leucospermum sp.	Graft compatibility	Rooting ability	Vigor of rooted cuttings	Plant size/stem diameter	Longevity	pH 6.5-8.5	Rel. high salts	Drought	Cold	Wet soils
catherinae	(B)	61	C	C	C	C	C	D	B	A
Conocarpodendron ssp. *Conocarpodendron* ssp.	B	71	D	A	A	B	B	B	C	C
Viridum (Durbanville)	B	(70)	D	A	A	B	B	C	C	C
cordifolium	A	100	C	C	C	C	C	C	C	C
cuneiforme	(C)	50	C	C	B	C	C	B	C	C
erubescens	(C)	(60)	C	C	C	C	C	B	C	C
formosum	B	56	B	B	B	C	C	D	C	B
fulgens	(B)	78	C		B	A	B	C	D	C
gmndiflorum	(B)	66	B		C	B	B	B	C	C
guenzii	(B)	(60)	C	B	B	B	B	D	C	B
patersonii	A	(100)	A	A	A	A	B	C	D	C
p/uridens	B	14	C	B	A	B	B	B	B	C
proecox	(B)	100	B	B	B	A	B	C	C	C
pmemorsum	(B)	56	B	A	A	C	C	B	B	C
reflexum	C	(66)	B	B	B	C	C	C	A	B
rodolentum	(C)	51	C	C	C	A	B	C	C	C
saxosum	(C)	(60)	D	D	D	B	B	C	B	C
truncatum	(C)	61	D	D	C	A	B	C	D	C
utriculosum	(C)	29	C	C	C	C	C	B	C	C
vestitum	(A)	42	C	C	C	C	C	B	C	C

Real or expected compatibility is based on grafting results with 6 exceptional candidates and on taxonomic relationships, respectively. A = excellent; B = good; C = average/normal; D = unsatisfactory relative to *L. cordifolium.* Rooting values (except those in parentheses) ex Jacobs 1982 (Brits 1990c).

Tal et al. (1992a) showed that cytokinins and GA_3 had strong effects on multiplication, but that a medium containing BA was better than zeatin. GA_3 at 1 to 2 mg/L was essential for rapid proliferation and elongation of the shoots, providing nearly double the shoot increase of BA alone. GA_3 also enhanced shoot length, an important consideration in handling shoots during subculturing. Light intensities of the level of 230 $\mu mol \times m^{-2} \times s^{-1}$ enhanced in vivo rooting compared to lower intensities. The auxins, IAA, IBA, and NAA, all improved rooting over the use of no auxin, but the best rooting was with 1 mg IBA/L. Hardening off was successfully accomplished using plantlets with 3 to 5 nodes, fog (delivering 0.25 mm water/h), and high levels of light (14,000 lux). In conclusion, research results have laid the groundwork for commercial micropropagation of *Leucospermum,* but conventional systems of vegetative propagation are more widely used.

B. Environmental Responses

1. Light.

Jacobs and Minnaar (1980) determined that light intensity reductions of up to 50% did not slow the rate of flower development, but flower quality, as assessed by the number of styles per flower head, receptacle length and diameter, and inflorescence dry weight, decreased with decreasing light intensity. Jacobs (1983) proposed that there was a quantitative response to light intensity because heavy shading prevented flower initiation. Napier (1985) found that shading plants when they had been induced led to reduced carbohydrate in the leaves and a loss of the induced state. The reduced capacity of deheaded shoots to initiate an inflorescence during winter may be more related to low light energy relationships than to a short photoperiod (Jacobs 1980). Jacobs and Minnaar (1980) ruled out a major role for light intensity and stated that the main factors affecting rate of flower development in pincushion were temperature and shoot size.

2. Temperature.

In the areas of South Africa where *Leucospermum* spp. are native, the mean annual temperatures are 13 to 16°C and the monthly mean is below 20°C (Ben-Jaacov 1986). *Leucospermums* are frost-sensitive, and growers have observed plant loss in severe frosts. Diverse protea-growing areas such as Israel, western Australia, and California achieve greater extremes (Ben-Jaacov 1986). In the commercial production area of Hawaii, the range is from a monthly minimum daily mean of about 13°C during winter to a maximum daily mean of 25°C in late summer, but the daily mean seldom exceeds 20°C. The protea-producing area of the island of Madeira at 500 m above sea level has winter/summer ranges of 10-18/15-25°C (Blandy 1996).

Prior to establishing that flowering was under photoperiodic control, Jacobs (1976) and Jacobs and Honeyborne (1979) proposed that the accumulation of heat units (from 4.4°C to the average daily temperature beginning 1 May onwards in South Africa) controlled the rate of floral development. Following removal of a primary inflorescence bud, about 925 heat units above a 5.8°C base temperature were required to mature 90% of secondary flower buds that began to develop. Fewer days were required in late spring than early spring as a response to greater heat unit sums per day, about 8.5 early on to about 20 by mid-summer. Jacobs (1976) also suggested that the exploitation of warm and cool growing regions could extend the production period from August into January.

Criley et al. (1990) reported a 120-day development period for inflorescences of 'Vlam' once floret initiation began in the fall, with about one-fourth of the heat units accumulated in the last month of development. Heat unit accumulation (from a base of 6°C to the mean daily temperature from 1 September) was uneven, varying from 14 units/day in mid-fall to 10 in mid-winter under Hawaii conditions, with an average of 12.8 heat units per day over the period of development. The heat unit total was 1536 units from floret initiation until 50% bloom was achieved. They concluded that under short photoperiods with high light intensities, floral development could be rapid if temperatures were not

limiting.

Application of the light and temperature results may be difficult to achieve for field-grown pincushion plants, but possibilities exist for potted plants. One scenario would impose 12 hr SD during the high light period of the year on potted plants grown at 18-20°C. Flowering could be expected about 4 months after the development of a 1 cm bud.

3. Cold Tolerance.

In South Africa, most *Leucospermum* species are indigenous to frost-free areas of the Cape (Ackerman 1995) (Table 2.4). When grown outside their natural habitats, they experience both warmer and cooler temperatures. As a general statement, they will tolerate brief exposure to temperatures as low as -3°C. *L. cordifolium* is affected by severe frost, while species from higher elevations, such as *L. tottum* and *L. vestitum,* are more cold tolerant (Vogts 1980). *L. lineare,* from elevations of 300 to 1000 m, is another cold-tolerant species. Research on cold acclimation has not been reported, but growers have shared knowledge about plant survival during episodic cold periods through the newsletter of the IPA.

4. Soils.

Most of the *Leucospermums* are indigenous to nutrient-poor, coarse, acidic, sandstone-derived soils. A few species are indigenous to soils derived from limestone and with a high pH. Vogts (1980) and Matthews and Carter (1993) have described the native locales of several important commercial species, including *L. cordifolium, L. vestitum,* and *L. tottum.* The weathered Table Mountain sandstone soils (pH 4.5 to 6.5) of the Caledon and Bredasdorp districts support populations of *L. cordifolium,* while *L. vestitum* is found on similarly acidic soils in mountainous areas of the West Cape north to the Cedarsburg range. Weathered sandstone soils support *L. tottum* in mountainous areas of the Cape. *L. lineare* is found on gravelly clay soils derived from granite in mountains of the southern Cape.

The *Leucospermums* seem adaptable to a variety of soil types within a narrow range of pH and fertility levels, as evidenced by their culture in Hawaii and the Canary Islands (volcanic soils), southern California and Israel, Australia, and several regions of southern Africa. Soilless culture has also been successful using either 10 cm slabs of rockwool or crushed volcanic rock (Calo 1986).

Table 2.4. Origin and altitudinal distribution of some of the *Leucospermum* species grown in commercial cultivation (Rebelo 1995).

Leucospermum sp.	Habitat	Elevation (m)
Conocarpodendron ssp. *conocarpodendron*	Granite and sandstone soils	to 160
cordifolium	Sandstone soils	30 to 500
glabrum	Cool, southern slopes on peaty soils	150 to 500
lineare	Granite-derived clays	300 to 1000
patersonii	Restricted to limestone soils	50 to 300
reflexum	Near streams on sandstone soils	1000 to 2000
tottum var. *tottum*	Sandstone slopes	300 to 2000
vestitum	Varied, on rocky sandstone slopes	60 to 1350

C. Cultural Practices

1. Spacing.

Planting densities are governed by two considerations: the ultimate size of the plant and the method of maintenance. One commercial grower recommended that *Leucospermum* be planted 3 m apart in rows (Matthews 1982). An Australian recommendation is 1.7 m in-row and 3.5 m between rows (Matthews and Matthews 1994). A South African grower reported a spacing of 1.75 × 0.75 m (7580 plants/ha), but planting distances would change with changes in pruning method (Steenkamp 1993). As good drainage is required, hardpan should be broken up and the soil rototilled. If posts and wire supports are used, the height of the lowest wire will depend on the size of bush being planted, but may be as low as 15 cm from the ground. Additional wires are installed later. The main leaders of the plants are fastened to the wire by clips of the type used in the culture of various vining fruits.

2. Pruning.

Management of proteas began with minimal attention to the plant structure. However, as with many other woody plants, pruning was found beneficial because heading back increased lateral shoot production and controlled plant height and shape for ease of harvest and to facilitate spraying. Brits et al. (1986) pointed out that a balance between thinning and heading back is necessary to stimulate vegetative growth while minimizing production of non-marketable short flowering branches.

Brits et al. (1986) distinguished between proteas with a lignotuber and ordinary non-lignotuberous species. Some *Leucospermum* species (*L. saxosum, L. cuneiforme*) are lignotuberous, which means they produce an enlarged base consisting of thickened wood and bark on which numerous axillary and adventitious buds are visible. The lignotuber provides a source of new shoots when veld fires damage the higher parts of the plant. Both fire and pruning down to the lignotuber serve to rejuvenate the plant. In contrast, older shoots of the non-lignotuberous species tend to die back to the base, and pruning is used to remove old, nonproductive shoots or to stimulate lateral breaks on young (1- or 2-year-old) wood.

Leucospermum is pruned differently from *Protea* (Brits et al. 1986; Matthews and Matthews 1994) (Fig. 2.3). Strong flowering branches of the current season are headed back to 7-15 cm during or soon after flower harvest to produce bearing branches for the ensuing season. The early cutback permits a longer growing season and, potentially, a longer stem. Thinner, later-flowering branches are cut to their origins, as new shoots that might sprout from a short, thin stub result in a cycle of short branches, which again produce short branches. Producers normally thin the non-marketable flowering branches in a separate operation at the end of the flowering season. Strong flowering branches of lignotuberous species are headed back to within 30 cm of the base of the plant at a point just above well-developed buds.

Other aspects of pruning of *Leucospermum* parallel practices followed in managing other woody plants (Brits et a1. 1986). Old flower heads and seed heads are removed during postharvest follow-up pruning. Vigorous shoots of 10 to 15 cm length that developed during flowering are allowed to remain. Young, actively growing dominant shoots should be pruned back to 20 to 40 cm. poorly branching and short, thin shoots and dead and diseased shoots are removed. Seedling plants and rooted terminal cuttings of *Leucospermum* are headed back during vegetative growth flushes to improve plant shape and remove horizontal branches lying on the ground (Matthews and Matthews 1994). Flower heads that form on rooted cuttings should be removed to encourage lateral shoot growth. The prevalence of disease in the aerial portions of the plant will dictate the use of disinfectant on the pruning shears and protective sealants on pruning wounds 1.5 cm diameter or greater. Matthews and Matthews (1994) distinguish between *L. cordifolium* and other species of *Leucospermum* in recommending that the number of flowers per bush of the *cordifolium* types be strictly limited by pruning during the early years of bush development to achieve a more upright bush habit and longer stems. Yr 1: 0

Plate 1 *Banksia serrata* painted by Celia Rosser. Courtesy of Monash University.

Leucospermum cordifolium 'Vlam'

Plate 2 Leucospermum species that have contributed to the commercial assortment of pincushion cut flowers or potted plants *(L. oleifolum).* Photos by P.E. Parvin and R. A. Criley. (Continues on next page)

Leucospermum tottum

Leucospermurn conocarpodendron subsp. *conocarpodendron*

Leucospermurn lineare

Plate 2 Leucospermum species that have contributed to the commercial assortment of pincushion cut flowers or potted plants (*L. oleifolum*). Photos by P.E. Parvin and R. A. Criley. (Continues on next page)

Leucospermum vestitum

Leucospermum oleifolum

Leucospermum patersonii

Plate 2 Leucospermum species that have contributed to the commercial assortment of pincushion cut flowers or potted plants (*L. oleifolum*). Photos by P.E. Parvin and R. A. Criley. (Continues on next page)

Leucospermum reflexum var. *luteum*

Leucospermum reflexum

Leucospermum glabrum

Plate 2 Leucospermum species that have contributed to the commercial assortment of pincushion cut flowers or potted plants *(L. oleifolum*). Photos by P.E. Parvin and R. A. Criley.

Flw; Yr 2: 4 Flw; Yr 3: 10 Flw; Yr 4: 25 Flw; Yr 5: 50 Flw; Yr 6: 60 Flw. In their program, pruning is done at flowering and for a month or so afterwards.

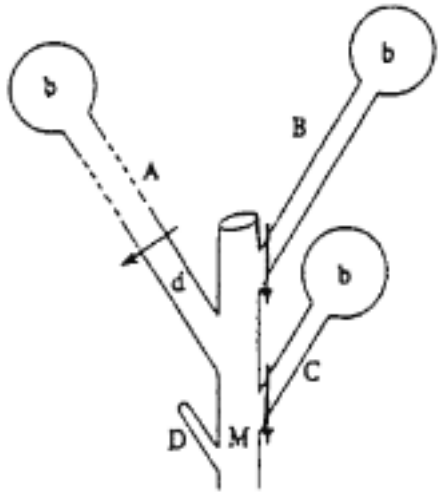

Fig. 2.3 Schematic representation f four types of schoots borne on productive Leucospermum plants and suitable pruning sites. A: strong flowering branch, the base of which is left when the flower is cut; B: weak flowering branch of marketable length; C: Weak, non-marketable flowering branch-both B and C are cut flush with the parent branch thinning cuts); D: thin, vegetative schoot that is left to develop in another growing season. b= flower; M= parent branch. Source: Brits et al. 1986.

Pruning is also used to influence flowering, principally to delay it. Early fall pruning to leave 10 to 15 shoots of 10 to 15 cm length was evaluated by Malan and Jacobs (1994) as a means to delay flowering through the production of shoots physiologically incapable of responding to short day inductive conditions. Night break lighting between 20:00 and 04:00 and supplemental irrigation were additive in prolonging stem growth. Naturally short day-lengths in spring were expected to result in reproductive development and an extended flowering season. The system was unsuccessful, however, because changes in growth habit during the cool, reduced-light-intensity days of winter resulted in few marketable stems. This study should be repeated, however, with other cultivars or in warmer regions to determine if temperature or light intensity were truly limiting.

3. Disbudding.

Following up on work by Jacobs and Honeyborne (1978), Brits (1986e) and Jacobs et al. (1986) demonstrated that removal of the primary inflorescence bud about two months prior to normal flowering led to the development of secondary inflorescence buds and a later harvest. Brits (1977) had previously demonstrated that application of ethephon to the branches prevented development of the primary inflorescence and activated the secondary inflorescence buds; later flowering was the result. Timing, however, was important, as late treatments caused loss of yield and decreased flower quality. Brits (1986e) suggested that it was necessary to select cultivars that would respond favorably to deheading or ethephon treatments. Both normally flowering and late-flowering cultivars were responsive.

Although all buds on a shoot have a potential to develop as flowers, normally the first bud to develop inhibits reproductive development of other buds. In a few species such

as *L. erubescens* and *L. saxosum* more than one flower develops, but on most large-flowered species, this is uncommon and undesirable for packing and shipping. Malan and Roux (1997) note that the characteristic of producing multiple flower buds does permit extension of the production season by removing the primary bud and allowing a secondary bud to develop. Since the second bud was suppressed in its initial development, it flowers later (Jacobs 1983, 1985). Malan and Jacobs (1990) had previously observed that decapitation of the terminal 5 cm of a growing shoot caused axillary bud break that was vegetative during natural or artificial long days but that resulted in development of an inflorescence in the uppermost axillary bud during the shorter day-lengths of fall. The capacity of these axillary buds to develop as inflorescences was lost as days lengthened in the spring. Between 42 and 56 SD cycles were necessary for inflorescence development and late winter decapitation provided too few SD for reproductive development.

Cultivar differences exist in the responsiveness of axillary buds to develop as inflorescences (Jacobs and Honeyborne 1978; Jacobs 1980, 1983). Disbudding of the primary inflorescence of 'Golden Star' in South Africa as late as October 15 was possible without crop loss (Jacobs and Honeyborne 1978), but 'Red Sunset' buds regenerated as vegetative shoots. September 15 was considered as the latest date at which disbudding would still provide a crop. Malan and Roux (1997) stated that the flowering time of early-flowering cultivars such as 'Ballerina' and 'Starlight' could be delayed better using disbudding techniques than later-flowering cultivars (Table 2.5).

The disbudding operation is more complex than merely delaying flower production because it impacts upon the next year's crop as well. Malan and Roux (1997) caution that the most vigorous shoots should not be disbudded, as these will be the early harvest of flowers and from their stubs develop the shoots for the next season's crop. Shoots of average vigor may be disbudded to produce a late crop, while weak shoots (<40 cm) do not respond well to disbudding. Disbudding can be done in groups to time the later crops for demand peaks. The practice of disbudding should only be applied to plants under a well-managed regime of pruning, fertilizing, and irrigating in which the vigor of the plant allows a predictability of the later production.

Table 2.5. The period of delay from normal peak flowering time, at Elsenburg, South Africa, following disbudding of Leucospermum cultivars during the period indicated (Malan and Roux 1997).

Cultivar	Normal flowering	Disbudding Period				
		Late April	Late May	Late June	Late July	Late August
		Weeks delay				
Tested on most vigorous shoots (mostly 60 to 80 cm long)						
Sunrise	late July	3-4	7-8	13-14	16-17	16-17
Luteum	early Sept.	3 month distribution of disbudded shoots				
Gold Dust	early Sept.	2-3	4-5	6-7	8-10	11-12
Scarlet Ribbons	mid Sept.	0	1-2	3-4	5-6	6-10
Flamespike	mid Sept.	0	0-1	0-2	4	6-7
Helderfontein	late Sept.	0	2-4	6-7	-	-
Yellowbird	late Sept.	0	0-1	1-2	4-6	4-8
Ballerina	early Oct.	0	0-3	2-4	4-7	7-11
Caroline	early Oct.	0	0-1	0-2	1-4	4-7
Red Sunset	early Oct.	0	0	0-3	3-4	4-7
Gold Star	mid Oct.	0	0	0	0-3	2-6
Vlam	late Oct.	0	0	0-1	2	5-7
Goldie	late Oct.	0		0	0-1	0-1
Tested on average shoots (40 to 60 cm long)						
Succession I	early Sept.		4-5	4-5	5-7	5-8
Succession II	early Oct.		0-1	1-4	4-6	5-7
High Gold	early Oct.		1-3	3-5	5-6	8-10
Starlight	early Nov.		0-2	1-4	1-7	3-8

4. Irrigation.

Water requirements for most Proteaceae have not been determined. In the mountainous regions of the Cape where many *Leucospermum* species are found, rainfall (@ 400 to 1000 mm) is concentrated in the winter months, while a few species are found in the summer rainfall (600 to 1000 mm) regions inland and further north. In the western Cape province, pincushions are cultivated without supplemental irrigation, relying on natural winter rainfall of 600 to 700 mm.

Malan and Jacobs (1994) reported that shoot growth cessation could be prevented during the dry fall by weekly irrigation at the rate of 27 L/mz (calculated from the author's description of their methodology), but night break lighting was required to continue the effect through winter. They concluded that water stress was the main cause of cessation of shoot growth prior to inductive SD in the autumn. However, many shoots were incapable of uninterrupted apical growth, and the development of distal axillary shoots rendered the shoots unmarketable as flower stems. Winter shoot production through the use of night break lighting and irrigation was not an effective approach to delay flowering until summer in 'Red Sunset' pincushion.

In a typic eutrandept, medial isothermic soil, commonly denoted as a loam at the Maui Agricultural Research Station (Kula, island of Maui, Hawaii, USA), where an average annual rainfall of 45 to 100 cm rainfall occurs, an irrigation rate of 5.5 to 7.5 L per plant per day was determined optimum (Wu et al. 1978). Less water was used in fumigated fields where the stress of root-knot nematodes was absent. The presence of root-knot nematodes increased water requirements by nearly 2 L per day. A rate of 3.8 L per day could achieve 80% of optimum yield during drought situations. The latter rate is similar to Malan and Jacobs (1994) rate of 27 L/mz, but is less than the 35 L per week recommendation of Furuta (1983).

5. Nutrition and Fertilization.

Unique to the Proteaceae are clusters of finely branched even-length rootlets occurring throughout the shallow root system of most species (Purnell 1960). The rootlets are crowded together along the axis of the lateral roots and are covered with long root hairs. They do not appear to have mycorrhizal associations, but it is reported that they are microbially induced (Malajczuk and Bowen 1974). The masses have a lifespan of about 6 months before shrivelling and disappearing. Such root masses are known as proteoid roots, and through their large surface areas they are thought to be responsible for K and P absorption (Lamont 1986; Vorster and Jooste 1986a). Grierson and Attiwill (1989) found increased H+ ion concentrations in leachates of proteoid roots, but also found increased levels of reduced manganese, and suggested that unidentified chelating compounds were released as well, since high amounts of aluminum have been found in leaves of Proteaceae. Lamont (1986) cautions that management practices such as cultivation will damage proteoid roots, and weed control is essential to reduce competition between the shallow proteoid roots and shallow-rooted weeds. Since the proteoid roots are concentrated in the leaf litter and surface layers of the soil, proteaceous species tend to be sensitive to chemical treatments, whether they be fertilizer, nematicides, or fungicides.

Phosphorus absorption in proteoid roots of *Protea compacta* showed a peak between pH 4 and 5.5 (Vorster and Jooste 1986a). Analyses also showed that proteoid roots were more effective in absorbing potassium than were ordinary roots. However, proteoid roots also accumulated their P, acting as sinks, while ordinary roots readily translocated P to the aerial parts (Vorster and Jooste 1986b). Inclusion of sucrose in experimental solutions stimulated the translocation of P from the proteoid roots, suggesting an energy-dependent mechanism for translocation from proteoid roots to the aerial parts. Proteoid roots were metabolically more active in P absorption at 35°C than at lower temperatures, while ordinary roots increased their rate of P absorption over the range of 15 to 35°C (Smith and Jooste 1986). Proteoid roots also displayed a higher oxygen uptake than did ordinary

roots.

Grierson and Attiwill (1989) demonstrated that proteoid roots can acidify their immediate environment. pH values of 4.2 to 4.4 were reported in the leachates of proteoid roots of *Banksia integrifolia,* while associated leaf litter and soil 5 cm away had pH values of 7.1 and 5.5 to 6.5, respectively. They concluded that nutrient uptake is enhanced by lower pH and the release of organic chelating compounds from the roots. With *Protea cynaroides,* periods of active growth of proteoid roots immediately precede bud differentiation and bud development (Hanekom et a1. 1973) and thus correlate with periods requiring high nutrient uptake.

Although the above results were obtained with *Protea compacta, P. cynaroides,* and *Banksia integrifolia,* the principles may be extended to *Leucospermum.* The mass of fine proteoid roots permits greater diffusion of oxygen around them. Their sugar and oxygen requirements and greater metabolic activity in both ion absorption and translocation suggest proteoid roots play a unique role in the nutritional status of these plants. The proteoid roots die off during the dry summers and are replaced each winter with the return of winter rains, a period when inflorescence development takes place.

Both numbers and mass of proteoid roots increased during *L. parile* seedling development (Jongens-Roberts and Mitchell 1986). Mobilization of P to the canopy occurred in 1- to 2-year-old plants, while in 5- to 6-year-old flowering plants, P level declined in the non-reproductive parts of the plant. In young plants, root production and foliar phosphorus content increased during the winter, but there was a marked decline in both in older plants.

The phosphorus-phobia vis-à-vis the Proteaceae is widely circulated in the commercial literature [c.f., "Provided phosphate is totally withheld, average pH levels of 5 will be acceptable..." (Riverlea Nursery undated)] and has received attention from researchers (Allemand et al. 1995; Malan 1996). Rates of fertilization considered normal for other woody plants often caused phytotoxicity to proteas, and Munro (1990) related that growers were advised not to supply P in their fertilizer programs. Nichols (1981) classified *L. cordifolium* among the highly sensitive proteas as a result of experiments providing young plants with 1 to 2 kg P/M3 of soilless potting medium. Sanford (1978) reported very little effect of phosphorus addition (as treble superphosphate) of up to 400 kg P/ha in field culture, although there was a slight increase in marketable yield. Foliar content of P was not correlated with yields of flowers per plant. One Australian grower (Bowden 1987), however, reported that his proteaceous plants responded to low levels of slow-release forms of P. His account suggests a need to examine the form in which P is applied. Trials of 0.1% potassium dihydrogen phosphite as a foliar spray for *Phytophthora cinnamomi* control showed no trace of phytotoxicity in several proteaceous species, including *L. reflexum,* while providing a high degree of control of the pathogen (Wood 1987; Turnbull and Crees 1995). Similar effectiveness was observed on four *Leucadendron* species (Marks and Smith 1989).

Matthews (1982) suggested that soils used for *Leucospermum* culture should have a pH of 5 to 5.5, K and P levels below 20, Ca below 10, and Mg below 30. On the basis of New Zealand Ministry of Agriculture and Forestry soil analysis, the following nutrients levels (units not specified) were considered suitable for Proteaceae: Ca, 6; P, 4 to 6; K, 4 to 6; and Mg, 8 to 12 (Salinger 1985). In Hawaii, a minimum soil content of 32 ppm (P_20_5), 0.117 meq K, and a pH of 5.5 to 6.1 were recommended (Munro 1990).

In soilless culture using rockwool slabs or crushed volcanic rock, satisfactory growth of *L. tottum* and *L. reflexum* was achieved using a fertility regime of 50 ppm N, 15 ppm P, 25 ppm K, and 1 ppm microelements. The pH was maintained between 5.5 and 6.5 by addition of sulfuric acid (Calo 1986). In pine bark and sand, root development, plant height, and branching of containerized *L. cordifolium* plants were satisfactory with N levels of 50 and 100 ppm and P levels of 4.5 and 9 ppm in twice-weekly liquid feeding (Matthews 1993).

Parvin (1986) reported on the application of tissue analysis to understanding the nutritional requirements of *Leucospermum.* Samples of recently matured leaves from the most recently matured vegetative flush of growth were collected from healthy green,

field-grown plants. The analyses (Table 2.6) were used to define a baseline against which abnormal plants could be compared. Seasonal variation existed, but only calcium and magnesium showed large differences between the vegetative growing period of summer and the inflorescence development period of late fall, with higher values for the former than the latter. Sanford (1978) found little relationship between amounts of N, P, and K applied as fertilizer and foliar levels of the same nutrient. In his study, foliage N ranged from 1.27 to 1.38%, P was in the range of 0.14 to 0.16%, and K ranged from 0.62 to 0.67% in recently expanded leaves.

Using sand culture, Claassens (1986) determined that *Leucospermum cordifolium* responded better to ammonium than nitrate forms of N, although this species tolerated nitrate better than did the genus *Protea.* Analyses for the highest dry matter yield showed somewhat higher tissue concentrations for P, K, and Ca and lower N than did Parvin's fieldgrown plants (Table 2.6). He also analyzed the flower heads of unfertilized veld plants and his fertilized sand culture plants and found trends to be similar except for nitrogen. Claassens concluded that higher N levels contributed to higher yields as well as to a higher nutrient content, and that N in the ammonium form is the predominant element that needs to be managed in culture. Witkowski (1989, 1990) reported that *L. parile* stored N in leaves and twigs and used it during inflorescence production during the next year. Claassens's (1986) study was cited by Brits (1990c), with the additional information that certain ecotypes originating on calcareous soils tolerated higher concentrations of $N0_3$, NH_4, P, alkalinity, and total salts than ecotypes originating from more acidic soils. Brits suggested that such characteristics might be a useful guide to selecting rootstocks. Malan (1996), on the other hand, offered the opinion that fertilization may be so dependant upon variety and site characteristics that recommendations would need tailoring to specific conditions.

Table 2.6. Foliar and flower head tissue analyses of *Leucospermum cordifolium.* (Parvin 1986 and Claassens 1986).

	Content (% Dry Weight)			
	Foliage		Flower Head[z]	
Element	Parvin[y]	Claassens	Veld	Sand culture
N	1.18	0.86	0.50	2.00
P	0.09	0.12	0.08	0.15
K	0.49	1.39	1.40	1.60
Mg	0.22	0.20	0.60	0.60
Ca	0.53	1.05	0.20	0.25
S	0.14			

[z] Claassens 1986.
[y] Content for microelements (ppm): Al (190), Cu (6), Fe (118), Mn (248) and Zn (30).

6. Production Period.

Although there are nearly 100 *Leucospermum* cultivars available, the exporters see a need only for a few lines that cover the entire marketing period. Since a cultivar typically blooms for only 4 to 6 weeks, approximately 6 to 8 cultivars flowering in succession would cover the late winter to late spring marketing period (Brits 1992b). These would include the basic color lines and early, mid-season, and late production periods.

Parvin (1974) reported that 65-75% of the total crop of *L. cordifolium* 'Hawaiian Sunburst' was harvested during the December through February time period in Hawaii. During a three-year study, beginning with 6-year-old plants, the per-plant yields averaged 600 to 650 flowers. Approximately three years transpires under Hawaii

conditions from initial seeding or rooting of cuttings before commercial levels of flower harvesting develop (Parvin 1974). Jacobs (1976) suggested that the flowering season could be extended by developing clonal selections from early- and late-flowering seedling populations (Fig. 2.4). His data showed that 50% of the crop could be harvested in 14 to 29 days, but through suitable selections, the marketing season could be extended over four to five months. *Leucospermum* releases of the ARC Fynbos Unit extend the season from mid-August (late winter) to mid-November (mid-spring) (Table 2.7).

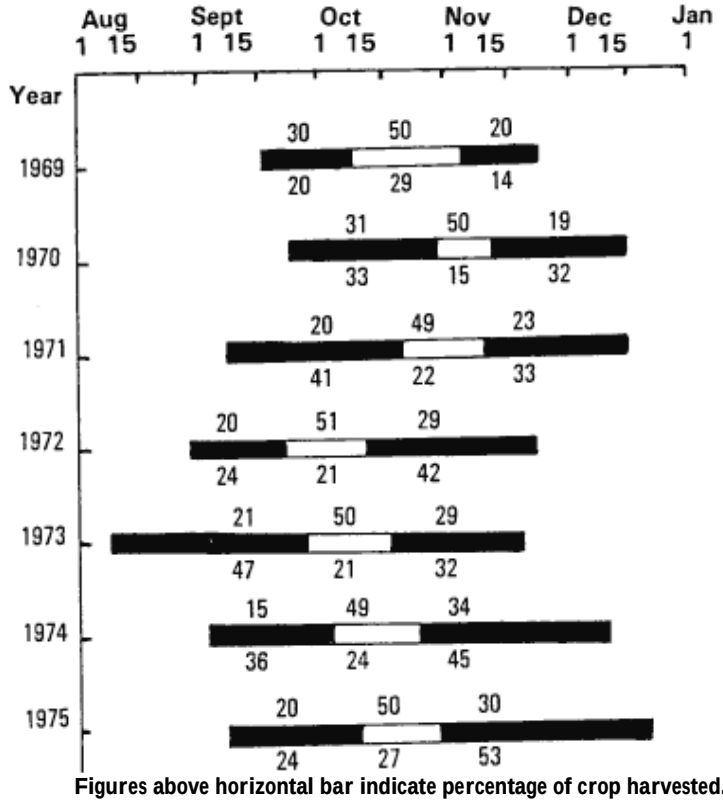

Fig. 2.4 Distribution of flowering in a seedling population of *Leucospermum cordifolium* in South Africa. Source: Jacobs 1976.

7. Growth Regulator Studies.

Long, strong stems are desired by the cut flower growers, but some *Leucospermum* species and hybrids produce stems too short to be of commercial value. Napier et al. (1986a,b) investigated the influence of single and multiple sprays of GA at 1000 mg/L on a hybrid *of L. conocarpodendron* × *L. cordifolium* during the summer vegetative growth stage. They noted that GA applications were ineffective in causing elongation when shoots were reproductive, but internodes between basal bracts of the shoot were elongated. Multiple applications of GA caused a marked increase in stem length without affecting shoot diameter. The dry weight per unit length of shoot was decreased because of smaller leaves. In a concentration comparison, GA at 750 mg/L applied five times at three-week intervals provided optimal shoot elongation, while

higher concentrations caused damage to the leaves and shoot tip, and shoot diameter was thinner.

Table 2.7. Color and flowering periods in the western Cape (South Africa) for 17 *Leucospermum* cultivars released by the Fynbos Unit of the Agricultural Research Council of South Africa (Brits 1992b).

	Flowering Period		
Color	Early[z]	Mid-season[y]	Late[x]
Yellow		'Yellow Bird' *L. cordifolium*	'Goldie' *L. cuneiforme*
		'Luteum' *L. reflexum*	
		'High Gold' *L. cordifolium* × *L. patersonii*	
Red	'Sunrise' *L. cordifolium x L. patersonii*	'Flamespike' *L. cordifolium*	'Vlam' *L. cordifolium*
		'Fire Dance' *L. cordifolium*	
Pink/Pastel/ Novelty	'Succession 1' *lineare-type*	'Scarlet Ribbon' *L. glabrum* × *L. tottum*	`Pink Star' *L. cordifolium*
	'Helderfontein' *L. glabrum*	'Tango' *L. glabrum* × *L. lineare*	`Caroline' *L. cordifolium* × *L. tottum*
			'Starlight' *lineare-type*
		'Succession 2' *lineare-type*	'Ballerina' *lineare-type*

[z] Middle August to end of September
[y] Middle September to end of October
[x] Late September to mid-November

In a similar field study on a *L. conocarpodendron* × *L. cordifolium* hybrid, Malan and Jacobs (1992) reported that a single GA_3 spray at 500 mg/L, when shoots resulting from pruning were 10 to 17 cm long, markedly increased the number of shoots longer than 30 cm when compared to control plants. Pruning was done in late winter to leave a stub about 20 cm in length, and the GA application was made 10 to 12 weeks later. Their study included multiple applications, but only up to 3, a month apart, and shoot length increased with multiple applications, as in Napier's study. Internode length was affected only slightly (no data presented), but node count was increased significantly. Their final recommendation of 500 mg GA_3/L was based on the economics of GA application, higher concentrations being uneconomic in their opinion.

Application of the cytokinin benzylaminopurine (BA) to developing inflorescences of 'Red Sunset' increased the number of florets in the inflorescence as well as dry weight, but also caused abnormal peduncle growth (Napier et al. 1986b). A single application made early in the development of the inflorescence increased floret number by 45%, while multiple applications added only slightly more, although dry weight of the inflorescence increased as the number of BA applications increased to four. Malan et al. (1994c) reported that apices of BA-treated shoots were larger than those of untreated shoots and more bract and flower initials were produced as a result, thus confirming the observations of Napier et al. (1986a). Spray applications of BA after inflorescence initiation stimulated the development of several inflorescence buds on the same branch,

a process that ended in the abortion of the inflorescence buds (Wallerstein and Nissim 1988).

Dupee and Goodwin (1990) reported that application of gibberellin (GA_{4+7} or GA_3) or paclobutrazol to initiated flower buds enhanced flowering by 3 to 9 days. Terminal bud removal delayed flowering, while terminal bud removal and treatment of the next bud with GA_{4+7} hastened the development of the secondary bud. Spray applications of GA to initiated inflorescences accelerated development, but also caused flower bud abortion (Wallerstein and Nissim 1988). Ethephon (960 mg/L) is also being used on mother plants to induce multiple branches on shoots to be harvested and used as cuttings for potted plant production (Brits et al. 1992).

The use of auxins for rooting of cuttings is treated under propagation.

Ethephon application (500 mg/L) to decapitated shoots reduced their responsiveness to inductive short days (Napier and Jacobs, 1989). Ethephon also enhanced the loss in responsiveness to short days when the plants were grown under shade. It is not clear how ethephon interacts with the lowered carbohydrate status of the shoot to reduce flower initiation.

D. Plant Protection

1. Diseases.

Among the important diseases affecting *Leucospermum* are root and collar rots caused by *Phytophthora cinnamomi* Rands and *P. nicotianae* Breda de Haan, leaf spots and stem cankers caused by *Dreschslera dematioideo* (Bubak and Wrobl.) Subramanian and P. C. Jain, and *D. biseptata* (Saci and Roum) M. J. Richardson and E. M. Fraser, a stem and leaf scab caused by a *Sphaceloma (= Elsinoe* telomorph) sp., and a canker and dieback caused by *Botryosphaeria dothidea* (Moug:Fr) Ces and De Not. (Von Broembsen 1985, 1989; Von Broembsen and Van der Merwe 1985; Knox-Davies et al. 1988; Kent 1989; Nagata and Ferreira 1991, 1993). *Botrytis cinerea* Pers.:Fr also colonizes young shoot tips and buds of *Leucospermum* (Cho 1977). The aerial diseases are favored by conditions where dew or fog persist in the mornings and are transmitted by splashing water and cuts caused by pruning and flower harvest. The *Dreschlera* group and *Sphaceloma (Elsinoe)* require free water for conidial germination (Benic and Knox-Davis 1983; Kent 1989).

The first report of verticillium wilt on any protea species appeared in 1991 (Koike et a1. 1991), when affected plants of *L. cordifolium* collapsed and died. Symptom expression included terminal shoot wilting, fading of foliage to light green and eventual collapse and browning of the entire plant. Brown flecking and streaking were apparent in the stem xylem tissue. *Verticillium dahliae* Kleb was isolated and its pathogenicity confirmed by inoculation into and reisolation from cuttings of *L. cordifolium* cv. Firewheel.

In the long term, breeding for disease resistance is a desirable alternative to fungicide use, but with the past emphasis on breeding for flower qualities, little progress has been made. Some progress has been reported in breeding for *Phytophthora* tolerance and *Dreschlera* resistance (Von Broembsen and Brits 1985, 1990), but all species evaluated lacked resistance. Good tolerance was shown for several hybrids and species selections and some tolerance appeared to be expressed within *L. cordifolium* (Von Broembsen and Brits 1990). Leonhardt et al. (1995) reported some resistance to *Sphaceloma* (*Elsinoe* scab disease) in *L. conocarpodendron* and *L. reflexum.* They have also found some interspecific hybrids with resistance to *Sphaceloma, Botrytis,* and *Dreschlera.* Matthews (1988) reported that *L. patersonii* showed some resistance to pincushion scab with a cultivar 'Goldie' completely resistant.

Protective fungicides (e.g., mancozeb, iprodione, chlorothalonil) are recommended, as well as regular sanitation to remove diseased or dead plant parts. Control of canker and dieback was achieved by a single spray application of benomyl immediately after pruning. Since *Leucospermum* is extremely susceptible to

Phytophthora (Von Broembsen and Brits 1985), control measures include avoiding poorly drained sites, planting disease-free nursery material, and fumigating the soil with methyl bromide prior to planting. Soil solarization has also been recommended (Knox-Davies 1988). Systemic fungicides have given inadequate control or are phytotoxic.

Control measures for many foliar diseases include roguing, sanitation, disinfection of pruning shears, and application of fungicides. Over-reliance on broad-spectrum fungicides such as benomyl has fostered resistance among some pathogens (Cho 1977). Due to the ever-changing spectrum of chemical controls, it is impractical to attempt to list effective materials, but useful resources include *Protea Diseases* (Von Broembsen 1989), *Protea Diseases and Their Control* (Forsberg 1993), and the occasional publication of *The Protea Disease Letter* (Nagata and Ferreira 1991, 1993) by the University of Hawaii.

An interesting biological control approach against *Phytophthora cinnamomi* utilized selected strains of *Pseudomonas cepacia* (Turnbull et al. 1989). Among the Proteaceae, *Leucospermum* was still susceptible to the root rot when inoculated with *Pseudomonas cepacia,* but plant mortality was slightly reduced. The promise of biological control, at least for *Leucospermum,* remains unfulfilled.

2. Nematodes.

Root-knot nematodes can severely limit growth and productivity of *Leucospermum* (Cho and Apt 1977). Heavily infected plants show stunting and chlorosis, followed by death of the plant. Treatments with phenamiphos and the fumigant dibromochloropropane (DBCP) increased shoot growth and flower production (Cho et al. 1976). The root-knot nematode [*Meloidogyne incognita* (Kofoid and White) Chitwood] decreases cut flower yields by at least 25% in infected fields compared to fumigated fields with an optimal irrigation regime (Wu et al. 1978). Under drought conditions or with minimal irrigation however, yields were comparable.

3. Insect Pests.

Three general categories of insect pests that damage proteas are (1) flower visitors, which may or may not damage the flowers but which are quarantine problems because the flowers must be marketed insect-free; (2) leaf feeders, leaf miners, and sap suckers, which cause aesthetic damage to the foliage of exported cut flowers; and (3) borers, which use protea stems and flowers as their hosts (Coetzee 1987a, 1987b). Occasionally centipedes and snails are found in the flower heads. A "Witches Broom" stem proliferation condition in protea may be caused by a mite *(Aceria proteae)* (Coetzee 1987a). Seed predation is a problem both in the wild and for propagators of proteas from seed (Coetzee and Giliomee 1987). Effective registered pesticides exist for some of the pests, but differ from country to country.

4. Weeds.

Nishimoto (1975) reported little or no injury from high rates of dichlobenil and oxadiazon (Ronstar) on trickle-irrigated *Leucospermum* planted 8 months prior to treatment. However, slight to severe injury was reported from simazine, ametryne, and diuron, especially at high rates. Weed control from all treatments was good. DeFrank and Rauch (1988) achieved acceptable weed control from pre-emergent sprays of oxadiazon and oxyflurofen 2% + oryzalin 1%, but noted that a black plastic woven ground cover suppressed all weed growth, which has since become an accepted weed control practice in Hawaii. For grass weed control, DeFrank (1990) recommended the post-emergent herbicides: fluazifop-butyl (Fusilade), sethoxdim (Poast), DPX 6202 (Assure), and RE-36290 (Selectone). DeFrank and Rauch (1988) achieved satisfactory post-emergence grassy weed control with the manufacturer's recommended rate of fluazifop-P, but noted that a 4X rate could damage *Leucospermum* flower buds.

E. Postharvest Studies

1. Handling and Storage.

Except in southern California, proteas tend to be grown in areas far distant from their markets. As most proteaceous flowers are heavy and/or bulky, air shipment is expensive, and shippers have investigated slower shipment methods, including seafreight. Pincushions are normally harvested with at least the first row of styles open, but this varies with the cultivar and destination. For packing into boxes, inflorescences with too many open styles are not desired because of tangling. On average, about 50% of the styles are open (Matthews and Matthews 1994).

Research on postharvest handling practices has shown that the pincushion protea will tolerate cool, dry, long-term storage and still provide a useful vaselife. *L. cordifolium* flowers that were cooled and hydrated at 1°C in water, wrapped in newsprint and bagged in plastic film withstood periods of three and four weeks of 1°C storage, and after rehydration, possessed an average vaselife of 8 days, versus 9 days for untreated controls (Jones and Faragher 1990). Haasbroek et al. (1973) successfully stored *L. cordifolium* at 1.7°C for 3 and 4 weeks without significant deterioration in vaselife. Downs and Reihana (1986) found significant varietal differences in vaselife following a period of simulated transport, with the New Zealand cultivar Harry Chittick at 35.5 days, a Hawaii hybrid of *L. lineare* × *L. cordifolium* at 29.7 days, and a South African hybrid *(L. glabrum* × *L. conocarpodendron)* Veldfire at 16.9 days.

Parvin (1978) improved vaselife of *Leucospermum cordifolium* by 44 to 48% through the use of a 2 to 4% sucrose plus 200 to 600 ppm hydroxyquinoline citrate "preservative" solution. Silver nitrate at 1000 ppm was not beneficial for the cultivars of *L. cordifolium* but improved vaselife for the *L. conocarpodendron* × *L. cuneiforme* hybrid, 'Hawaii Gold' (Parvin and Leonhardt 1982).

Since the mature, expanded pincushion flower occupies as much room in a shipping carton as a standard chrysanthemum, investigations were undertaken into the revival of wilted flowers with extruded styles, which could be packed more tightly. Flowers pulsed with a preservative prior to partial dehydration (20% loss of FW) and storage (24 h at 13°C) could be revived, although vaselife was not as long as with fresh cut flowers (Criley et al. 1978a, 1978b). *Leucospermum* flowers cut in bud (7 cm diameter) offered better promise, however, with full development and less loss of vaselife than flowers cut at a younger stage (Criley et al. 1978a; Parvin and Leonhardt 1982).

2. Insect Eradication.

A variety of approaches has been used to eradicate insects from the flower heads before shipping. Maughan (1986) reported that fumigation of various *Protea* spp. with methyl bromide, carbon dioxide, nitrogen, sulfur dioxide, dichlorvos, pyrethrum, and combinations killed varying amounts of insects, but often damaged the flowers or decreased vaselife. Treatments combining carbon dioxide with pyrethrum or diclorvos required exposures up to 30 h for 100% kill, but did not produce marked damage. Magnesium phosphide gas plus dichlorvos also has given excellent control (Wright and Coetzee 1992), as has a pressurized aerosol of dichlorvos (Coetzee 1987b; Wright 1992). Vapor heat treatments of 10 min at 56°C or 66°C decreased vaselife of cut *Banksia prionotes* by 21% and 49%, respectively, while hot water dips of 30 min at 46°C or 10 min at 56°C damaged the inflorescences and reduced vaselife by 25% and 37%, respectively (Seaton and Joyce 1993).

Gamma irradiation of protea flowers effectively killed earwigs, spiders, weevils, millipedes, and ants after 50 minutes of exposure (0.1 to 2.9 megaRads) without serious leaf blackening, but the experiments did not include *Leucospermum* (Wright and Coetzee 1992). At a dose required to kill insects (10 k Gy), flowers and leaves of *Banksia* were damaged (Seaton and Joyce 1992). In the only similar work mentioning *Leucospermum,* inflorescences with 50% of the styles reflexed were subjected to 30 Krads of gamma irradiation (Haasbroek et al. 1973). Evaluation of the flowers and foliage

after irradiation, 36 h storage at 15°C, and rehydration in a preservative solution showed little or no damage and a vaselife of 28 days versus 23 days for blooms with no irradiation treatment. Since corroborating data is lacking, it is not clear whether *Leucospermum* is more tolerant to gamma irradiation than other proteaceous flowers or whether the conditions of this experiment were unique.

3. Grades and Standards.

For many years, harvest of pincushions from natural stands in the veld resulted in mixed quality and lack of uniformity of the product (Littlejohn et al. 1995). This situation improved as pincushions moved to more distant cultivation areas and seedlings and selections were planted out. Little effort was made to manage the plants for longer, straighter stems. Initially, the wholesale and retail florists accepted mixed qualities, but the existence of standards for most floricultural crops stimulated a similar request for the proteaceous cut flowers as well. An early attempt to gain approval for grades and standards for cut pincushion flowers (Hawaii Dept. Agr. 1980; Table 2.8) failed to enlist grower support. A major deficiency of this proposal was acceptance of short stem flowers. The Flower Export Council of Australia (1992) circulated a draft grades and standards proposal (Table 2.9).

Where they languish, grades and standards need to be implemented, if only to improve communication in the overseas flower markets that exporters have targeted. The IPA itself should develop a set of standards for stem length and straightness; flower shape and freedom from defects, insects, and diseases; and descriptions for single- and multiple-headed stems. Tables 2.8 and 2.9 present a platform from which to start.

Table 2.8. Standards proposed for *Leucospermum cordifolium* by the Hawaii Department of Agriculture (1980).

	Class (Grade)	
Standard	Extra fancy	Fancy
Stem length from cut end to base of flower head	> 23 cm	15 to 23 cm
Flower	Full head, well-formed and symmetrical, well developed, more than 1/2 styles reflexed, well colored, and typical of the species.	Full head, well-formed and symmetrical, well developed, more than 1/2 styles reflexed, well colored, and typical of the species.
	Clean, properly trimmed, free from injury.	Clean, properly trimmed, free from injury.
	Angle of flower head not more than 90^0 to the stem.	Angle of flower head not more than 90^0 to the stem.
Foliage	Leaves stripped from lower 3/4 of stem.	Leaves stripped from lower 3/4 of stem.
	Slight defect or blemish permitted.	Slight defect or blemish permitted.
Stem straightness	Curvature not to exceed 2.5 cm from a straight line.	Curvature not to exceed 2.5 cm from a straight line.
Tolerances for defects and off-size	Not more than 2% by count may fail to meet the requirements of the grade or the stem length.	Not more than 2% by count may fail to meet the requirements of the grade or the stem length.

Table 2.9. Flower Export Council of Australia proposed standards (1992) for cut Proteaceae *(Leucospermum).*

	Class (Grade)	
Standard	Extra class	Class 1
Minimum length	60 cm	40 cm
Flower	Well formed.	Reasonably well-formed.
	Sound, clean, uniform, of good color and size, no abnormal external moisture, fresh in appearance, insect- and disease-free.	Sound, clean, uniform, of good color and size, no abnormal external moisture, fresh in appearance, insect- and disease-free.
	Proportion of reflexed styles < 5%.	Proportion of reflexed styles < 5%.
	Flowers not hidden by leaves.	Flowers not hidden by leaves.
Foliage	90% leaves intact on not less than 50% of stalk below flower head.	90% of leaves intact on not less than 50% of stalk below flower head.
Clonal	Flowers of clonal origin.	Flowers typical of the variety.
	Typical of variety and species.	Typical of species.
Single bloom	Stems straight (no more than 10° bend).	Straight stem with flower head no more than 45° bend.
Tolerance for defects and blemishes	5%	10%

F. Genetic Improvement

One of the first *Leucosperm* um hybrids to be registered was a red hybrid named 'Mars', selected in 1969 by the late F. C. Batchelor on his Protea Heights farm from a *Leucospermum cordifolium* population after five generations of mass selection (Brits 1984a, 1985a). As of the fourth edition of the International Protea Register (International Registration Authority: Proteas 1997), 30 cultivar names have been registered and another 58 have been noted but not registered for selections and interspecific hybrids of *Leucospermum.*

Breeding objectives for proteas have mostly focused on new flower colors, improved productivity, and a longer season of bloom, but characteristics such as improved postharvest life, disease resistance, and slender, longer, and straighter stems, reduced leaf pubescence, and smaller leaves have also received attention (Brits 1992a, 1992b; Ito et al. 1990; Leonhardt et al. 1995). *L. lineare* has been used to contribute slender, light-weight stems with narrow, pubescence-free foliage, all qualities sought by flower exporters (Leonhardt et al. 1995). *L. lineare* contributes earliness to hybrids with *L. cordifolium,* while *L. tottum* contributes a later flower season (Jacobs 1976). Interspecific hybrids of *L. lineare* with *L. cordifolium* have been selected that markedly extend the normal flowering season in South Africa (Brits 1992b). Active breeding programs are being conducted at the Fynbos Research Station, Elsenburg, South Africa (Brits 1992a, 1992b; Littlejohn et al. 1995) and at the Maui Research Station of the University of Hawaii (Ito et al. 1978, 1979, 1990, 1991; Leonhardt et al. 1995), and in Israel (Shchori et al. 1995).

Breeding and selection require 10 to 15 years, although some hybrids have been produced in less than 10 years (Ito et al. 1990). In Israel, evaluation of hybrids between *L. patersoni* and *L. conocarpodendron* yielded four high-yielding cultivars tolerant of high pH soils and a rootstock cultivar in only four years after planting out (Shchori et al. 1995). Ackerman et al. (1995) selected plants tolerant to high pH, calcareous soils, from seedlings of *L. patersoni.* One selection, designated 'Nemastrong', was also tolerant to nematodes. A cross between *L. patersonii* and *L. conocarpodendron,* designated 'Carmeli', also demonstrated excellent resistance to high pH and calcium. Both selections root well from cuttings and have good grafting characteristics.

G. *Leucospermum* as a Pot Plant

While a number of the Proteaceae may be grown as potted plants, the *Leucospermums,* with their relative ease of rooting and attractive floral display, have the greatest potential (Sacks and Resendiz 1996). Plants for sale need to be offered with several buds open. High light intensity is necessary for flowering (Jacobs and Minnaar 1980; Napier and Jacobs 1989; Ackerman et al. 1995) as well as for rapid rooting of cuttings. Research on the photoperiod responsiveness of *Leucospermum* (Wallerstein 1989; Malan and Jacobs 1990) indicates that daylength manipulation may have implications for potted flowering plant production as well.

Leucospermum species suitable for potted plants are of two types: those having a single large inflorescence, such as *L. cordifolium, L. lineare,* and *L. tottum;* and those with small multiple inflorescences (conflorescences) such as *L. oleifolium, L. muirii,* and *L. mundii* (Ackerman et al. 1995; Brits et al. 1992; Brits 1995a). It is important to select material that will root rapidly and support flower initiation and development on a young root system (Ackerman and Brits 1991; Brits et al. 1992).

1. Production.

Some pinchusions do not respond well to a short production cycle and must be grown on a longer cycle of 18 to 24 months (Ackerman et al. 1995). These include the multiple-headed species and some single-headed types. Branched cuttings are produced on the mother plant, rooted in late autumn, and kept under production an extra year to flower in the second season. Sacks and Resendiz (1996) use a 20-month production program, rooting cuttings in the summer, transplanting to 10-cm pots, and pinching to induce branching the following spring and potting up to 16-cm pots. Salable pots with 5 to 6 buds per plant are produced a year later.

The growing medium should be lightweight but capable of holding sufficient water and nutrient cations (Brits et al. 1992). A medium of 10 peat:40 pine bark:50 river sand supplied with a liquid feed at each irrigation (77 ppm N, 5 ppm P, 63 ppm K, 23 ppm Ca, 8 ppm Mg, 1.8 ppm Fe, and a microelement complex) proved satisfactory (Ackerman et al. 1995), while Ben-Jaacov et al. (1989) reported successful cultivation in media of 4 coarse peat:4 fibrous peat:2 vermiculite No. 6 or 3 volcanic tuff (8 mm):1 peat in 10-cm pots.

Brits (1990a) provided a rapid production method using cuttings that had set buds on the mother plant (Fig. 2.5). Following rooting, the inflorescences developed, producing a marketable potted plant within 6 to 8 months after harvesting of the original cuttings. As one single flowering stem, the plants were not marketable because of weak stems and lack of fullness, but several single-stem cuttings per pot is feasible (Brits et al. 1992). Branched, budded cuttings are useable, but cultivar selection for the capacity to continue inflorescence development is necessary to avoid bud abortion during or following rooting. Alternative protocols for rapid pot plant production are illustrated in Fig. 2.6. Brits et al. (1992) suggested that taking the cuttings in late summer (earlier than the semi-hardwood stage) would overcome the problem of abortion of the primary flower bud and allow rooting to occur before initiation of flower buds. They suggested heading back soft terminals to harder subterminal wood.

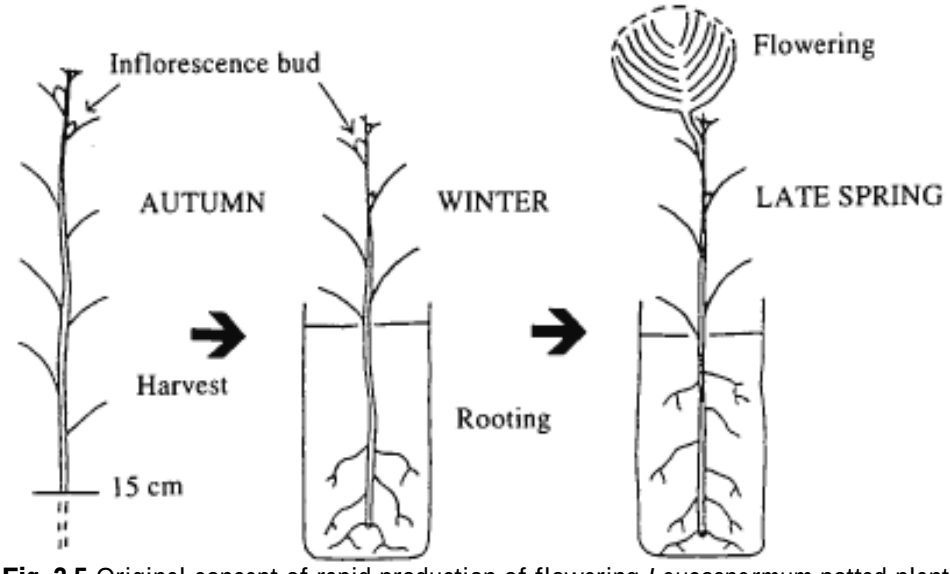

Fig. 2.5 Original concept of rapid production of flowering *Leucospermum* potted plants from semi-hardwood cuttings rooted while bearing a flower bud. Source: Brits et al. 1992.

POT PLANT PRODUCTION SYSTEMS

Month of activity

S O N D J F M A M J J A S O N
A.
Harvest cuttings during flower initiation. Select for shoots of at least 3.5 mm diameter. Select for multiple branched cuttings with desirable angle to main stem and short enough to be proportional to final pot size.
Flower initiation in the field
Rooting period: Harvest cuttings, Root growth
Resume flower development
Flowering
8 months
B.
Shoot tips of mother plants are pinched and headed back, and branch-stimulating compounds such as BA and ethephon are applied. Harvest cutting early – during active growth. Root during late summer and allow flower initiation at normal time.
Rooting period: Harvest Root growth
Flower initiation on own roots
Flower development
Flowering
10 months

Fig. 2.6 Alternative rapid production systems for *Leucospermum* potted plants in the southern hemisphere using cuttings harvested in different physiological stages. Source: Brits et al. 1992.

Yoshimoto (1982) successfully rooted cuttings with branches stimulated by removing 6 to 10 cm of tip during spring and summer, but he was not successful in forcing flowering in the next season. At that time, the application of high light and photoperiod requirements was unknown. A significant advance in production of potted *Leucospermum* 'Ballerina' was reported by Brits et al. (1992). Branched shoots (Fig. 2.7) produced by spraying 960 mg ethephon/L on strongly elongating primary shoots about 10 cm long on the mother plant were rooted and manipulated as potted plants. The resulting shoots had a wider angle to the primary shoot compared to hand-pinched controls and produced a more desirable shape for marketing. Observations from other studies (Brits et al. 1986; Jacobs and Minnaar 1980; and Napier 1985) suggested that shoot diameter was important for good flower initiation, and that cultivars should be selected for their capacity to produce flowers on relatively thin stems (ca. 3.5 mm diam.). Flowers were initiated on stem diam. of 4 to 5 mm in cut flower types, but on stems too long for well-proportioned potted plants. Species producing multiple inflorescences, such as *L. mundii* and *L. oleifolium,* were also recommended.

Fig. 2.7. A shoot of *Leucospermum* treated with ethephon to induce multiple laterals. Photo: Criley.

The *L. lineare* × *L. tottum* hybrid 'Ballerina' has been shown to have a high propensity to develop flowers even after cutting back (Brits et al. 1992; Ackerman et al. 1995) (Fig. 2.8). In one experiment in which primary shoots on mother stock plants were tip-pinched, BA was applied, and the resulting shoots shaped on the mother plant before taking the shoot as a cutting. Following treatment with 4000 ppm KIBA, non-induced, branched cuttings of two cultivars rooted well in 4 to 5 weeks. 'Ballerina' tolerated the manipulations better than did 'Tango' (a hybrid of *L. glabrum* × *L. lineare)* with 80% of the rooted plants flowering on several branches the next spring versus a very low proportion for 'Tango'.

Growth regulators are being used to induce branching (Brits et al. 1992) and improve compactness, increase leaf number, and increase shoot diameter, with a concomitant improvement in the capacity to initiate inflorescences (Ackerman and Brits 1991; Ben-Jaacov et al. 1990; Brits 1995a). These uses may apply to cutting

manipulations on the stock plant as well as to plants already growing in containers. Brits et al. (1992) proposed a scheme for the rapid production of potted *Leucospermum* using paclobutrazol and BA on the mother plants (Figure 2.9). Ethephon may cause some shoot length reduction and is additive with paclobutrazol (Brits 1995a).

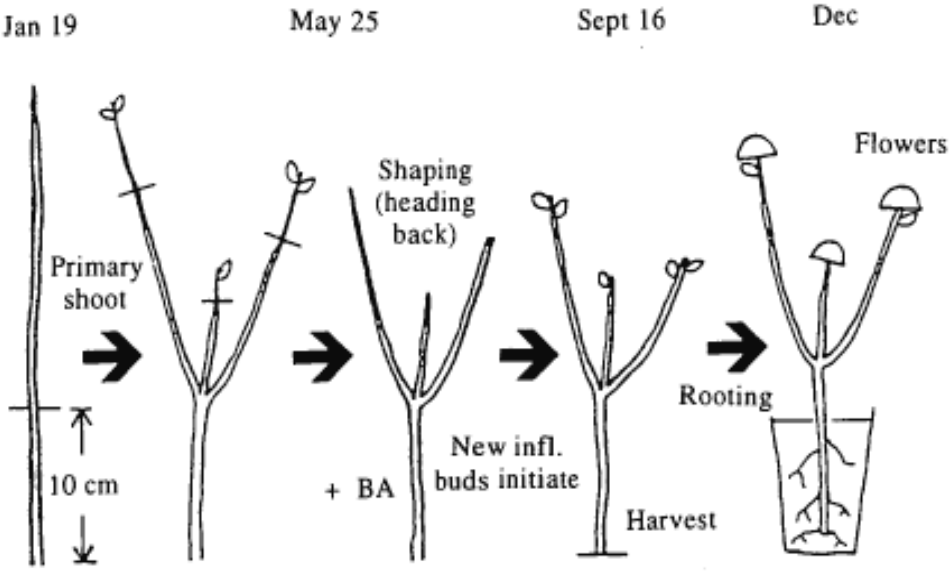

Fig. 2.8. Diagram of sequential manipulations performed on 'Ballerina' *Leucospermum lineare* × *L. tottum* shoots, followed by rooting in early spring and resulting in branched potted plants flowering in December in the southern hemisphere. Source: Brits et al. 1992.

2. Postproduction.

Budded *Leucospermum* plants abort their young flowering buds if moved into low indoor light conditions. Ackerman et al. (1995) recommend that the first row of styles be released on the inflorescence as the minimum developmental stage. Following storage in darkness for up to 8 days at 4°C and 90% RH, budded plants of 'Ballerina' continued to flower without damage or reduction in quality. Under similar conditions, *L. oleifolium* and *L. mundii* suffered some bud damage and leaf discoloration and flowered for 17 and 7 to 10 days, respectively (Ackerman et al. 1995).

IV. CROP POTENTIAL AND RESEARCH NEEDS

As developing nations seek sources of foreign currency to support development and improve conditions for rural peoples, the export of flower crops has been an important component. However, such nations do not support research into the new floral crops, and the sources of knowledge will be the very nations whose growers will lose market share to the new competition. Nonetheless, a 1997 listing of IPA members revealed only 13 different nations and did not include any from Asia or Central/South America. The same impetus that moved rose, carnation, and chrystanthemum production to Colombia, Ecuador, Mexico, and Kenya will also drive *Leucospermum* production to suitable climatic regions in nations with low land and labor costs. Interest is being shown in areas as diverse as Taiwan, China, Korea, southern France, Corsica, Chile, and El Salvador.

Development of new protea-producing regions will come from joint ventures with existing growers.

Since the market for proteas of all types is not yet saturated, particularly in terms of year-round availability, there is still room for both domestic and foreign production to increase. The few researchers involved with production of cut flowers and potted proteaceae have much work ahead of them before crop production practices reach the levels of sophistication attained by roses or carnations, for example. The challenge for producers is to identify and prioritize where to put limited financial resources in support of long-term as well as short-term needs.

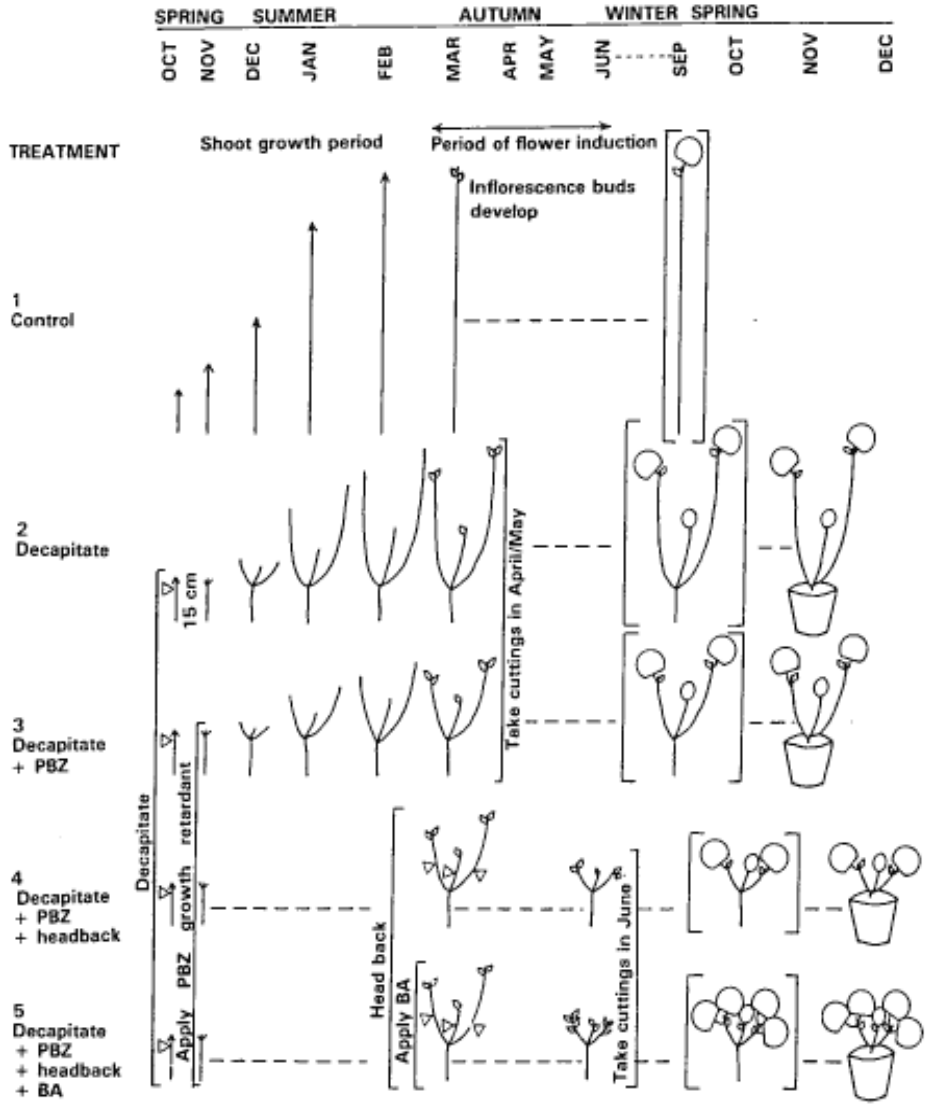

Fig. 2.9. Diagrams of basic rapid production systems of *Leucospermum* in the southern hemisphere. Seasonal manipulations are done on the mother plant primary shoots and on rooted cuttings and include, progressively, 1: control; 2: branching treatment; 3: growth retardation with paclobutrazol (PBZ); 4: shaping of pot plant

by heading back laterals; 5: benzyladenine treatment to increase number of inflorescence buds in types bearing conflorescences. Source: Brits et al. 1992.

At the Sixth Biennial Conference of the IPA, Parvin (1991b) observed that the first decades of protea production were producer-driven: the novelty value was high, the supply was low, and almost any protea brought to market could be sold. He ventured that as wholesalers, retailers, and the ultimate consumer begin to appreciate quality, the markets will be driven by consumer preferences. Education of the consumer, determining consumer preferences, and controlling production to grow what the consumer wants are the future for the industry.

The research needs of *Leucospermum,* as separate from other Proteaceae, are not so distinct, and there is a great deal of overlap in such lists (Brits et al. 1992; Brits 1995c; Malan 1995). The categories for needed research range from gaining a better understanding of the biology and physiology of the subject plant to learning about marketing opportunities and requirements.

Gathering and learning more about the varied germplasm is a high priority, especially with South African flora threatened by wild gathering, land clearance for crops and animals, and other forces inflicting loss of habitat. In the *Leucospermum* collections at the Fynbos Unit of the South African Agricultural Research Council, some forms can no longer be found in the wild. The germplasm base is especially valuable for breeding and crop improvement (Littlejohn 1995). Plant breeders have much to learn about the genetic bases for productivity, disease resistance, flower color, ease of propagation, and possibilities for manipulating flowering time.

Nutrition remains an area of concern because of off-color foliage disorders, interactions with soil pH and soil type, and inadequate standards for tissue analysis and their interpretation as a guide to fertilization. Malan (1996) notes that the interaction of substrates, growing techniques, and nutrition on proteoid root development is unknown. The suggestion that ammonium nitrogen is favored by Proteaceae should be followed up, as well as alternative forms of phosphorus for fertilization. Development of *Leucospermum* as potted plants also requires an understanding of the fertilizer regime. The interactions of major and minor elements with the flowering process are not known, and this could be important in the timing of fertilizer application on growth and flowering.

Increasingly, attention is being turned toward practices that spread seasonal production over longer periods, improve quality, and permit better management of the plants. Other culture and management issues requiring research include: salinity tolerance, irrigation frequency and amount, pruning for optimal flower production and plant growth habit, and the interaction of nutrition with vegetative and reproductive phases of growth. The culture of *Leucospermum* under protected cultivation and soilless culture systems is receiving attention in areas where the climate is marginal for outdoor culture (Allemand et al. 1995; Montarone and Allemand 1995).

While vegetative propagation is not the problem with *Leucospermum* that it is with other Proteaceae, research continues to find more efficient and less costly systems. Bringing tissue culture from a laboratory level to commercial production volumes also represents a challenge, if not to research, then to the ingenuity of commercial laboratories. The introduction of rootstocks, such as 'Spider', (Van der Merwe et al. 1991) and 'Nemastrong' and 'Carmeli' (Ackerman et al. 1997) that are tolerant to diseases, easy to root as well as suitable for the technique of cutting grafting, and compatible with other species and hybrids, may accelerate plantings of *Leucospermum* in previously inhospitable sites. Israeli research has proven the value of adaptability testing in the development of rootstocks suitable to local soil types.

Pest control remains an on-going problem area, not only for new insects, but also because of diminishing availability of registered chemical controls. Insect presence in cut flowers limits their use and export and is the impetus for finding improved practices to prevent their presence, remove them, or kill them (Seaton and Woods 1991; Wright and Coetzee 1992). Ants, while not damaging pests on their own, are well known for "managing" colonies of other insects that they bring into the inflorescences, and effective

control measures need to be developed. The practices of Integrated Pest Management (IPM) have not been elaborated for *Leucospermum,* although the principles developed for other crops will certainly apply (Wright 1995).

Control of diseases and nematodes faces the same problem of diminished availability of registered chemicals. The stem and collar rots caused by *Phytophthora* spp. are particularly difficult because the most effective fungicide, metalaxyl, is not registered for field use in protea. At present, use of *Phytophthora*-tolerant rootstocks offers the best approach, while the traditional breeding approach will require many years to implement and may still find no genes for resistance in the species. The technologies of genetic engineering may yield useful results once resistance genes are identified.

The minor crop designation under which all protea fall is a deterrent to rapid advances in finding herbicides that can be used among proteas, but progress can be expected here, especially when registrations permit a broad designation for ornamental use. Specific weeds may still pose a problem, however. The use of groundcover or sod-crops that can be mowed and managed to reduce their competition with the shallow-rooted proteas offers some promise, especially when other advantages may accrue, such as nematode-repelling properties, reservoirs for predaceous insects, and nutrition (through the use of nitrogen-fixing legumes).

Postharvest research is needed to determine optimum storage conditions, vaselife following pre-conditioning and storage treatments, hybrids with good vaselife, packing and shipping conditions, management of diseases, and disinfestation of insects. The post-production characteristics of potted *Leucospermum* and the production practices that influence them are also in need of elaboration.

Marketing research is high on the list of priorities of commercial growers in all parts of the world. The needs range from product selection to identification of consumer wants, from postharvest handling and storage to packaging, and from identifying seasonal sources to the markets requiring the products available at any given time.

At the Seventh Biennial IPA Conference in Harare, Zimbabwe, Kobus Steenkamp, Farm Manager of Protea Heights near Stellenbosch, recounted the story of a farmer who had won a million Rand in a lottery. Asked what he would do with the money, he replied, "I will just carry on farming until the money is finished." Mr. Steenkamp added, "I think one can run a sound business with proteas, but not easily get rich."

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3

Protea: A Floricultural Crop from the Cape Floristic Kingdom*

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I. INTRODUCTION

Protea, the most widely known genus of the Proteaceae, is now an important floral crop. Other genera in this family that are widely used in floriculture are *Leucospermum* (Criley 1998), *Banksia* (Sedgley 1998), and *Leucadendron. Mimetes*, *Serruria*, *Aulax*, *Telopea*, *Grevillea*, *Isopogon*, and *Paranomus* are used to a lesser extent. The name *Protea*, given by Linnaeus in 1753, referring to the Greek mythical god, Proteus, who could change his shape at will, is truly an apt name due to the wide diversity of this genus. The genus *Protea* is only found in sub-Saharan Africa and currently 114 species are described (Rourke 1980), with 14 subspecies recognized (Rebelo 1995). The tropical *Protea* species are widely distributed across sub-Saharan Africa and comprise 35 species (Beard 1992). Three of these tropical species are found in the summer rainfall region of South Africa: *P. caffra, P. gaguedi*, and *P. welwitschii*. The 89 species of *Protea* found in Southern Africa may be sub-divided into 20 groups of closely related species, shown in Table 3.1 (Rebelo 1995). The Cape Floristic Kingdom, a small strip of land between the towns of Grahamstown in the east and Clanwilliam in the west (Fig. 3.1) is home to 69 endemic species of *Protea* (Rourke 1980). It is from these species that the commercially utilized species derive, and include the stately *P. cynaroides* with a flower diameter of up to 25 cm and *P. scolymocephala* with a flower diameter of approximately 5 cm. The Cape Floral Kingdom, one of the world's six plant kingdoms, is also known as the Flora Capensis or the fynbos biome. This plant kingdom, ranking alongside the Holarctic, Palaeotropic, Neotropic, Australasian, and Antarctic Kingdoms that cover vast areas of the globe, is unique. Plants in this region are adapted to hot dry summer conditions and primarily acidic, nutrient poor soils. It comprises only 0.04% of the earth's surface, but due to its remarkable plant species diversity (>8500 species of flowering plants) and high level of endemism, has been classified as a distinct phytogeographic region (Bond and Goldblatt 1984).

Table 3.1. Taxonomic groupings within the genus *Protea* (summarized from Rebelo 1995).

Group Common Names	Species
Rodent Sugarbush	*P. amplexicaulis* (Salisb.) R.Br., *P. humiflora* Andrews, *P. cordata* Thunb., *P. decurrens* E. Phillips, *P. subulifolia* (Salisb. ex Knight) Rourke
Grassland Sugarbush	*P. caffra* Meisn., *P. petiolaris* (Hiern) Baker & Wright, *P. simplex* E. Phillips, *P. parvula* Beard , *P. dracomontana* Beard, *P. nubigena* Rourke
Shaving Brush Sugarbush	*P. inopina* Rourke, *P. glabra* Thunb., *P. rupicola* Mund ex Meisn., *P. nitida* Mill.
Red Sugarbush	*P. enervis* Wild
Mountain Sugarbush	*P. angolensis* Welw., *P. rupestris* R.E. Fr., *P. madiansis* Oliv., *P. rubropilosa* Beard, *P. comptonii* Beard, *P. curvata* N.E. Br., *P. laetans* L. E. Davidson
Savanna Sugarbush	*P. welwitschii* Engl., *P. gaguedi* J.F. Gmel.
Moorland Sugarbush	*P. asymmetrica* Beard, *P. wentzelana* Engl.
King Sugarbush	*P. cynaroides* (L.) L.
Snow Sugarbush	*P. scolopendriifolia* (Salisb. ex Knight) Rourke, *P. scabriuscula* E. Phillips, *P. cryophila* Bolus, *P. pruinosa* Rourke
Spoonbract Sugarbush	*P. roupelliae* Meisn., *P. eximia* (Salisb. ex Knight) Fourc., *P. compacta* R. Br., *P. obtusifolia* H. Beuk ex Meisn., *P. susannae* E. Phillips, *P. burchellii* Stapf, *P. longifolia* Andrews, *P. pudens* Rourke

True Sugarbush	*P. repens* (L.) L., *P. aristata* E. Phillips, *P. lanceolata* E. Mey. ex Meisn.
Bearded Sugarbush	*P. laurifolia* Thunb., *P. neriifolia* R. Br., *P. lepidocarpodendron* (L.) L., *P. lorifolia* (Salisb. ex Knight) Fourc., *P. coronata Lam.*, *P. speciosa* (L.) L., *P. stokoei* E. Phillips, *P. grandiceps* Tratt., *P. magnifica* Link, *P. holosericea* (Salisb. ex Knight) Rourke
Dwarf-tufted Sugarbush	*P. lorea* R. Br., *P. scorzonerifolia* (Salisb. ex Knight) Rycroft, *P. aspera* E. Phillips, *P. scabrapiscina* R. Br., *P. piscina* Rourke, *P. restionifolia* (Salisb. ex Knight) Rycroft, *P. denticulata* Rourke
White Sugarbush	*P. subvestita* N.E. Br., *P. lacticolor* Salisb., *P. punctata* Meisn., *P. mundii* Klotzsch, *P. aurea* (Burm.f.) Rourke, *P. venusta* Compton
Bishop Sugarbush	*P. caespitosa* Andrews
Eastern Ground Sugarbush	*P. tenax* (Salisb.) R. Br., *P. foliosa* Rourke, *P. vogtsiae* Rourke, *P. intonsa* Rourke, *P. montana* E. Mey. ex Meisn.
Western Ground Sugarbush	*P. acaulos* (L.) Reichard, *P. angustata* R. Br., *P. laevi* R. Br., *P. convexa* E. Phillips, *P. revoluta* R. Br.
Shale Sugarbush	*P. mucronifolia* Salisb., *P. odorata* Thunb.
Rose Sugarbush	*P. scolymocephala* (L.) Reichard, *P. acuminata* Sims, *P. canaliculata* Andrews, *P. nana* (P.J. Bergius) Thunb., *P. witzenbergiana* E. Phillips, *P. pityphylla* E. Phillips
Penduline Sugarbush	*P. recondita* H. Beuk ex Meisn., *P. effusa* E. Mey. ex Meisn., *P. sulphurea* E. Phillips, *P. namaquana* Rourke, *P. pendula* R. Br.

While the prominent use of *Protea* today is as fresh or dried flower, the plant has had many uses in the past. Early European settlers in South wagon wheels. The bark of *P. nitida* was used in the tanning of leather and the leaves as a source of black ink (Rourke 1980). *Protea* also had their uses in traditional medicine (Van Wyk et al. 1997). The nectar of *P. repens*, which is produced in copious amounts, was used by early European settlers as a remedy for chest disorders after being boiled to a syrup. The bark of *P. caffra* is used to treat bleeding stomach ulcers and diarrhoea.

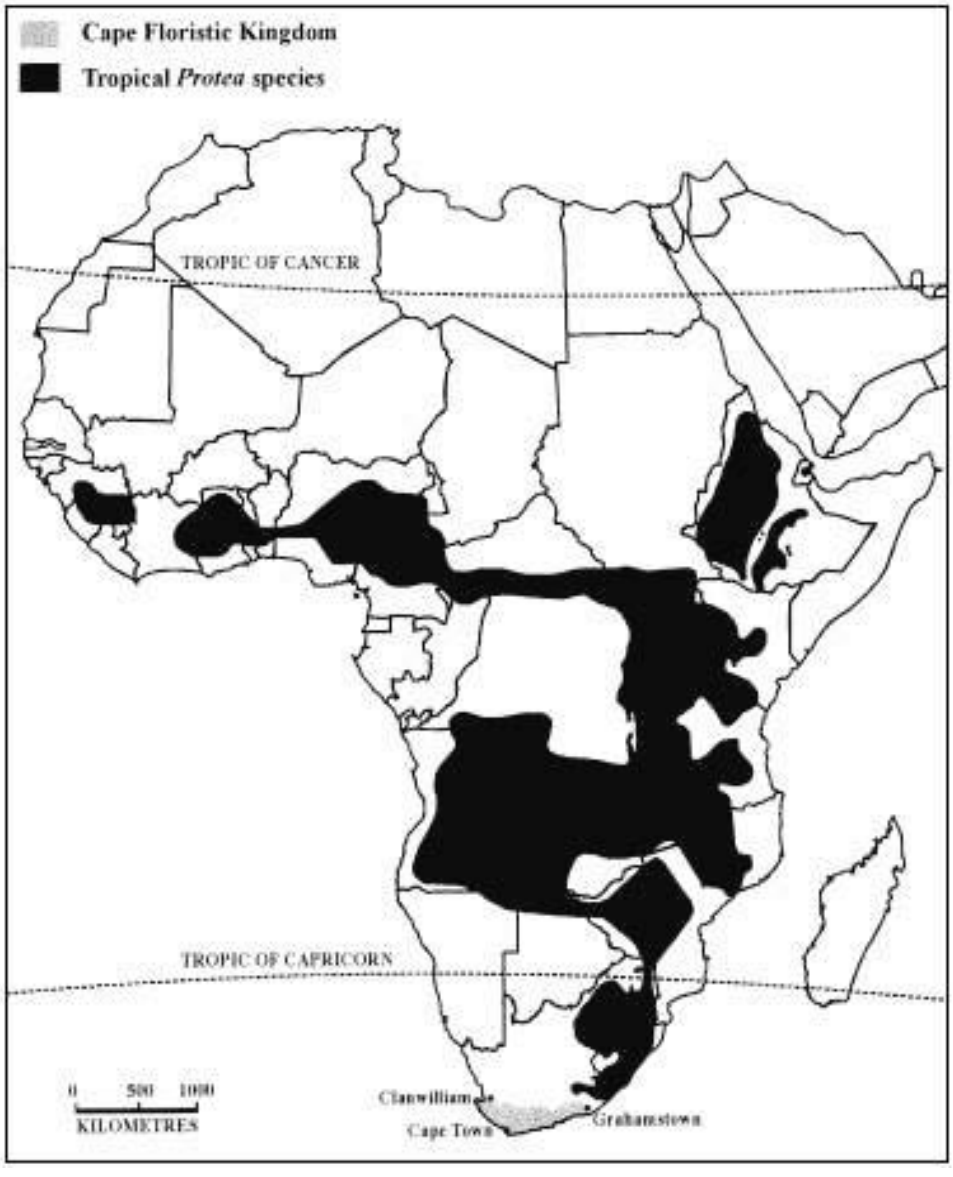

Fig. 3.1. Map of Africa, depicting the Cape Floristic Kingdom and the distribution of tropical *Protea* throughout Africa.

II. HISTORY

A. Taxonomy and Cultivation

The early taxonomical and cultivation history of *Protea* has been reviewed by Rourke (1980). A Dutch trade group collected the first *Protea* in 1597 and in 1605 Clusius described *P. neriifolia*. Paule Hermann of the Netherlands collected *Protea* on

Table Mountain in 1672, but the descriptions were published in 1737. Sir Hans Sloane of London described *P. repens* in 1693 and Plukenett did likewise for *P. scolymocephala* and *P. cynaroides* in 1700.

European collectors of exotic plants were the first cultivators of Proteaceae, from achenes collected by Masson in 1774. *P. repens* was the first recorded *Protea* species to flower outside its natural habitat. In 1803, *P. cynaroides* flowered in the collection of the Earl of Coventry, Croome, Worcestershire. The largest collection of 35 species was grown by George Hubbert in 1805 in the suburbs of London and, by 1810, 23 species of *Protea* were already grown at Kew Gardens. The Dutch and French showed great enthusiasm for *Protea* cultivation during this period. The first commercial distributors of *Protea* achenes were the London firm, Lee and Kennedy. Among their clientele was Josephine, wife of Napoleon. The industrial revolution in Europe and the British Isles, in the early 1800s, led to wide-scale heating of greenhouses and concomitant high humidity, conditions under which *Protea* would not grow, leading to a loss of interest in their cultivation. It was only in 1981 that *P. cynaroides* flowered once again in Kew Gardens.

In this rich floral kingdom, the South African wild flower industry had a humble origin. Street hawkers began selling flowers, picked in the surrounding mountains, on the streets of Cape Town, a tradition still in existence (Coetzee and Littlejohn 1995). In the 19th century, European church groups established settlements on their mission stations in the rural areas of the Cape, for people originating from the Khoi-San tribes, as well as slaves imported from the East, and European settlers. These inhabitants of the mission stations, at Elim and Genadendal, were the first exporters of dried indigenous flowers to Europe in 1886 (Krüger and Schaberg 1984).

However, no interest was shown in the cultivation of *Protea* in the 19th century. In 1910, A. C. Buller cultivated *P. cynaroides* commercially for the first time on his farm near Stellenbosch. In 1913 the National Botanical Garden of South Africa at Kirstenbosch was established and proteas were among the first plants cultivated. The first seed trader selling proteaceous achenes was Kate Stanford, who issued a catalogue in 1933 (Rourke 1980). Ruth Middelmann greatly promoted sales of proteaceous achenes, exporting achenes to countries such as New Zealand, the United States of America (California), and Australia (Lighton 1960). The Kirstenbosch botanical garden also introduced a system for the selling of achenes of plants from the Flora Capensis soon after its establishment.

Frank Batchelor established the first commercial plantation on his farm in Devon Valley near Stellenbosch, the farm later to be known as Protea Heights, where he harvested the first flowers in 1948. In 1953 *P. cynaroides* was part of a floral basket sent as a gift from the people of the Cape to Queen Elizabeth on the eve of her coronation (Lighton 1960). This is the first documentation of fresh *Protea* being exported. Buller and Batchelor can be viewed as the fathers of the fresh, cut flower protea industry in South Africa.

The commercialization of the dried flower industry began in the mid 1950s, with the Middelmann family exporting large quantities of dried flowers by ship to Europe. Today there are over 400 flower harvesters collecting plant material from the wild and delivering it to large dried flower businesses for drying and processing for export. In the South African dried flower industry, six *Protea* species are used (Table 3.2), from which a large number of products are created (Coetzee and Middelmann 1997). Twenty different products that originate from *P. repens* are sold (Wessels et al. 1997), with more than 20 million inflorescences of *P. repens* harvested in the natural habitat annually to supply the market. The proteaceous material used in the dried flower industry is primarily harvested from the natural habitat and can have negative effects on the ecology of the fynbos, the re-establishment of the species after fire, and the genetic variability within a population (Coetzee and Littlejohn 1995).

Table 3.2. Important *Protea* species used in the dried flower trade.

Species	Trade Name
P. repens	Repens flower, rosette
P. compacta	Compacta flower, rosette
P. magnifica	Barbigera flower
P. susannae	Susannae rosette
P. neriifolia	Neriifolia bud
P. obtusifolia	Obtusifolia flower

The fresh cut flower industry utilizes 12 *Protea* species and a number of interspecific hybrids, listed in Table 3.3 (Coetzee and Middelmann 1997). Approximately 350 growers cultivate Proteaceae commercially. Although some species of *Protea* are still harvested in the natural habitat and sold as fresh cut flowers, a recent survey indicated that more than 80% of the cut flower *Protea* are from cultivation (Wessels et al. 1997). In 1997 the *Proteaceae* hectarage under intensive cultivation in South Africa was in excess of 400 ha, of which 50% were *Protea* (Middelmann and Archer 1999). A further 1,000 ha of broadcast sown plantations were recorded. During 1998, 3,666 tons of fresh cut flowers were exported from South Africa, of which 30% was represented by genus *Protea*. The top-selling products exported by South Africa are *P. magnifica, P. repens*, and *P. eximia*, representing 58% of exports of flowering stems. Large quantities of bouquets, many containing *P. eximia* or *P. compacta*, are also exported from South Africa. Export and local sale of *Protea* is throughout the year, with a peak in export quantities during October.

Table 3.3. Important *Protea* species used in the fresh cut flower trade (Middelmann and Coetzee, 1997), with their natural flowering times in the Southern Hemisphere (Rebelo 1995).

		Flowering time											
Protea Species	Trade name	J	F	M	A	M	J	J	A	S	O	N	D
P. compacta					*	*	*	*	*	*			
P. cynaroides	King[z]	*	*	*	*	*	*	*	*	*	*	*	*
P. eximia	Duchess[z]							*	*	*	*	*	*
P. grandiceps		*								*	*	*	*
P. lacticolor			*	*	*	*	*						
P. magnifica	Barbigera[z] or Queen[y]	*						*	*	*	*	*	*
P. mundii		*	*	*	*	*	*	*	*	*			
P. nana								*	*	*	*		
P. neriifolia	Mink[y]		*	*	*	*	*	*	*	*	*	*	
P. pityphylla						*	*	*	*	*			
P. repens	Sugarbush[y]	*	*	*	*	*	*	*	*	*	*	*	*
P. scolymocephala	Scoly[z]							*	*	*	*		

[z]South Africa
[y]USA

B. Research

The domestication of *Protea* in South Africa began in 1913, with the inauguration of the National Botanical Garden at Kirstenbosch. The establishment of a collection of

Proteaceae led to the publication of an article on cultivation, titled "The cultivation of proteas and their allies" (Matthews 1921). It was only in the late 1950s that a scientific manual was published on protea cultivation: *Proteas: Know Them and Grow Them* (Vogts 1959). Due to the growing interest in South Africa in proteas as a floricultural crop, the South African Department of Agriculture initiated a research program on proteas in the 1960s, under the leadership of Dr. Marie Vogts. The first research phase dealt with the identification, collection, and establishment in cultivation of the protea species in South Africa with floricultural potential. The collection of economically important species was established at Oudebosch near Betty's Bay. Ten years of research resulted in the identification of horticultural variants within species. The characteristics of these variants were stable when propagated by achenes (Vogts 1971). In 1973, a breeding and selection program was initiated at Tygerhoek, near Riviersonderend, about 150 km from Cape Town. The collection of proteas was moved from Oudebosch to the new site. The first *Protea* cultivar resulting from this program was Guerna (Plate 1), a *P. repens* selection (Brits 1985). During the period 1988 to 1992 the germplasm collection of Proteaceae, or what is known as the field genebank (Littlejohn and de Kock 1997) was moved from Tygerhoek to a new site, Elsenburg, an experimental farm near Stellenbosch. In April 1992, the genebank collection was transferred to the Agricultural Research Council (ARC), a non-profit, non-governmental organization. The ARC is responsible for the maintenance of the field genebank and to research the commercialization of Southern African Proteaceae.

Research in other countries where *Protea* is cultivated has been undertaken by various research organizations, with individuals within the organizations playing critical roles. In Hawaii, research on propagation, cultivation, selection, and diseases has been undertaken since the 1960s by the University of Hawaii. In California, the University of California has played an instrumental role in importing new plant material and in research on leaf blackening. Proteaceae research in Australia is conducted by a number of different organizations in Western Australia and Queensland, while in New Zealand the Horticulture Research Centre in Levin conducted Proteaceae research (Matthews and Carter 1983). In France, research on cultivation in soilless medium under glass at the Sophia Antipolis INRA station is underway, and in Tenerife, Spain, the University of La Laguna is active in Proteaceae research. The Volcani Institute in Israel has done excellent research on cultivation of Proteaceae in calcareous soils. However, worldwide research on Proteaceae as a horticultural crop is decreasing, although many problems for cultivators of cut flowers still exist. In the 1980s an active International Protea Working Group was inaugurated (Lamont 1984) but, by the late 1990s, the membership had dwindled to five researchers.

C. World Industry

The Proteaceae of Southern Africa are also cultivated in many other countries, such as Australia, Chile, El Salvador, France, Israel, New Zealand, Spain (Canary Islands), Portugal, the United States of America (California, Hawaii), and Zimbabwe (Leonhardt and Criley 1999). Cultivation in many countries developed simultaneously with the industry in South Africa.

In Australia, the Botanical Garden in Adelaide began cultivating Cape flora in 1871 (Lighton 1960). The cut flower industry in Australia gained impetus when immigrants from South Africa, such as the Wood family, sold their farm in South Africa in 1984 and emigrated to Western Australia with large quantities of seed. Today, South African Proteaceae are cultivated in South Australia, Victoria, New South Wales, Queensland, and Western Australia, but no data exists on the extent of cultivation of the genus *Protea*. Large commercial plantations are especially found in the Busselton/Margaret River area of Western Australia. The largest nursery producing potted plants of various Proteaceae species is situated in Monbulk, Victoria, and is owned and run by the Matthews family. In New Zealand, origins are unclear, but it is widely believed

that South African Proteaceae were brought there by soldiers returning from the Anglo-Boer War during the period 1899 to 1906 (Matthews and Carter 1983). In 1922, Duncan and Davies Nursery offered *P. repens* in their catalogue and Stevens Brothers began selling proteaceous cut flowers in 1945. Achenes imported from South Africa were used to hybridize the well-known *Leucadendron* cultivar, Safari Sunset. A *Protea* cultivar that originated from New Zealand is the *P. repens* hybrid, Clark's Red. Proteaceae cut flowers are an important New Zealand export commodity, and are sold primarily to Japan and the Far East. There are no statistics on the extent of *Protea* plantations (Soar 1998).

The industry in Hawaii developed from a research project on new cut flower crops at the University of Hawaii. While a visiting Professor in Hawaii, Sam McFadden, University of Florida, imported a wide variety of propagative material in 1964. Included were proteaceous achenes. In 1968, Phillip Parvin joined the Faculty as Research Horticulturist at the Maui Agricultural Research Center, and spent the next 25 years assisting in the development of the protea cut flower industry in Hawaii. Today, approximately 60 ha of Proteaceae are cultivated in Hawaii (Wilson 1998).

The cultivation of South African Proteaceae in California was promoted by Howard Asper of Escondido, who imported many species during the 1960s. Today, approximately 450 ha are under woody Southern Hemisphere plants for cut flower production, of which approximately 20% is the genus *Protea* (Perry 1998).

Zimbabwe is a recent entrant to the international trade in Proteaceae. The primary initiators of cultivation on a commercial scale were the Miekle family in the late 1970s. The first *Protea* cut flower exports were made in 1981. The Australian cultivar Pink Ice was cultivated on a large scale in Zimbabwe, but recent problems with disease and insects have drastically reduced the hectarage. Other *Protea* cultivars and species are being used and approximately 78 ha are under plantations, with 140 ha of other Proteaceae (Middelmann and Archer 1999).

The area under cultivation of Proteaceae in South America is approximately 8 ha, with 0.5 ha in Chile (Lobos 1998) and 7.5 ha in El Salvador (Veltman 1998). Spain and Portugal have approximately 30 ha of cultivated Proteaceae, located mainly on the islands of Madeira (Fernandes and Blandy 1998) and Tenerife (J. A. Rodríguez-Pérez, pers. comm.).

III. REPRODUCTIVE BIOLOGY

The genus *Protea* range in size from small prostrate shrubs, some with underground stems, to large trees. All are evergreen, woody perennials with sclerophyllous leaves suited to withstand periods of hot, dry weather. Regeneration can take place through sprouting from the lignotuber in some species or by release of achenes, from infructescences maintained on the plant. The foliage varies from fine needle-like leaves in *P. aristata* to the petiolate oval or obovate leaves of *P. cynaroides*. The commercially valuable product in *Protea* is the terminal inflorescence. It is the size and color of the involucral bracts of the inflorescence, which range from greenish white through all shades of orange, pink, red to brownish-red that give the *Protea* their aesthetic appeal. The genus *Protea* is distinguished from all other African genera of the Proteaceae by its flowers. The perianth is bipartite, bilaterally symmetrical with the three adaxial perianth segments fused from the base of the tube to the tips of the limbs, forming a distinct sheath, while the abaxial perianth segment separates completely from the adaxial perianth sheath, falling free as each individual flower opens (Rourke 1980). Each flower is composed of four perianth segments and the individual flowers are aggregated together on the inflorescence, surrounded by a prominent involucre of colored and often tufted bracts. The involucral bracts provide the main floral display. The individual flowers develop spirally from the outer edge of the involucral receptacle. Three anthers are attached to the three fused perianth segments; the fourth anther is attached to the free perianth segment. The central pistil consists of an ovary containing a single ovule, a long

style and a small stigmatic region at the tip of the style enclosing the stigmatic groove. The distal portion of the style is specialized to form the pollen presenter, the external morphology of which varies between species (Rourke 1980). The pistil of *P. repens* can be roughly divided into four major regions: the stigma, a vertebra-shaped upper style, a heart-shaped lower style, and the ovary (Van der Walt and Littlejohn 1996a). The upper pistil is modified to form the pollen presenter, an elongated, ridged structure where pollen is deposited prior to anthesis and a longitudinal obliquely placed terminal groove on the upper adaxial side of the stigma, the stigmatic groove. A layer of interlocking epidermal cells fringes the margin of the stigmatic groove. A stylar canal appears to run the length of the style, surrounded by densely packed transmitting tissue. The stylar canal joins up with the cavity formed between the ovule and the inner ovary wall. The ovary is partially embedded in the woody involucral receptacle of the inflorescence and contains one acutely obovate-shaped ovule. The observed pistil structure of *P. repens* is very similar to *P. cynaroides* (Vogts 1971), *Macadamia* (Sedgley et al. 1985), and *Banksia* (Clifford and Sedgley 1993). In all cases the style is woody, containing many sclerenchyma cells, but in *Macadamia* and *Banksia* the stylar canal does not extend along the entire length of the style.

Trichomes are found on the outer surface of the ovary. After flowering, the fertilized ovules develop into obconic achenes, densely pubescent with long straight hairs, brown, rust-colored, black, or white (Rourke 1980). The viable achenes tend to be found in distinct groups, or clusters on the receptacle, which may be a mechanism to reduce insect predation (Mustart et al. 1995). It appears that the plant actively controls the clustering, but the mechanism of control is unknown. The achenes formed may be stored in infructescences, the woody flower receptacle enclosed by woody involucral bracts, on the plant (Bond 1984, 1985), with release being triggered when water supply to the infructescence stops, such as during a fire, at plant death, or when insects consume the infructescence stem. *Protea* adapted to arid conditions, such as *P. glabra* and *P. nitida*, release their achenes four to seven months after flowering. The function of the trichomes on the achenes is fourfold: (1) expansion of drying achenes assists in forcing the achenes from the drying infructescence, (2) on an airborne achene they assist with buoyancy in high winds, (3) they assist in anchoring the achene to the ground, and (4) they orientate the achene on the soil surface to ensure optimum water uptake for germination (Rebelo 1995).

The flowers of *Protea* are protandrous, with the anthers dehiscing prior to the flower opening (Van der Walt and Littlejohn 1996b; Vogts 1971). The anthers deposit their pollen on the pollen presenter. During anthesis foraging fauna collects the pollen. Three types of fauna assist in pollination of *Protea*: birds (predominantly *Promerops cafer*, the Cape Sugarbird); small mammals such as mice, rats, and voles; and many types of insects (Collins and Rebelo 1992). The shape of the style in mammal pollinated *Protea* is curved (Plate 2), while bird and insect pollinated species have straighter styles. It is generally accepted that the *Protea* with large conspicuous inflorescences are bird pollinated, but species differ in dependency on birds as pollinators. Inflorescences of *P. nitida, P. cynaroides*, and *P. repens* bagged to exclude bird pollinators, but not insects, set achenes at the same rate as unbagged inflorescences (Coetzee and Giliomee 1985; Wright et al. 1991). In *P. neriifolia*, *P. magnifica*, and *P. laurifolia* the bagged inflorescences set significantly fewer achenes.

At anthesis the stigmatic groove has not yet become receptive to pollen. In a study on *P. repens* and *P. eximia*, the stigmatic groove was open at its widest between three and six days after anthesis (Van der Walt and Littlejohn 1996b). The number of pollen tubes per style and the achene set recorded from controlled pollination indicated that peak receptivity of the stigma was between two and six days after anthesis. Stigmatic secretions in *P. eximia* increased as the stigmatic groove opened.

The genus *Protea* has an inherently low achene set, between 1% and 30% under natural pollination conditions (Rebelo and Rourke 1986; Esler et al. 1989). Reasons cited for low achene set range from direct plant control of achene set numbers, pollinator

limitation, insect and mammal predation, and poor nutrition. The percentage of florets with pollen tubes, the percentage of ovules penetrated by a pollen tube, and the achene set in *P. repens* and *P. eximia* are highly correlated, indicating that entry of a viable pollen tube into the stylar canal results in a viable achene. In *P. repens* the achene set from controlled self-pollination, open pollination, and pollination between different clones of *P. repens* resulted in the same high achene set percentages of between 40% and 74% (Van der Walt 1995), while the achene set of *P. eximia* did not exceed 10%. This is contrary to the generally accepted view that all *Protea* are obligatory cross-pollinators (Horn 1962) and supports the observation that achenes resulting from insect pollination are likely to be from self pollen (Wright 1994a). Pollination does not occur without a pollen vector, such as an insect or bird (Brits 1983).

IV. CROP IMPROVEMENT

A. Genetic Variability

The growth habit differences between species range from the Eastern and Western ground sugarbushes that have underground stems, to upright bushes typified by *P. eximia*, and to trees, such as *P. nitida* (Rebelo 1995). Some species have a lignotuber (a swelling of the stem at or just below ground level, covered in dormant buds that can regenerate after a fire), such as *P. cynaroides* and *P. welwitschii*, but most species do not. *Protea* are described as evergreen, but species differences occur, with some species having leaves that live for one year, e.g., *P. nitida*, and others with leaves remaining on the bush for up to 6 years, e.g., *P. neriifolia*. Leaf shape varies from the narrow, elongated leaves of *P. longifolia* to the ovate leaves of *P. cynaroides* that have a prominent leaf stalk. Interspecific hybrids exhibit characteristics intermediary to the parental species, allowing for ease of identification of the parents of interspecific hybrids (Vogts 1989). The color of the involucral bracts varies from brown, through shades of deep crimson, red and pink, to white or pale green, both within and between species. Further variation in flower appearance occurs due to differences in the color of the trichome tufts, or beard, at the ends of the inner and outer involucral bracts, especially in *P. magnifica*.

Plant species with a predominantly outcrossing breeding system generally show high levels of phenotypic variability. The amount of phenotypic variability within species differs widely between species of *Protea*. In species with a wide habitat range, such as *P. cynaroides*, *P. neriifolia*, and *P. magnifica*, distinct horticultural forms (Plate 3) can be recognized (Vogts 1989). Studies indicated that the variation observed between seedling populations of *P. cynaroides* sampled from different localities was consistent when the plants were cultivated at a single locality, and therefore had a genetic basis (Vogts 1971). This was useful in selecting achene propagated populations that could flower at different times of the year and thus supply marketable flowers for 12 months of the year.

In species with smaller habitat ranges, such as *P. compacta*, few observable differences are recognized between populations (Vogts 1989). Currently studies using RAPD-PCR analysis are being done by the Agricultural Research Council in South Africa to compare the extent of variation between species with a wide habitat range and those with a small habitat range. This information will assist in determining the extent to which populations must be sampled from, to try to maximize the variation within species kept in genebanks, botanical gardens, and in cultivation.

There is a high level of genetic variation present in *P. neriifolia* based on analysis of segregation after self-pollination (G. M. Littlejohn, unpubl.). Measurements of various traits on mature seedling plants obtained by self-pollination of a single selected clone of *P. neriifolia* showed significant variation between seedlings. The type of traits measured included growth habit, plant height, flower color, leaf length and width, inflorescence length and width, inflorescence mass, style length, and the concealment of the inflorescence by the leaves. Genetic improvement is closely linked to the process of

Plate 1 *Protea repens* cv. Guerna, the first *Protea* cultivar released in 1978 from the South African Proteaceae breeding project.

Plate 2 *Protea holosericea*, a mammal-pollinated, endangered species found in two isolated population in the Worcester district within the Cape Floristic Kingdom.

Plate 3 The large-leaf, summer flowering horticultural variant of Protea cynaroides in its natural habitat.

Plate 4 *Protea* cv. Sheila, a putative hybrid between *P. magnifica* and *P. burchellii*, is an example of an interspecific hybrid produced by natural pollen vectors and selected for its unique involucral bract color, flower head shape, and the plant vigor.

Plate 5 *Protea cynaroides* cv. Madiba, the result of controlled hybridization, was selected for its late spring flowering time, red involucral bract color, small leaves, thin stems, and strong plant vigor.

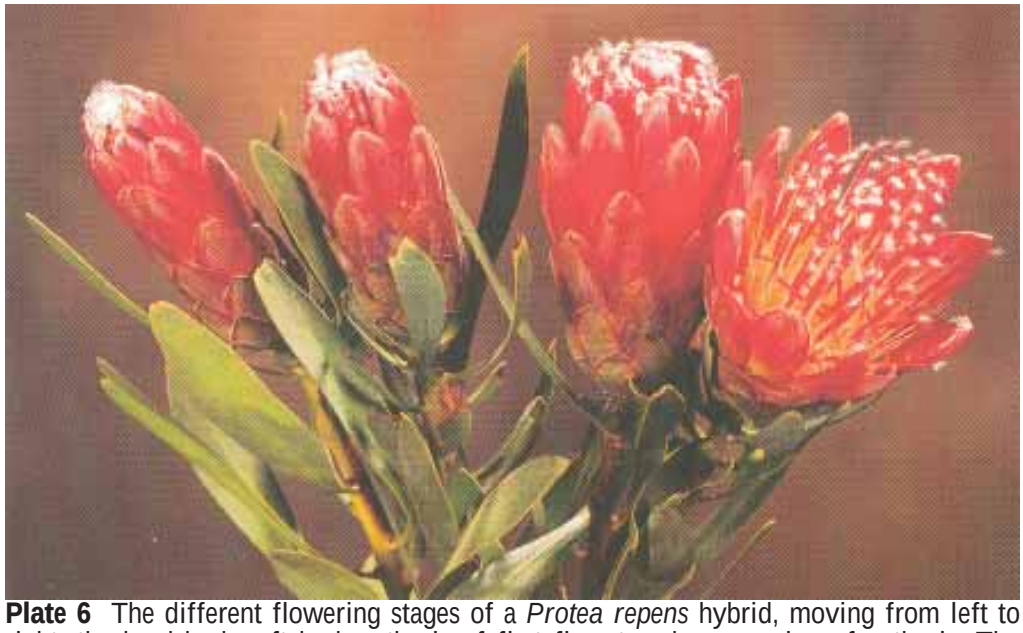

Plate 6 The different flowering stages of a *Protea repens* hybrid, moving from left to right, the hard bud, soft bud, anthesis of first florest and progression of anthesis. The correct cut flower harvesting stage is from soft bud to anthesis of the first florets.

domestication of an essentially wild plant, such as the *Protea* (Brits et al. 1983). Domestication generally follows three phases: (1) the harvesting of wild flowers; (2) the selection of superior populations or clones; and finally, (3) the development of new variations by hybridization, aimed at improving traits of importance in cultivation (Brits 1984). In a woody, perennial plant the breeding process is lengthy. The duration from collected wild plant material to acceptance of a cultivar developed by controlled hybridization can take up to 40 years (Fig. 3.2). This time span allows only for evaluation at one site, and no regional evaluation. Regional evaluation would increase the time span by four to six years (Wessels et al. 1997).

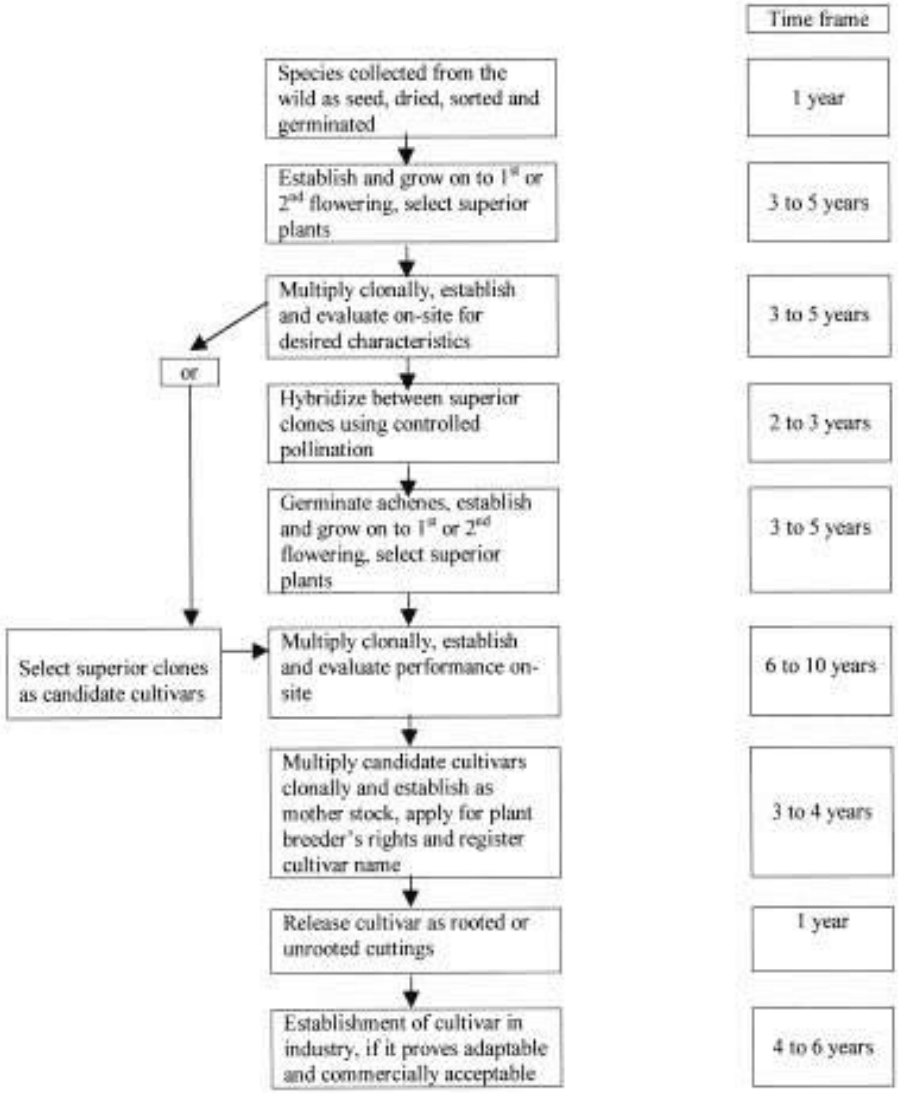

Fig. 3.2. Sequence of events and time lapse in the development of a *Protea* cultivar, from selection of wild harvested material through controlled hybridization and the selection of a superior hybrid.

B. Selection

The first stage in selection is the selection of species suitable for cultivation. Vogts (1989) provided *Protea* enthusiasts with a book on the Proteaceae and information on how to cultivate them. Of the species described in the book, 150 were identified as suitable for cultivation, with 86 having very good market potential (Brits et al. 1983). Characteristics sought for in suitable species included: attractive and arresting appearance, color, shape and size of flower head, foliage attractive but not dominating; flower head neither hidden nor pendulous; erect growth providing long, straight flower stems; good cultivation potential and ease of achene propagation; stability of characters; desired flowering time; post harvest quality; no obnoxious odor.

Selection within a species can take two forms: selection for an improved population or selection of a unique individual from a population that is propagated clonally. Both of these methods have been used in *Protea*. The identification of horticultural variants within certain *Protea* species identified populations suitable for use in initiating mass selection for improving populations (Vogts 1989).

Brits (1985) documented the selection of an achene propagated cultivar of *P. repens*, Guerna, which comprised 18 similar clones. Achene propagation or clonal propagation could be used. The success of selection of unique individual plants from within a population is dependent on the level of genetic variation present in the population from which one is selecting (Vogts 1989). Selection criteria for single plant selections are determined by the flower traits together with the producer requirements. These are summarized in Table 3.4. Single plant selections that have become successful cultivars include *P. eximia* cv. Fiery Duchess, *P. magnifica* cv. Atlantic Queen, and *P. cynaroides* cv. Red Rex (see Table 3.5).

Table 3.4. The characteristics desirable in a single plant selection for use as a cut flower cultivar.

Production characteristics	Flower characteristics
High yield	Flower head color
Growth vigor	Flower head shape
Longevity	Attractive foliage that does not conceal flower head
Ease of rooting	Terminal flower with no secondary growth (bypass)
Good regeneration after pruning	Straight stems
Tolerance to different soil types	Stems longer than 40 cm
Tolerance to cold	Ease of packing
Tolerance to heat	Resistance to leaf blackening
Insect resistance	Vase life of 10 days minimum
Ability to shift flowering time	Involucral bracts that retain their turgidity and color and do not brown under hot, dry conditions
Disease resistance	Ease of removal of leaves on lower flower stem

Table 3.5. Some cultivars in *Protea*, selected predominantly from chance hybrids or as single plant species selections, and recorded in the International Protea Register (Sadie 1998).

Putative parentage	Cultivar names[z]
P. burchelli/P. longifolia	Nomad (SA)
P. compacta/P. burchellii	Brenda (SA)

P. compacta/P. eximia	Pink Duke (SA)
P. compacta/P. magnifica	Andrea (SA), Lady Di (SA), Margot (SA), Pink Velvet (SA)
P. compacta/P. neriifolia	Carnivalz (SA)
P. compacta/P. obtusifolia	Red Baron (SA)
P. compacta/P. susannae	Pink Ice (Aus)
P. cynaroides	Artic Ice (NZ), Attaturk (Zim), Clarez (SA), Ivory King (Zim), Florindinaz (SA), Madibaz (SA), Red Rexz (SA)
P. cynaroides/P. grandiceps	Cottontop (SA), King Grand (SA)
P. cynaroides/P. compacta	Valentine (SA)
P. eximia	Duchess of Perth (Aus), Fiery Duchess (SA)
P. eximia/P. susannae	Baron (Aus), Cardinal (SA), Sylvia (SA)
P. glabra/P. laurifolia	Helzaan (SA)
P. lacticolor/P. mundii	Ivy (SA)
P. laurifolia/P. sulphurea	Pretty Annez (SA)
P. magnifica	Atlantic Queen (SA), Chelsea (SA)
P. magnifica/P. burchellii	Sheilaz (SA), Kurrajong Rose (Aus)
P. magnifica/P. laurifolia	Princess (SA)
P. magnifica/P. longifolia	Pinitaz (SA), Possum Magic (Aus)
P. magnifica/P. neriifolia	Pacific Queen (NZ), Venetia (SA)
P. magnifica/P. obtusifolia	Candidaz (SA), Ruthz (SA)
P. magnifica/P. susannae	Susara (SA)
P. mundii/P. subvestita	Empathy (Zim)
P. neriifolia	Frosted Fire (Aus), Pretty Belindaz (SA)
P. neriifolia/P. repens	Nataliaz (SA)
P. neriifolia/P. longifolia	Barber's Hybrid (NZ), Anneke (SA)
P. obtusifolia	Davidz (Is), Jossefz (Is), Michalz (Is), Shlomoz (Is)
P. pityphylla/P. effusa	Ansiz (SA), Lizlz (SA), Petrouxz (SA), Riaz (SA)
P. pudens/P. longifolia	Pixiez (Aus)
P. repens	Embers (SA), Guerna (SA), Rubens (SA), Sneyd (SA), Sugar Daddy (SA)
P. repens/P. longifolia	Liebencherryz (SA)
P. repens/P. mundii	Sweet Suzyz (SA)
P. repens/P. aristata	Venusz (SA)
P. repens/P. aurea	Clark's Red (NZ)
P. repens/P. pudens	Kurrajong Petite (Aus)

Key: z Protected by plant breeder's rights, or under application; Aus = Australia, Is = Israel, NZ = New Zealand, SA = South Africa, Zim = Zimbabwe

Early in the development of the fledgling protea industry in South Africa, it was observed that chance occurring interspecific hybrids produced new, unique flower forms, the plants often exhibiting greater vigor than either parental species (Vogts 1989). This led to the active search for interspecific hybrids by growers and the selection of many of these as cultivars, all clonally propagated by means of cuttings (see Table 3.5). This was also the impetus behind the initiation of a controlled breeding program, based primarily on the development of interspecific hybrids.

C. Hybridization

The controlled pollination method developed for *Leucospermum* has been extensively used in *Protea* hybridization (Brits 1983). The method entails covering the inflorescence of the female parent to exclude all possible pollinating fauna after removing any flowers with dehisced anthers. Two days later the unopened flowers are all removed from the center of the inflorescence, leaving a single ring of approximately 40 to 60

flowers that are newly opened. The pollen from the pollen parent is applied by using a style with pollen on the pollen presenter as a "brush" applicator. The inflorescence is re-covered. Mature achenes are harvested between nine and twelve months later. The achene set obtained by using this technique in *Protea* have been dismally small (Brits 1992), except in the case of intraspecific hybridization in *P. cynaroides* and *P. repens* (Table 3.6).

Table 3.6. Controlled hybridization results in *Protea* using the *Leucospermum* hybridization technique (Brits 1983).

Female parent	Male parents	Average achene set (%)
P. aristata	*P. aristata, P. repens*	0
P. compacta	*P. compacta, P. eximia, P.* cv. Sylvia	1.2
P. cynaroides	*P. cynaroides*	20.4
P. eximia	*P. eximia, P. eximia/P. compacta, P. repens*	0
P. pudens	*P. repens, P. obtusifolia, P.* cv. Ivy	0
P. repens	*P. repens*	24.6

Modifications to this technique have been made, using information gleaned from the studies of natural pollination. Firstly, it has been found that viable achenes are often found clustered on the involucral receptacle and this appears to be under direct control of the female plant (Wright 1994a,b; Mustart et al. 1995). Secondly, visual observation of the involucral receptacle indicates that space could be a limiting factor in achene development, similar to that observed in *Banksia* (Fuss and Sedgley 1991a,b). Therefore the pollination technique was modified so that at the first visit after bagging the inflorescence only 10 to 20 flowers are pollinated, with the removal of the next spiral of flowers. This is done repeatedly over three to four successive visits to pollinate flowers on the inflorescence, with a final visit to remove the central, remaining flowers. While very time consuming, the increase in success of obtaining mature, viable achenes makes the effort worthwhile (Table 3.7).

The full scope of interspecific hybridization can only be utilized if pollen can be successfully stored for use on species or clones flowering at different times of the year. The pollen of four *Protea* species was successfully stored for 12 months, desiccated, either at –18°C in an ordinary household deep freeze or in liquid nitrogen (Van der Walt and Littlejohn 1996c).

D. Interspecific Hybridization

Interspecific incompatibility can be exhibited at different stages during the reproduction process or in the interspecific hybrid plant. The simplest form of incompatibility takes place prior to fertilization, where pollen tube growth from a "foreign" species cannot grow down the style of the seed parent and no fertilization occurs (Van Tuyl 1989). Studies on *P. repens* and *P. eximia* indicated that the ten-fold decrease in achene set observed after interspecific pollination compared to intraspecific pollination was due to pollen tube growth being interrupted while growing down the style of the female parent (Van der Walt and Littlejohn 1996a). High correlation was observed between the number of flowers in which pollen tubes observed entered the ovule and the percentage achene set recorded. This indicates that in these two species, post fertilization mechanisms to inhibit interspecific hybridization were not active.

Table 3.7. Some successful cross combinations obtained in *Protea* by using the modified controlled pollination technique.

Seed parent	Pollen parent	Achene set (%)
P. aurea	*P. lacticolor/P. mundii*	19
P. neriifolia	*P. holosericea*	9
P. magnifica/P. laurifolia	*P. holosericea*	20
P. pudens	*P. acuminata*	63
P. pudens	*P. nana*	27
P. neriifolia/P. burchellii	*P. holosericea*	8
P. eximia	*P. compacta*	16
P. compacta/P. neriifolia	*P. repens/P. aristata*	1
P. lepidocarpodendron/P. neriifolia	*P. magnifica/P. neriifolia*	5
P. magnifica/P. laurifolia	*P. neriifolia*	2
P. lepidocarpodendron/P. neriifolia	*P. laurifolia/P. magnifica*	8
P. eximia/P. susannae	*P. compacta*	5
P. compacta	*P. compacta/P. burchellii*	15
P. compacta	*P. longifolia/P. burchellii*	15
P. burchellii	*P. compacta/P. burchellii*	8
P. magnifica/P. laurifolia	*P. magnifica/P. obtusifolia*	1

Incompatibility can also be detected in poor vigor and growth of interspecific hybrids. In general, interspecific hybrids in genus *Protea* are vigorous (Brits 1983). A further level of incompatibility is chromosomal incompatibility, leading to loss of sexual reproduction capacity in interspecific hybrids. Pollen grain infertility is a good indicator of meiotic disturbances during the development of the pollen grains (Van Tuyl 1989). In genus *Protea* the fertility of pollen ranges from 0% in the case of *P. cynaroides* interspecific hybrids to 89% in a *P. laurifolia* hybrid (Van der Walt and Littlejohn 1996b). No pattern of relatedness between parental species and pollen fertility was detected. Pollen size varied significantly between and within species. Meiotic analysis of interspecific hybrids of *Protea* has not yet been done and is complicated by the small size of the chromosomes and the woodiness of the flowers. No differences in the basal chromosome number of 12 have been recorded between species (De Vos 1943).

E. Cultivars

The aim of a breeding program is to develop cultivars (see Table 3.5) suitable for commercial exploitation for cut flower production. Currently cultivars of genus *Protea* originate from three sources: selection of individual superior plants from within species, selection of chance hybrids (Plate 4), and selection from achenes obtained from controlled hybridization (Plate 5) (Table 3.8). The parentage of chance hybrids is deduced from knowledge of characteristics of taxonomic importance between the seed parent and possible pollen parents growing in the vicinity of the seed parent.

Prior to 1973, commercial plant resources were undescribed and traded collectively under their old specific names, e.g., *P. barbigera* Meisn. for *P. magnifica* Link. In 1973 an international cultivar registration program for Proteaceae was launched, South Africa having obtained authority from the International Society for Horticultural Science to act as the International Registrar of all protea cultivars falling within the South African genera (Brits et al. 1983). Some of the well known *Protea* cultivars incorporated in the international register are listed in Table 3.5.

Table 3.8. Examples of cultivars derived from different sources within genus *Protea*.

Source	Cultivar name	Putative parentage
Selection of superior plants within species	Fiery Duchess	*P. eximia*
	Atlantic Queen	*P. magnifica*
	Snow Queen	*P. magnifica*
Selection of chance interspecific hybrid	Cardinal	*P. eximia/P. susannae*
	King Grand	*P. cynaroides/P. grandiceps*
	Susara	*P. magnifica/P. susannae*
Selection derived from controlled pollination	Madiba	*P. cynaroides/P. cynaroides*
	Clare	*P. cynaroides/P. cynaroides*

V. PHYSIOLOGY

Protea exhibits some unique physiological traits, such as the role of roots in water and nutrient uptake and carbohydrate metabolism in the cut flowering stems. The understanding of many physiological processes is incomplete, but this provides a fertile area for continued research.

A. Flowering

Protea species growing in their natural habitat are observed to flower at distinct times of the year (see Table 3.3). The majority of commercially used *Protea* flower naturally during the autumn to spring months of the Southern Hemisphere. The high demand for flowers in Europe, the dominant market for South African Proteaceae, is mid spring to mid summer, a time when few species flower. This has resulted in studies aimed at elucidating how flowering is initiated and if it can be manipulated.

The *Protea* stem grows in spurts (called flushes) during loosely defined growth periods during the year. This produces clearly defined growth flushes on the stem. Under the climatic conditions of the Western Cape, the predominant growth periods are: Winter (March to August), Spring (September to November), Summer (December to January), and Autumn (February to March) (Malan 1993). The number of flushes, ranging from none to two, produced during each growth period, is influenced by the environmental conditions and the species. The *Protea* inflorescence is borne terminally on a shoot consisting of two or more growth flushes. The flushes arise in succession from a distal axillary bud, with flushes exhibiting strong apical dominance during active growth.

Inflorescence initiation in *Protea* cultivar Carnival, a putative hybrid between *P. compacta* and *P. neriifolia* takes place after cessation of growth of the spring or summer flush under conditions in the Western Cape, South Africa. Generally two or more successive flushes are required for an inflorescence to initiate (Greenfield et al. 1993). A spring flush must be subtended by at least one previous flush for flower initiation to take place. Although not investigated in other species or hybrids, the requirement for at least two growth flushes subtending a flower is likely to hold for all other species. In some species, such as *P. neriifolia*, flowers are produced on secondary growth flushes that initiate below the current flower head, during the same season. This appears to be species specific, and will only occur on flowering stems with a large diameter (G. M. Littlejohn, pers. obs.). A minimum diameter of the flush subtending the inflorescence, a possible requirement for flowering to take place, has not been determined for any of the *Protea*. There are indications that the sink capacity of the stem plays a role in the ability of a stem to initiate an inflorescence (De Swardt 1989). Pruning studies on *Protea* cv. Carnival have shown the possibility of manipulating the flowering time, stem length, and production of mature bushes by manipulating the pruning time (Gerber et al. 1993;

Hettasch et al. 1997). Pruning the plant during the early spring months results in no flowering in the following spring, probably due to limited leaf area. Inflorescences are initiated on the spring and summer flushes of the following year, resulting in peak flowering during February as opposed to normal peak flowering during April. The bearing cycle of the plant is transformed in this way from an annual cycle to a biennial cycle. This also allows each stem to develop more growth flushes, which results in longer stems and a greater marketable harvest.

The precise environmental and intraplant factors triggering inflorescence initiation are still unclear. Dupee and Goodwin (1990a) observed flower initiation on the first spring flush in *P. neriifolia* cv. Salmon Pink, while seedlings of the Long Leaf variant of *P. cynaroides* initiated flowers on the summer flush as well as the autumn flush. The flowering time and number of flowers harvested from different *Protea* species changed, depending on the site at which they were planted (Dupee and Goodwin 1990b, 1992). A delay in flowering, of approximately six months, and a reduction in flower number occurred at the site with the highest altitude, lowest mean winter temperature and largest difference in day length between summer and winter. 'Guerna' produces only 18 flowers per bush during the period of December to February at 33° South, compared to 86 stems per bush at 21° North spread over twelve months of the year (Table 3.9). In other cultivars, differences in flower time and flower number per plant per annum occurred when grown in Hawaii or South Africa. While flower numbers can be accounted for by differences in soil fertility, the time of flowering appears dependant on differences in day length. It would appear that in the absence of clear environmental cues, such as changes in day length, many *Protea* produce a flower on a stem when sufficient carbohydrate source is available in the stem. This latter method is employed by 'Sylvia', a backcross of *P. susannae* on a hybrid between *P. eximia* and *P. susannae* (Malan and Le Roux 1995). Although 'Sylvia' naturally flowers during the late summer and autumn in South Africa, flowering over the full year can be obtained if pruning is scheduled to occur throughout the year.

Table 3.9. Comparison of flowering times and flower yield of *Protea* cultivars grown in Hawaii (21°N, 900 m) and South Africa (33°S, 177 m), with flowering season corrected to the Southern Hemisphere.

		Months Flowering												
Cultivar[z]	Location[y]	J	F	M	A	M	J	J	A	S	O	N	D	Flowers harvested
Guerna	Hawaii	*	*	*	*	*	*	*	*	*	*	*	*	86
	South Africa	*	*										*	18
Brenda	Hawaii				*	*	*	*						210
	South Africa				*	*								20
Cardinal	Hawaii	*	*					*	*	*	*	*	*	31
	South Africa	*	*	*	*	*	*							35
Red Baron	Hawaii		*	*	*	*	*	*	*	*	*	*		86
	South Africa			*	*	*								24
Sylvia	Hawaii	*	*	*	*	*	*	*	*	*	*	*	*	66
	South Africa	*	*	*	*	*								38

[z]Refer to Table 3.8 for parents.

[y]Hawaii data based on Criley et al. (1996); South African data based on Littlejohn (unpublished).

B. Propagation

1. Sexual Reproduction.

The fruits of the *Protea* species are held on the woody receptacle enclosed by the involucral bracts. The *Protea* species found in the savanna areas outside the Cape Floral Kingdom release their achenes between two and four months after flowering (Rebelo 1995). The Eastern Ground and Western Ground *Protea* (Table 3.1) generally release their achenes one to two years after flowering. The remaining species store the achenes in the infructescence indefinitely, a process called serotiny. The achenes are subject to large variations in temperature and the infructescence may become waterlogged during heavy rains, but germination will only take place after the achenes fall to the ground (Rebelo 1995). About 80% of viable achenes will germinate within 90 days, if kept sufficiently moist and at temperatures ranging from 5° to 25°C (Van Staden 1966). The duration from fertilization until harvest of achenes of *Protea* affects the germination rate and amount of achenes germinating (Van Staden 1978; Le Maitre 1990). Dormancy seems to be imposed by a low temperature requirement and by the action of the pericarp, which prevents simultaneous germination of all achenes (Deall and Brown 1981). Scarification, stratification, and incubation in pure oxygen improved the germination of *P. compacta* (Brown and Van Staden 1973). Treatment of *P. compacta* with Promalin, a solution containing GA4/GA7 and benzyladendine, increased germination, as did a stratification treatment of 60 days at 5°C, but treatment with GA3 reduced germination (Mitchell et al. 1986). Rodríguez Pérez (1995) observed an improvement in germination after imbibition with GA3 in *P. neriifolia* and *P. eximia*, but no significant difference in *P. cynaroides*. The optimum cues for maximum germination are likely to differ between the *Protea* species, as has been observed in Leucospermum (Brits 1990c).

2. Vegetative Propagation.

Members of the Proteaceae can be propagated by vegetative cuttings. The selection of single plants for use as clonally propagated cultivars depends upon the ability to propagate the plant material vegetatively. Most commercial *Protea* species are propagated by using approximately 20 cm long terminal, semi-hardwood cuttings (Malan 1993). Sub-terminal cuttings can be successfully used in some cultivars (Harre 1995) and may be the preferred type of cutting (Montarone et al. 1997). Sub-terminal cuttings of 'Sylvia' and 'Cardinal' delivered more vigorous plantlets with improved branching complexity at an earlier age. Rooting of leaf bud cuttings is also possible in *P. obtusifolia* (Rodríguez Pérez 1992). In general a 5 sec basal dip in indole butyric acid at 1,000 to 4,000 ppm is followed by setting the cuttings in well aerated medium with intermittent mist and bottom heat at 22° to 25°C (Malan 1993; Harre 1995). Rooting generally occurs within six to 16 weeks. Auxin concentration (Perry 1988), auxin carrier (Gouws et al. 1990), and hormone mixtures (Criley and Parvin 1979; Gouws et al. 1990) all influence rooting success. Specific requirements have to be adapted for each cultivar for optimum results (Harre 1995). The frequency of misting (Perry 1988), bottom heat temperature, light intensity, and rooting medium aeration (Harre 1995) also affect rooting. The time of harvesting cuttings is important in *Protea,* where growth flushes are not always well synchronized (Malan 1993), because the physiological status of the new growth flushes may not be consistent. Scarring of the base of the cutting is effective in promoting rooting of some *Protea* cultivars (Rodríguez Pérez 1990). Control of diseases while plants are rooting is important to ensure success (Benic 1986) and includes proper sanitation in the mother plants.

3. Grafting.

Grafting of *Protea* has focussed on using alkaline tolerant *P. obtusifolia* as a rootstock (Brits 1990a,b). The most successful method is the grafting or budding onto cuttings. The cutting can be rooted or unrooted. With unrooted cuttings, rooting and graft union are achieved simultaneously in a mist propagation facility. This latter technique has

been successfully applied to *Leucadendron* (Ackermann et al. 1997). Factors requiring more research in *Protea* grafting are ease of rooting of the rootstock and selection for low phenolic production in the rootstock and scion, or methods to control blackening of the cut surfaces (Brits 1990b). Low grafting success in *Protea* was not ascribed to incompatibility between scions and rootstock. An extensive search for rootstocks within Proteaceae resistant or tolerant to root rot caused by *Phytophthora cinnamomi* highlighted successful scion and rootstock combinations within the different genera and indicated combinations where graft incompatibility occurred (Moffat and Turnbull 1995). *P. cynaroides* grafted successfully onto a variety of *Protea* species, but graft union failure occurred after one to two years, with eventual death of the scion. The most successful rootstocks tested were *Protea* cultivar Pink Ice and *P. roupelliae*.

4. Tissue Culture.

Tissue culture techniques for propagation of *Protea* (Rugge 1995) have been developed. The major problem in genus *Protea* is the browning of the tissue due to phenolic compounds (Malan 1993), however, shoot proliferation has been obtained in *P. repens, P. obtusifolia*, and *P. cynaroides*. Successful transplanting of rooted shoots to soil has not been achieved. Callus and proteoid roots have been raised from mature cotyledons of *Protea* (Van Staden et al. 1981).

B. Water and Nutrient Uptake

Most species of *Protea* are adapted to nutrient-poor soils derived from Table Mountain Sandstone, with a pH (KCl) between 4 and 6 and a clay content of less than 20%. *P. obtusifolia* is found only on limestone calcareous sands with a pH (KCl) as high as 8 and *P. susannae* on the fringes of the limestone areas with pH (KCl) in the region of 6 to 7. *P. laurifolia* can be found on shale soils with a higher silt content. The two rare species, *P. mucronifolia* and *P. odorata*, are adapted to growing on shale derived soils (Rebelo 1995).

The most striking adaptation of the Proteaceae to the nutrient-poor soils on which they are found is the presence of proteoid roots, first described by Purnell (1960). The root system of *Protea* consists of a deep tap root, primarily a root for sourcing water, and shallow, lateral roots in the upper five to 10 cm that bear clusters of proteoid roots. Proteoid roots are specialized lateral roots that are diarch, show limited growth, and do not undergo secondary thickening. They bear profuse root hairs that are ephemeral and sometimes branched. Under natural conditions they first appear on roots of seedlings about six months old when the cotyledons are just withering away. The proteoid roots enable the plant to efficiently extract soil phosphorus (Lamont 1982), nitrogen, and potassium (Vorster and Jooste 1986a,b). In *Protea* growing under seasonally dry conditions, such as their natural habitat, proteoid roots are seasonal structures. Proteoid and other roots are only formed during the wet season (Lamont 1983). Shoot growth is predominantly during the dry, warm season. High nutrient levels in the soil, especially phosphates, inhibit the formation of proteoid roots in many of the Proteaceae (Grose 1989; Silber et al. 1997). Proteaceae are also characterized by highly efficient utilization of P within the plant (Grundon 1972; Grose 1989). The use of tissue and soil samples to determine the seasonal nutritional requirements has not been entirely successful (Parvin 1986). Seasonal and interplant differences in the cycle of growth flushes makes interpretation of leaf samples difficult (Barth et al. 1996). Leaf nutrient composition for 'Pink Ice' was studied in detail and the results are summarized in Table 3.10. The range in nutrient concentrations is given for the two periods of the year, i.e., mid summer and late autumn through winter, when the variation between samples and plants was the least. Significant positive and negative correlations were observed between nutrients, e.g., N concentrations were positively correlated with P, K, Na, and Zn and negatively correlated with Ca, Mg, and Fe concentrations. These significant relationships may indicate synergistic and antagonistic interactions between nutrients that need to be considered

when interpreting plant nutrient data.

Research effort has focused on the cultivation of *Protea* in soilless media (Montarone and Allemand 1993). This has led to clarification of the total plant uptake of nutrients for certain species and clones (Montarone and Ziegler 1997). It is obvious that differences between species exist in terms of their requirements for different nutrients (Claassens 1986).

Table 3.10. Range in mean nutrient concentrations of leaf samples of *Protea* cultivar Pink Ice during two periods of the year [z].

Nutrient	December to February	May to August
	(% dry weight)	
N	0.82–0.83	0.77–0.86
P	0.06–0.07	0.05–0.06
K	0.37–0.41	0.18–0.21
Ca	0.46–0.51	0.63–0.68
Na	-	0.14–0.18
S	0.11–0.13	0.09–0.10
	(mg/kg)	
Cu	-	3.5–4.5
Zn	12–15	-
Mn	43–44	-
Fe	-	51–54

[z]Data from Maier et al. (1995).

Water requirements of the different species grown under soilless conditions differ (Montarone and Ziegler 1997), with *P. cynaroides* requiring twice the amount of water required by *P. eximia*. Water requirements can be deducted by knowledge of where species grow naturally, i.e., species growing in wet valleys or near water sources have higher water requirements than species preferring dry areas (Manders and Smith 1992). *Protea*, however, will not grow under waterlogged conditions (Vogts 1989).

Investigations on the water requirement of cultivated *Protea* under irrigation indicated that maintenance of a high soil water capacity was essential to the field survival of rooted cuttings of the *Protea* cv. Cardinal (Van Zyl et al. 1999). Active consumption of water continued throughout the year and maintenance of high soil water levels increased the shoot lengths and biomass production on cultivar Cardinal in comparison with lower soil water levels.

C. Postharvest Physiology

In the genus *Protea*, vase life reduction is associated with the phenomenon of leaf blackening due to oxidation of phenolic compounds in the leaves (McConchie et al. 1991). The vase life of *Protea* is generally three to four weeks, but postharvest leaf blackening reduces the vase life to approximately one week.

Discoloration of *Protea* leaves can be induced by mechanisms such as pre-harvest mechanical damage, insect or fungal attack, or excessive heat; however, postharvest leaf blackening occurs on leaves without any physical damage (Jones et al. 1995). Although pre-harvest conditions such as waterlogging, drought, and harvesting stems from aged plants have been reported to affect the extent of leaf blackening (De Swardt 1979), little is known of the possible mechanisms involved.

Symptoms of leaf blackening occur within 2 to 5 days after harvest in *P. eximia* and *P. neriifolia* (McConchie et al. 1991). The extent of leaf blackening varies widely

between species (McConchie and Lang 1993), clones within species (Paull and Dai 1989), and the time of year. Paull and Dai (1989) found a reduction in leaf blackening if inflorescences were harvested in the afternoon compared to the morning and if inflorescences were harvested when the involucral bracts had just opened rather than at the soft bud stage. Fumigants used for insect disinfestation of inflorescences after harvest can also increase leaf blackening (Coetzee and Wright 1990; Karunaratne et al. 1997).

Removal of the inflorescence significantly delays the onset of leaf blackening (Reid et al. 1989; Dai 1993). The inflorescence continues to expand after harvest and exhibits a high rate of respiration (Ferreira 1986) with a large volume of nectar production when open (Cowling and Mitchell 1981). Removal of the inflorescence, girdling of the stem just below the inflorescence (Dai 1993; Reid et al. 1989), adding 2.5% to 5% of sucrose to the vase solution (Dai 1993), or placing the floral stems in bright light (Reid et al. 1989) delays or even prevents leaf blackening. The starch and sucrose concentration in leaves declines in stems held in the dark rather than in the light (McConchie et al. 1991; Bieleski et al. 1992).

The physiological basis of leaf blackening is still poorly understood. It appears to be a complex cascade of events that lead to the oxidation of phenolic compounds (Jones et al. 1995). This occurs, either enzymatically via polyphenol oxidase or peroxidase, or non-enzymatically after cleavage of phenolic glycosides by glucosidases. It is still not clear if membrane degradation occurs during leaf blackening (Jones et al. 1995). A reduction in leaf carbohydrate levels is coincident with leaf blackening. Dai and Paull (1995) concluded that leaf blackening in *Protea* is a result of depletion of carbohydrate by the inflorescence. This was due primarily to the sugar demand for nectar production.

VI. PRODUCTION

A. Cultivation

Cultivation techniques, describing the basic cultivation practices in different regions of the world, have been published in books by Matthews (1993), Vogts (1989), and Harre (1995). The Agricultural Research Council of South Africa has compiled a handbook on cultivation of Proteaceae (1998).

The cultivation of *Protea* is limited by the availability of suitable soils and climatic conditions (Vogts 1989). The soils must be well drained and acidic, except in the case of lime tolerant species such as *P. obtusifolia*. Clay content less than 20% is preferred, but up to 50% clay will be tolerated by some species as long as the drainage is excellent. Hot, humid conditions are not well tolerated by *Protea* and sufficient air movement is required for healthy growth. High light intensity is required. *Protea* are generally cultivated without protection and in open soil. In South Africa, two forms of cultivation are practiced: intense cultivation of clonal and seed material in rows, and broadcast seed sowing. The latter is used primarily for *P. repens* and other species used in the dried flower industry (Coetzee and Littlejohn 1995). Cultivation under glass in soilless media is possible (Montarone and Allemand 1993) and is considered economically viable in the south of France.

The general recommendation is to use a between row spacing of 3.5 to 4.0 m and a within row spacing of 0.8 to 1.0 m, giving a plant density of 2,500 to 3,560/ha. In practice, much closer spacing, with plant densities of up to 6,000/ha, is used by many farmers. The most important factors determining plant spacing are the size of the farm implements available to the farmer and the size of the plantation. In plantations small enough to be managed with hand labor only, plants are more closely spaced, but in large plantations wide inter-row spacing is required for the mechanical equipment. Soil preparation prior to planting depends on the soil type and depth. In very shallow soils, ridging is recommended to improve the depth of soil available for plant growth. Ridging is also used to improve the drainage of heavy soil. In very rocky soil, or on very steep

slopes, no soil preparation is done. In soils of a good depth, liming and adjustment of the macro and micro nutrient levels by fertilization prior to soil preparation to a depth of 1 m is recommended.

Drip irrigation is the preferred method of supplying water to *Protea* during the dry season. Overhead irrigation is not suitable as it increases the possibility of diseases and large droplets can damage the flower heads and leaves. The *Protea* species and hybrids used in cultivation will tolerate dry summer periods, but sensitivity to lack of water during the winter varies, e.g., *P. repens* will tolerate dry winter conditions in a summer rainfall area, but *P. stokoei* will not. Inorganic and organic mulches are widely used. The choice of the type of mulch depends on the soil type, soil temperatures, and cost of the mulch. Low growing cover crops that have a low cutting frequency are recommended between rows to assist in weed control. Fertilization programs differ from locality to locality, depending on the chemical and physical properties of the soil, the biomass removed annually from the plants during harvest and pruning, and the cultivar being grown. The general recommendations are not to apply large amounts of phosphates, nor use fertilizers in which more than 50% of the nitrogen is bound in nitrates. Top-dressing with potassium during the life of the plant will be necessary.

Maintenance of the immature bushes requires pruning to develop a complex structure of bearers as soon as possible. Under conditions where the plants grow slowly, annual pruning is sufficient, but in warmer areas where plants grow faster, pruning will be required two to three times a year during the first two years. *Protea* cultivars are generally able to bear a harvest of flowering stems of sufficient length two to four years after planting, depending on the parentage of the cultivar. Bushes in production will be pruned to leave bearers for the following crop during the harvest of flowering stems, with additional pruning to remove unwanted vegetative stems as required. Pruning to achieve biennial production requires leaving a long bearer when the flowering stems are harvested. This long bearer is then re-cut during the early spring to remove any new shoots, thereby timing the initiation of the new shoots correctly for manipulation of the flowering time. The number of bearers, and therefore shoots per plant, at any stage of the plant's development is dependent on the cultivar and its interaction with the climatic and soil conditions.

Flowering stems are harvested at any stage between soft-bud, or anthesis of the outer ring of florets (Plate 6). The stems are best placed immediately in water, with cooling to 2° to 5°C within 60 minutes after harvest. Thereafter the cool chain should be maintained until the stems are sold to the florist or consumer. In exporting countries the cold chain is of necessity broken during air transport. The stem length categories for export standards from South Africa start at a minimum of 40 cm, with an increase in length of 10 cm for the next category. The stem length of the longest and shortest stem packed in a carton may not differ by more than 5 cm and the stem may not deviate by more than 5 cm from straight. The *Protea* with small flower heads, such as *P. nana*, may be exported from 25 cm in length and longer. Maximum allowable blemishes, either physical or due to disease, on the involucral bracts and leaves are also defined, but each importing country sets its own phytosanitary restrictions.

The cultivation of *Protea*, both within its natural habitat and in other regions is increasing annually (Middelmann and Archer 1999). Species such as *P. cynaroides* grow under a wide variety of conditions, but other species, such as *P. compacta* and *P. magnifica,* grow poorly when cultivated outside their natural habitat range. The interspecific hybrids registered as cultivars (Table 3.5) are generally easily cultivated under a diversity of conditions.

B. Pathogens Associated with Diseases of Protea

There are a number of unique pathogens associated with *Protea* species, as well as some wide host range pathogens that attack these plants. References are also made to fungi that attack proteas when they are cultivated outside their natural habitat (Forsberg

1993; Ziehrl et al. 1995; Swart et al. 1998; Swart 1999). The first protea disease was described by Cooke (1883) and since then more than 30 pathogens have been isolated from *Protea*, of which nine can be considered as economically important diseases of *Protea* species (Table 3.11). Diseases are one of the limiting factors in the commercialization of proteas. Diseases can lead to the total destruction of cultivated proteas. Infected foliage and/or stems of protea flowers are esthetically not acceptable and lead to phytosanitary problems during international trade. In the past, disease resistance was not taken into account with cultivar development, as selections were primarily aimed at flower characteristics (Knox-Davies et al. 1986). As a result epidemic disease problems can occur with intensive cultivation of clonal proteas.

The most important diseases of *Protea* species can be grouped into root diseases, leaf spot diseases, diseases of the shoots, stem and inflorescence, and the cankers. With the exception of one bacterial disease, all of these diseases are caused by fungi. There have been no confirmed reports of *Protea* infected by viruses.

1. Pathogens of Roots.

Phytophthora cinnamomi is an important root pathogen of Proteaceae in Australia (Forsberg 1993), New Zealand (Greenhalgh 1981), South Africa (Knox-Davies et al. 1986), and the U.S.A., especially Hawaii (Kliejunas and Ko 1976; Rohrbach 1983). The disease causes root and crown rot, and is commonly referred to as the sudden death syndrome. Infected plants become chlorotic and wilt as a result of extensive root rot (Von Broembsen 1979, 1989; Cho 1981). Most protea deaths occur during hot dry periods and on badly drained soils (Newhook and Podger 1972; Pegg and Alcorn 1972; Van Wyk 1973b).

Table 3.11. Economically relevant diseases of *Protea* species.

Pathogen	Name of Disease	Reference
Phytophthora cinnamomi Rands	Root and crown rot	(Van Wyk 1973a)
Batcheloromyces proteae P.S. Van Wyk and Knox-Dav.	Leaf spot	(Marasas et al. 1975)
Coleroa senniana (Sacc.) Müller & Arx	Leaf spot	(Saccardo 1910)
Leptosphaeria protearum Syd. and P. Syd.	Leaf spot	(Van Wyk 1973a)
Mycosphaerella proteae Sacc.	Leaf spot	(Van Wyk 1973a)
Mycosphaerella jonkershoekensis P.S. Van Wyk, Marasas and Knox-Dav.	Leaf spot	(Van Wyk et al. 1975a,b)
Phyllachora proteae Wakef.	Leaf spot	(Wakefield 1922)
Botrytis cinerea Pers: Fr.	Flower head blight	(Serfontein & Knox-Davies 1990b)
Collectotrichum gloeosporioides (Penz.) Penz. and Sacc	Anthracnose/tip die-back	(Benic & Knox-Davies 1983)
Armillaria luteobubalina Watling and Kile	Root pathogen	(Forsberg 1993)
Fusarium oxysporum Schltdl.: Fr.	Fusarium wilt	(Swart et al. 1998)
Macrophomina phaseolina	Root and collar rot	(Benic 1986)

(Tassi) Goid.		
Phytophthora nicotianae Breda de Haan	Root and collar rot	(Forsberg 1993)
Rhizoctonia solani J.G. Kühn	Damping-off	(Rohrbach 1983)
Rosellinia De not. sp.	Basal stem, crown or collar rot and root rot	(Forsberg 1993)
Verticillium dahliae Kleb.	Shoot wilting and chlorosis of foliage	(Forsberg 1993)
Pythium vexans De Bary	Damping-off	(Benic 1986)
Pseudomonas syringae Moffatt	Bacterial leaf spot	(Paine and Stansfield 1919)
Cercostigmina protearum (Cooke) U. Braun and Crous var. *protearum*	Leaf spot	(Crous and Braun 1996)
Clasterosporium proteae M.B. Ellis	Leaf spot	(Ellis 1976)
Coniothyrium Corda emend. Sacc. Species	Leaf tip disease	(Van Wyk 1973a)
Mycosphaerella bellula Crous and M.J. Wingf.	Leaf spot	(Crous and Wingfield 1993)
Teratosphaeria fibrillosa Syd. and P. Syd.	Leaf spot	(Sydow and Sydow 1912)
Teratosphaeria proteae-arboreae P.S. Van Wyk, Marasas and Knox-Dav.	Leaf spot	(Van Wyk et al. 1975a)
Trimmatostroma macowanii (Sacc.) M.B. Ellis	Leaf spot	(Ellis 1976)
Didymosporium congestum Syd.	Leaf spot	(Diodge 1950)
Dothiorella Sacc. sp.	Leaf spot	(Anon. 1991)
Chondrostereum purpureum (Perd.: Fr.)	Silver leaf	(Forsberg 1993)
Schizophyllum commune Fr.: Fr.	Trunk rot	(S. Denman, pers. comm.)
Sclerotinia Fuckel. sp.	Die back	(Benic 1986)
Phomopsis (Sacc.) Sacc. sp.	Die-back	(Orffer and Knox-Davies 1989)

P. cinnamomi can be isolated from seedlings with damping-off symptoms in seedbeds and from cuttings in nursery beds (Benic 1986; Forsberg 1993). Symptoms are generally less severe and develop more slowly on *Protea* than on other Proteaceae such as *Leucospermum* and *Leucadendron*. *Protea cynaroides, P. neriifolia,* and *P. repens* appear to be resistant to *P. cinnamomi*. Other soil-borne pathogens of *Protea* are listed in Table 3.11.

2. Pathogens of Leaves.

Protea species are generally more prone to leaf spot diseases than other Proteaceae (Van Wyk 1973a) and the only bacterium, *Pseudomonas syringae*, was isolated from the leaves of *P. cynaroides* in England (Paine and Stansfield 1919) and Australia (Wimalajeewa et al. 1983). Bacterial leaf spot has not been recorded in South Africa (Knox-Davies et al. 1986).

Batcheloromyces proteae Marasas is one of the economically important pathogens of *Protea* leaves. The leaf spots are not destructive but decrease the quality of the leaves

for commercial use. The most typical lesions are black, with a red-brown to purple-black discoloration of the leaf tissue (Marasas et al. 1975). The host range includes the following economically important proteas, *P. cynaroides, P. grandiceps, P. magnifica, P. neriifolia*, *P. punctata*, and *P. repens* (Marasas et al. 1975; Smith et al. 1983; Van Wyk et al. 1985; Knox-Davies et al. 1986; Swart 1999).

Coleroa senniana was first described by Saccardo (1910) on leaves of *P. gaguedi (P. abyssinica)* from North Africa. The fungus commonly occurs on leaves of *Protea* species in Southern Africa (Doidge 1941) and is, except for *Mycosphaerella proteae,* probably the most widespread pathogen of *Protea* species. *C. senniana* produces tiny black specks (pseudothecia of the fungus) on the upper surface of *Protea* leaves. On *P. magnifica* the specks are yellow to brown (Van der Byl 1929; Serfontein and Knox-Davies 1990a). *Coleroa senniana* occurs on leaves of summer and winter rainfall *Protea* throughout sub-Saharan Africa (Saccardo 1910) and was also isolated on cultivated *Protea* in California, U.S.A. (Swart 1999).

Leptosphaeria protearum causes leaf spots that are necrotic and sunken, with raised, dark brown margins (Van Wyk 1973a). Most economically important proteas are affected by *L. protearum*, but *P. mag nifica* is particularly susceptible. *Leptosphaeria protearum* appears specific to *Protea* species (Von Broembsen 1989).

Mycosphaerella proteae is the most common pathogen on *Protea* species in South Africa (Van Wyk 1973a) and the host range includes winter and summer rainfall proteas (Saccardo 1891; Sydow and Sydow 1914; Doidge 1921; Van Wyk et al. 1975a,b; Swart 1999). The leaf spots caused by *M. proteae* on the different hosts are quite variable in appearance but the spots are amphigenous and bright red-purple to red-brown. *Mycosphaerella jonkershoekensis* has so far only appeared on *P. repens* and *P. magnifica* (Van Wyk 1973a; Van Wyk et al. 1975a,b) and causes greyish to light brown leaf spots with raised, dark brown margins. *Phyllachora proteae* lesions are typically necrotic with a raised margin and move from the leaf tip inwards and finally cover the entire leaf surface (Wakefield 1922; Van Wyk 1973a; Van Wyk et al. 1975a). The host range includes *P. acaulis, P. magnifica, P. neriifolia*, and *P. repens* (Van Wyk 1973a; Van Wyk et al. 1975a). Van Wyk (1973a) stated that *Phyllachora proteae* must be reclassified as a species of *Botryosphaeria. P. proteae* has been reclassified as *Botryosphaeria proteae* Wakef. Denman & Crous. (Denman et al. 1999).

Vizella interrupta G. Winter, S. Hughes causes brown lesions on *Protea* leaves, which often coalesce. The ascocarps form black spots on slightly discolored leaf tissue on *Protea* species. The host range includes *P. cynaroides, P. grandiceps, P. magnifica*, and *P. neriifolia* (Van Wyk 1973a; Van Wyk et al. 1975b, 1976; Swart 1999).

3. Pathogens of Shoots, Stems, and Inflorescences.

Colletotrichum gloeosporioides, or colletotrichum die-back, is the most important disease of *Protea* species (Coetzee et al. 1988). The die-back of young shoot tips is the most characteristic symptom. Other symptoms include necrotic stem and leaf lesions, stem rot, sunken stem cankers, seedling damping off, seedling blight, and cutting die-back (Von Broembsen 1989; Forsberg 1993). *Colletotrichum* lesions on one side of the stem cause the new growth to bend. This is referred to as shepherd's crook disease of proteas. All economically important *Protea* species are affected by colletotrichum die-back in South Africa, Australia, and Hawaii (Greenhalgh 1981; Benic and Knox-Davies 1983; Benic 1986; Knox-Davies et al. 1986; Anon. 1991).

Botrytis cinerea causes blight of the flowering branches and inflorescence heads. In *Protea* species, *B. cinerea* is a strong, active pathogen that can invade actively growing tissues and inflorescences (Rohrbach 1983). Brown spots develop on the leaves and inflorescence buds. The lesions expand and inflorescence buds can be killed, with necrosis extending down the inflorescence stalks, causing death of affected parts and new shoots (Serfontein and Knox-Davies 1990b; Forsberg 1993). Infected shoot tips collapse, darken, and die. Bending of affected shoots is typical of botrytis damping-off (Forsberg 1993) and has been recorded on cuttings showing die-back symptoms (Benic 1986). The

host range includes *P. cynaroides* and *P. repens* in South Africa and Hawaii (Swart 1999).

4. Pathogens of Woody Stems.

Botryosphaeria species that cause cankers and die-back of injured tissue are a common problem and cause considerable losses in the production of *Protea* cut flowers. The most important species associated with *Protea* are *Botryosphaeria dothidea* (Moug.: Fr.) Ces and De Not., or *Botryosphaeria ribis* (Tode: Fr.) Grossenb. and Duggar. The host range includes *P. compacta, P. cynaroides, P. eximia, P. grandiceps*, and *P. repens* (Van Wyk 1973a; Knox-Davies et al. 1981; Swart 1999).

In South Africa, only two chemicals are registered for the control of diseases on proteas. Looking at the complexity of the proteaceous pathogens, as well as the lack of control strategies of the diseases, it becomes evident that diseases are the most limiting factor in the commercialization of proteas. To prevent the development of diseases, the breeding and selection of resistant or tolerant cultivars will play an important role in the future.

C. Phytophagous Insect Fauna of *Protea*

From studies on the insect guilds of *P. repens* (Coetzee and Latsky 1986), *P. cynaroides* and *P. neriifolia* (Coetzee 1989), *P. magnifica* and *P. laurifolia* (Wright 1990), and *P. nitida* (Visser 1992), it is clear that proteas harbor a rich and distinct entomofauna. Insects associated with *Protea* species play an important ecological role as pollinators (Coetzee and Giliomee 1985), folivores (Wright and Giliomee 1992), and seed predators (Myburg and Rust 1975). *Protea* insects of significant economic importance can be divided into flower visitors, endophagous or borers, folivorous insects, and sap-suckers.

1. Flower Visitors.

The nectar and pollen rich protea flower attracts more than 200 insect species (Gess 1968) with, in many cases, high population levels (Visser 1992). Sugar birds like *Promerops cafer* (Mostert et al. 1980) and rodents (Cowling and Richardson 1995) pollinate proteas and it is also possible for insects to successfully pollinate *Protea* species (Coetzee and Giliomee 1985). Collins and Rebelo (1987) suggested that bird pollinated seed would be of genetically higher quality than seeds resulting from insect pollination, as birds have a larger foraging range and this could result in greater heterozygosity. Insects pollinating *Protea* species are generalist flower visitors and it is possible that larger beetles (Coleoptera, Scarabaeidae) may be more important pollinators than smaller insects (Wright 1990), again due to the greater mobility of larger insects. The presence of insects in cut flowers is one of the most serious limiting factors influencing the South African protea industry (Wright and Saunders 1995). Research on the use of a negative pressure fumigation system, based on a forced cooling system, provided excellent insect control using dichlorvos aerosol (Wright and Coetzee 1992; Wright 1992).

2. Borers.

Inflorescences and infructescences of *Protea* species are attacked by the larvae of a range of insects (Coetzee and Giliomee 1987a,b). The endophagous predators of serotinous protea seed are listed in Table 3.12. Insect seed predation of canopy stored *Protea* seed banks may be a factor that reduces the potential of proteas to form monospecific stands (Wright 1994b). Borers attacking *Protea* infructescences are also an important guild of pests of cultivated *Protea*, attacking young shoots and flower buds (Myburg and Rust 1975). On *P. cynaroides,* the larvae of the protea butterfly, *Capys alphauses,* has been recorded destroying up to 40% of the flower buds. Endophagous larvae cause phytosanitary problems, when present in cut flowers. Infested infructescences serve as a reservoir where pest numbers can increase and orchard

sanitation is a practice that should be applied to reduce borer incidence (Coetzee et al. 1988).

Table 3.12. Endophagous insects of *Protea* species.

Genus	Species	Family	Order
Sphenoptera		Buprestidae	Coleoptera
Genuchus	*G. hottentottus* (Frabricius)	Scarabaeidae	Coleoptera
Euderes	*E. lineicollis* (Wiedemann)	Curculionidae	Coleoptera
Capys	*C. alphaeus* (Cramer)	Lycaenidae	Lepidoptera
Orophia	*O. ammopleura* (Meyrick)	Oecoporidae	Lepidoptera
Argyroploce		Torticidae	Lepidoptera
Bostra	*B. conspicualis* Warren	Pyralidae	Lepidoptera
Tinea		Tineidae	Lepidoptera

3. Folivorous Insects.

As the foliage of protea cut flowers must be esthetically acceptable, the leaves must be free of insect damage. Leaves of proteas are attacked by herbivores, leafminers, and gall forming insects. Leaf feeders can remove 5% to 22% of the leaf surface (Coetzee 1989; Wright and Giliomee 1992). Leaf miners cause scarring of leaves, which renders the final product unmarketable, while gall forming insects are a phytosanitary risk (Wright and Saunders 1995). Young protea leaves are protected by a range of unique anti-herbivore mechanisms such as phenolic compounds (tannins) and a pronounced cyanogenic capacity. Some species cover their young leaves with a thick layer of trichomes. This strategy has led to insects avoiding the more succulent and nutritious young leaves in favor of older, tougher leaves (Coetzee et. al. 1997). However, some of the most important herbivores on *Protea* species (*Bostra conspicualis* Warren, Pyralidae, Lepidoptera, and *Afroleptops coetzeei*) (Oberprieler), Curculionidae, (Coleoptera), have alimentary tract pH levels which suggest adaptation to a tannin rich diet (Wright and Giliomee 1992), which allows them to utilize older leaves in spite of the presence of tannins. Leafminers on *Protea* species are a guild of micro-lepidoptera that have successfully overcome the defense mechanism of young *Protea* leaves. The micro-lepidoptera belong to the families Phyllocnistidae, Incurvanidae, and Gracillaniidae. Only *Proteaphagus capensis* (Scoblein), Incurvariidae, found on *P. cynaroides* has been identified. The rest are still unknown and very little is known about their life cycle. Gall insects that belong to the Psyllidae (Hemiptera) can form galls on leaves of *P. repens* and cause phytosanitary problems.

4. Sap Suckers.

A selection of sap suckers feed on proteas. These can transfer diseases by means of their mouth parts, but cause little physical damage. Stressed plants can die when infestations are not controlled. Sedentary sap suckers include mealy bug (Pseudococcidae) and scale insect species of the Coccidae and Diaspididae (Coetzee 1989), which causes phytosanitary problems with the export of flowers.

Insects cause serious problems where proteas are cultivated in their natural habitat. Where proteas are cultivated outside their natural habitat, no serious insect problems have

been experienced. This indicates that insects cannot easily overcome the defense mechanisms of the genus *Protea.*

VII. CONCLUSION

Protea have become an established horticultural crop, with a world sale of approximately 8 million flowering stems. In South Africa 3.01 million stems are exported, 1.14 million sold through the formal market, and 1.01 million sold by the informal sector. Other producing countries do not have figures for sales of *Protea*, but total sales are estimated at 3.00 million. Less than 1.5 million stems are sold through the Dutch auction system annually. The total share of the world flower market filled by *Protea* is very small, but it is the flower identified with South Africa. *P. cynaroides* is the national flower of South Africa and is the symbol of its sports teams. In the Cape Floristic Region, Proteaceae is an important component of the agricultural sector and the industry provides many job opportunities. Cultivation in areas outside their natural habitat has increased dramatically, both within South Africa and in other countries with similar climate and soil conditions. This has led to large quantities of proteas on the international market originating from regions other than the endemic environment from which *Protea* originate. Thus the Cape region and the people who initiated the protea industry run the risk of losing their market share. The stipulations of the Convention on Biological Diversity, which focus on benefit sharing related to commercial exploitation of genetic resources, would appear to have no practical application to the *Protea* genetic material. *Protea* species propagation material is widely available from around the globe. The majority of the most widely used cultivars originate in South Africa, but practical and financially viable methods of ensuring that royalties are returned to the legal owners of cultivars are insufficient. Solutions to this problem are being sought.

An interesting pattern in the development of the indigenous cut flower industry in South Africa is that changes in the industry have most often been preceded by research activities. The challenge for South Africa is to produce high-quality blooms for the Western European market during the hot dry summer months. The majority of the *Protea* bloom during the early winter to late spring, while the Western European markets buy *Protea* during their Northern Hemisphere winter period from September to May. Selection and breeding has resulted in cultivars that flower in the summer, but more types are needed. It is also necessary to develop cultivars of similar appearance, but successive flowering periods, to provide a continuous supply of blooms to the market. An increase in the cultivation of the winter flowering species in the Northern Hemisphere could negatively impact on the Southern Hemisphere countries. Leaf blackening remains a problem in all regions where *Protea* are grown. Leaf blackening reduces the appeal of *Protea* to the consumer. It may be possible to reduce leaf blackening by genetic manipulation. If cultivars with reduced potential for leaf blackening can be developed, it would impact positively on the industry.

There are pests and diseases of *Protea* that are common to the different regions in which they are cultivated. South Africa has the challenge of cultivating *Protea* in their natural habitat, with all the co-evolved insects and pathogens present in the natural fynbos. It is necessary to continuously research chemical and biological control measures. Environmentally sound practices must include the breeding of disease resistant cultivars to reduce the dependence on chemical control.

Refinement of cultivation practices, such as pruning, fertilization, and irrigation, is required to maintain the economic return of *Protea* as a crop and to ensure the delivery of quality blooms to a very competitive international market. The challenges of cultivating *Protea* differ from region to region, but the basic plant physiology controlling the plant's reaction to environmental stresses remains the same. Funding for basic research has, in the past, been generously supplied by government organizations, but in the economic climate of the late 1990s, government support of research is dwindling. This is especially

true in South Africa, where flowers in general are still minor crops.

The international flower markets are always searching for new, exciting products. *Protea* can fulfill this demand. A larger variety of cultivars, with different forms and colors, longer vase life, exceptional quality, and extended availability during the year are needed to maintain and increase the market share. These goals will only be achieved by continued research.

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4

Leucadendron: A Major Proteaceous Floricultural Crop[*]

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I. INTRODUCTION

Many members of the Proteaceae are being used as fresh and dry cut flowers (Plate I and II). Some of these crops have been reviewed recently: *Leucospermum* (Criley 1998), *Protea* (Coetzee and Littlejohn 2001), and *Banksia* (Sedgley 1998). Recent publication on cultivation and diseases of Proteaceae are reviewed by Crous et al. (2004). The total number of Proteaceous cut stems around the world is about 100 million (Littlejohn 2001), and leucadendrons probably account for at least half of this total. Israel alone produces more than 35 million branches annually–about 25% of all the cut foliage exported from this country (Gazit 2002). All leucadendrons provide good cut foliage, but one of them, *L*. 'Safari Sunset', a *Leucadendron* hybrid developed some 40 years ago in New Zealand, is the most popular (Matthews 2002). This single cultivar accounts for about 90% of the proteas produced in Israel. Most of the scientific research on *Leucadendron* in Israel, especially with regard to commercial cultural practices, has addressed this cultivar.

Proteas, including leucadendrons, have been investigated and cultivated for over 250 years (Knight 1809; Linnaeus 1753) and still there are many myths regarding their uniqueness and thus their very special methods of cultivation. In fact, there is still relatively little solid, scientifically based information available on these plants. Three types of information have been consulted for this review: (1) scientific and technical publications; (2) books about proteas, some written for amateur botanists and nature lovers (Vogts 1982; Eliovson 1983; Rebelo 2001; Matthews and Carter 1983) and other books for commercial growers (Parvin and Criley 1991; Matthews 1993; McLennan 1993; Harre 1988, 1991; Salinger 1985; Matthews 2002); and (3) published and unpublished accounts of practical experience, provided mainly by Israeli farmers, extension specialists, and researchers. In general, for simplification, the name "protea" will be used, in this review, for all plants belonging to the Proteaceae. Growers of Proteas, including *Leucadendron*, on a worldwide basis cooperate and exchange information via the International Protea Association (IPA) (Brits 1984; Criley 1998).

II. BOTANY OF THE GENUS *LEUCADENDRON*

A. Taxonomy

About 100 years passed between the discovery of South Africa and the beginning of scientific description of the proteas. In 1737, Linnaeus described the first two species of *Leucadendron* (*L. argenteum* and *L. coniferum*), but it took a long time to understand and to classify the South African proteas. With the introduction of the binomial system of nomenclature by Linnaeus in his *Species Plantarum* (1753), only six species of plants were listed under the name protea. In the case of *L. argenteum*, Linnaeus became lyrical in his description and stated that "This tree is the most shining and splendid of all plants," but he then continued and wrote about the Silver Tree that: "*yes,* (it is) *like Proteus himself extremely variable and different*" (Williams 1972). The difficulties and misunderstanding were probably partly due to the fact that the genus *Leucadendron* is dioecious, and the male and the female plants are very different in appearance (Williams 1972). A general introduction to the origin of the protea family can be found in Criley's review on *Leucospermum* (Criley 1998), and the systematics and phylogeny of the African Proteaceae were reviewed recently by Rourke (1998). The taxonomy of the genus *Leucadendron* was revised about 30 years ago (Williams 1972).

Recent studies, based on gene-sequencing data, have contributed to the understanding of the genetics, systematics, and phylogeny of the African Proteaceae, including *Leucadendron* (Barker et al. 1995; Hoot and Douglas 1998; Tansley and Brown 2000). The genus *Leucadendron* is easily identified as having plants of separate sexes: the pistillate plants (known as female plants in the leucadendron literature) produce woody

conical, fruit-bearing flower heads, called "cones" (Rebelo 2001). The flower heads of the staminate plants (known as male plants in the leucadendron literature) do not form those conical flower heads. The conspicuous cones of the female plants consist of spirally arranged floral abracts, each of which covers a small flower (floret), and the bracts become hard and woody, forming the conical structures (Rebelo 2001).

There are also morphological differences between the male and the female plants: the males are usually more branched and often slightly larger than the females, with smaller leaves and flower heads (Rebelo a2001). Bond and Midgley (1988) reported great differences in stem diameter, leaf area, number of inflorescences and mass of each individual inflorescence between the sexes of *L. rubrum*, and some differences in these characters in *L. tinctum* also. There are other extreme phenomena of dimorphism that distinguish between the sexes in *L. rubrum* (De Kock et al. 1994).

Williams (1972) reviewed the taxonomic history of the main South African genera of Protea. Because emphasis had been placed on different features, the family had been divided into different genera in several different ways, and each genus into different groups of species. Williams a(1972) adopted R. Brown's (1810) approach and based his classification of *Leucadendron* on division into sections and sub-sections, mainly according to fruit and floral characters (Table 4.1). Rebelo (2001) is continuing his research on the taxonomy and distribution of the genus *Leucadendron*, and much of the more recent information can be found in his Protea Atlas Project (Rebelo 2004). Thorough knowledge of the generic relationships among the Leucadendrons is contributing greatly to their horticulture and breeding.

Rebelo (2001) simplified the use of Williams' (1972) classification of the Leucadendrons by adding the English common name "conebush" to the genus *Leucadendron* as well as common names to the subsections (Table 4.1); he described each of the sections, subsections and species. Species belonging to the section *Leucadendron* have round nuts or nutlets (fruits) and those belonging to the section *Alatosperma* have flat, winged fruits.

B. Distribution and Ecology

The distribution range of the genus *Leucadendron* is limited to the Cape geological series in the southern Cape Province (Cape Floral Kingdom), with a small outlier on the Cape geological series near the coast in Natal (Williams 1972). All leucadendrons, except 3, are found in the Cape Floral Kingdom (Rebelo 2001) and all of them are well adapted to the fynbos vegetation type (Cowling and Richardson 1995). The fynbos is the most common vegetative type of the Cape Floral Kingdom, contributing more than 80% of its species, including the leucadendrons (Goldblatt and Manning 2000). Rourke (1980) defined fynbos as the sclerophyllous vegetation of the southwestern Cape, composed mainly of plants having fine, hard, heath-like leaves, or stems. The exact distribution of the individual *Leucadendron* species was described by Goldblatt and Manning (2000), and distribution maps were presented by Williams (1972) and Rebelo (2001). The survival risk for leucadendrons species in nature is: 2 extinct, 16 endangered, 8 vulnerable, 17 naturally rare, and 1 uncertain (Hilton-Taylor 1996). Additional information is available at *www.nbi.ac.za/protea*. This situation is even more prevalent with regard to some of the local types and subspecies (Rebelo 2001). The South African Agricultural Research Council–Fynbos Unit has directed great efforts into the *ex situ* conservation of horticulturally important proteas, including leucadendrons (Littlejohn et al. 2000).

Table 4.1. Classification of the genus *Leucadendron* (modified from Rebelo 2001).

Section	Subsection name		Species
	Scientific	Common[z]	
Leucadendron	Villosa	Sandveld	*brunioides, cinereum, concavum, coriaceum, dubium, galpinii, levisanus, linifolium, stellare, thymifolium*
	Membranacea	Arid	*arcuatum, bonum, remotum, pubescens*
	Carinata	Ridge-seed	*nitidum, sericeum*
	Uniflora	Pauciflor	*ericifolium, olens*
	Aliena	Kouga	*singulare, sorocephalodes*
	Cuneata	Fuse-bract	*corymbosum, laxum, verticillatum*
	Nervosa	Jonaskop Silver	*nervosum*
	Leucadendron	Silver	*album, argenteum, dregei, rubrum*
	Nucifera	Sun	*barkerae, burchellii, cordatum, cadens, daphnoides, glaberrinum, gydoense, loranthifolium, meyerianum, orientale, pubibracteolatum, rodii, sessile, sheilae, tinctum, tradouwense*
	Ventricosa	Crown	*chamelaea, elimense, globosum, grandiflorum*
Alatospermum	Trigona	Delta-seed	*conicum, floridum, loeriense, macowanii, pondoense, roukei, radiatum, salicifolium, uliginosum*
	Brunneobracteata	Oilbract	*microcephalum*
	Alata	Sunshine& Clay	*coniferum, cryptocephalum, diemontianum, discolor, eucalyptifolium, flexuosum, foedum, gandogeri, lanigerum, laureolum, meridianum, modestum, procerum, salignum, spissifolium, strobilinum, stelligerum, xanthoconus*
	Compressa	Needle-leaf	*comosum, immordoratum, muirii, nobile, osbornei, platyspermum, spirale, teretifolium*

[z] Cone bush

The diversity, endemism, and distribution of leucadendrons and also of other Fynbos plants in the Cape Floristic Region are extensive. The rugged and dissected nature of the Cape landscape is a significant factor in the understanding of this diversity and endemism (Goldblatt and Manning 2000), as is the fact that after more than 250 years of

Leucadendron research (Linnaeus 1753; Knight 1809) new species belonging to this genus are still being discovered (A. E. Van-Wyk 1990; Rourke 1997). Many studies and publications address various ecological and distribution aspects of the place of the *Leucadendron* species in the natural vegetation (Midgley 1998). Fires are an important factor in the life cycle of leucadendrons and affect the germination of its serotinous species, as well as some of the myrmecochorous and therophilous species (T. Rebelo, pers. commun. 2004). The fire causes the releases of the seeds from the cones to the ground, making the germination possible (Bond 1985; Le-Maitre 1988, 1989; Le-Maitre et al. 1992; Midgley 2000). Flower harvesting methods, seed dispersibility, and seed size affect the distribution and ecology of leucadendrons (Stock et al. 1990; Mustart and Cowling 1993a,b; Midgley 1998). The type of soil, its nutrient levels, its pH and hence its nutrient availability, as well as plant competition and tillage of the heathland soil are also important determinants of the distribution of *Leucadendron* in its natural habitat (Davis and Midgley 1990; Davis 1992; Mustart and Cowling 1993a,b; Mustart et al. 1994; Richards et al. 1997a,b; Laurie et al. 1997).

Data regarding the climate of the Cape Region reveal average daily maximum temperatures of 28°C and 17°C in midsummer and midwinter, respectively. Extreme maxima reach 43°C in the summer and 30°C in the winter, and extreme minima reach 4°C in midsummer and -5°C in midwinter. Temperatures, especially leaf temperatures, are greatly affected by ocean breezes and overcast skies. Annual rainfall ranges from 3000 mm on some mountain peaks to less than 250 mm in some inland valleys (Schulze 1984; Goldblatt and Manning 2000). The soils of the Cape region have various geological origins, including sandstone, granite, and limestone (Goldblatt and Manning 2000), and accordingly, in nature, different species of *Leucadendron* grow in sandy or heavy, boggy soils, and in soils with high or low pH (Williams 1972; Eliovson 1983; Laurie et al. 1997).

III. WORLD INDUSTRY AND ECONOMICS

World trade in the three most widely used genera among the South African Proteaceae is estimated at 100 million stems annually, with the greatest volume involving a single *Leucadendron* cultivar 'Safari Sunset' (Littlejohn 2001). Littlejohn (2001) estimated the annual market volume of *L*. 'Safari Sunset' to be about 25 million stems; today, however, we know that the current volume is probably more than 40 million. A large proportion of the *Leucadendron* branches produced for the world market are of seed-propagated species and not of cutting-propagated cultivars (Table 4.2). This is especially true in the South African production of *Leucadendron*. Except for some hybrids, most of the seed propagated plants and those propagated vegetatively from unidentified clones are sold under the species name or under trade names. In many cases, the "old" synonymous species name is used as the trade/commercial name. In other cases, the species name is followed by an indication of whether the flower is male or female. The SAPPEX (South African Protea Producers and Exporters Association, undated) Catalogue includes 24 species and six cultivars of *Leucadendron* that are currently exported from South Africa.

The main leucadendrons sold on the Sydney market are: *L*. 'Silvan Red', *L*. 'Safari Sunset', *L. salignum* red, *L. salignum* yellow, *L. gandogeri* green and yellow, *L. laureolum* green and yellow, *L*. 'Tall Red', *L*. 'Inca Gold' yellow, *L*. 'Maui Sunset', *L. salicifolium*, *L. floridum* 'Pisa', *L*. 'Harvest'; leucadendrons with "cones" ("Christmas-nuts" as it is called on the Sydney market in the mid-summer, Christmas season) include: *L. galpinii* and *L*. 'Jubilee Crown'. More exotic Leucadendrons are: *L*. 'Katies Blush', *L*. 'Sundance', *L. tinctum*, *L. orientale*, *L. strobilinium*, *L. discolor* female (white), *L. discolor* male (yellow with red center), *L. argenteum*, and *L. elemense* (with "nuts" at Christmas; Scott 2000).

A. Types of *Leucadendron* Cut Branches

In analyzing the different types of *Leucadendron* cut products on the market, one may classify them into four main groups, more than one of which may be produced by a given species or cultivar during different seasons. The four main groups according to SAPPEX (undated) and L. J. Matthews (2002) include: (1) Foliage–cut branches are sold for their attractive foliage, which is relatively uniform along the whole length of the branch. The color of foliage varies among species and between specific clones: silver in silver tree (*L. argenteum*), green in 'green discolor' (*L. discolor*) and 'Pisa' (*L. coniferum* × *L. floridum*), and light green in male *L. platyspermum*. The product is available almost throughout the year, except when new growth is too soft. (2) Attractive colorful "heads"–in these branches, when vegetative growth is stopped or slowed down and flowering commences, the larger terminal leaves become colorful. These involucre leaves commonly mistakenly known as "bracts" (Rebelo 2001, 2004) change their color during the marketing season. The main colors are various shades of red and yellow. Particular examples are: *L.* 'Safari Sunset', *L.* 'Yaeli', *L.* 'Inca Gold', and *L.* 'Gold Strike'. Depending on the cultivar, the product may be available for long or short periods, though its shape and color may change in the course of the marketing season. (3) Male colorful "heads"–inflorescence and surrounding involucre leaves as in red and yellow discolors (*L. discolor*). The marketing season is extremely short (two to three weeks). (4) Branches terminating in attractive female cones–the main examples are females of: *L. teretifolium, L. linifolium, L. galpinii, L. coniferum, L. salicifolium, L. platyspermum*, and the cultivar 'Jubilee Crown' (*L. laureolum* × *L. salignum*). Some species or cultivars may be sold with attractive colorful involucral leaves and cones (e.g., *L.* 'Safari Sunset'). This type of product has a long marketing period.

Table 4.2. The main species and cultivars of *Leucadendron* in the international floricultural trade and their methods of propagation. (Sources: Cape Flora–South Africa, SAPPEX (Catalogue).

		Types of Plantation			
			Seedlings		
Botanical	Trade of cultivar name	Clones	All types of seedlings	Special types	Sex separated at harvest
L. argenteum	Silver tree	x	x		
L. coniferum	Sabulosum		x		
L. coniferum × *floridum*	Pisa	x			
L. discolor	Green Discolor	x	x		
L. discolor	Red Discolor	x		x	
L. discolor	Yellow Discolor	x		x	
L. floridum	Florida	x		x	
L. galpinii			x		
L. laureolum	Decorum Star				x
L. laureolum	Laureolum male				x
L. laureolum × *L. salignum*	Safari Sunset	x			
L. linifolium	Tortum female				x
L. linifolium	Tortum male				x
L. laxum	Smartrose		x		
L. laxum	Jubilee Crown	x			
L. meridianum			x		

L. muirii			x			
L. nervosum						x
L. nervosum	Nervosum male					x
L. platyspermum	Platy male		x			x
L. platyspermum	Platystar		x			x
L. rubrum	Rubrum female		x			x
L. rubrum	Rubrum male		x			x
L. salicifolium	Strictum	x				
L. salignum	Blush	x				
L. salignum	Red adscendens			x		
L. salignum × *L. eucalyptifolium*	Chameleon	x				
L. teretifolium	Cumosum		x			
L. xanthoconus	Salignum		x			
L. laureolum × *L. salignum*	Gold Strike	x				

B. Yield

It is difficult to assess the potential and the actual yields of leucadendrons. Yield may be counted in terms of production per plant or per hectare. In commercial plantations of *L.* 'Silvan Red', Barth et al. (1996) counted average annual yields of 314 and 219 marketable stems per plant on highly fertile and infertile sites, respectively. They indicated that the plants were 1.0 to 1.5 m wide, but they did not indicate the distances between plants. However, in Australia, the planting density is generally 2600 plants per hectare (Cecil et al. 1995), so that the average annual yield is almost 700,000 stems per hectare. *Leucadendron* 'Safari Sunset' is planted in Israel at spacings of 2 m between rows and at 0.8 m within the row, i.e., 6250 plants per hectare (Shtaynmetz 1998; Shtaynmetz et al. 2004a). When planting is done in the spring, the average annual yields are 60,000, 150,000, 240,000, and about 400,000 marketable stems per hectare in the first, second, third, and fourth year onwards, respectively (Shtaynmetz et al. 2004a). The discrepancies between the Australian and Israeli figures may be related to the different cultivars and/or to the fact that in Israel the figure is solely for quality exportable stems.

IV. HORTICULTURE

A. Genetic Improvement

In the early days of the protea industry, flowers were harvested from natural plant stands. Even now, many of the *Leucadendron* branches, especially those produced in South Africa, are harvested from natural fynbos or produced on seed-propagated species, rather than on cuttingpropagated, selectively bred cultivars. The first dedicated, scientific breeding of proteas–which included *Leucadendron* as an important component–was started in South Africa in 1973 (Brits 1983; Brits et al. 1983). The breeding of *Leucadendron* was initially based on the extensive collections that Marie Vogts had made, from nature, of so-called "commercial variants" (botanical ecotypes) of the best variations of species, and which she subsequently established in cultivation (Brits et al. 1983). However, the trend towards production of high-quality cultivars of *Leucadendron* started in other countries, rather than South Africa (Littlejohn et al. 1995). Leucadendrons are easily reproduced by cuttings, therefore the improvement process has to produce only a single superior plant; the new cultivar can then be developed simply by multiplying this plant by means of cuttings. There are several ways to select the superior single plant from

which to develop a new cultivar: taking cuttings from superior plants grown in the natural fynbos or in seedpropagated plantations, or developing superior variations by controlled or uncontrolled hybridization (Brits 1983). Hybrid seeds may be produced from crossing variants of the same species (intraspecific), or from crosses between species (interspecific). Hybrid plants may be produced by planting the parent plants in the same field and waiting for crosspollination to take place naturally (open pollination) and then collecting hybrid seeds, or by artificial, controlled pollination (van den Berg and Brits 1995).

In *Leucadendron*, the genetic variations available are vast and as yet largely untapped (Brits 1983; Littlejohn et al. 1995; van den Berg and Brits 1995). In 1995, Littlejohn et al. (1995) stated that the techniques to successfully hybridize any Proteas at will were not yet available, and that there was a need to overcome difficulties of low seed set and crossincompatibility between species.

The natural pollination modes in *Leucadendron* differ among species; some species are wind pollinated and others depend on specific insects (Hattingh and Giliomee 1989). In their review, Collins and Rebelo (1987) indicated that the pollination biology and breeding systems of Australian and southern African Proteaceae resemble one another. Proteas exhibit low seed set relative to the number of flowers available, and functional abandromonoecy (overcrowded, functional and non-functional flowers on the same receptacle) seems to be the main cause of poor seed set (Hattingh and Giliomee 1989).

Originally, leucadendrons were marketed mainly as green/foliage type flowers. Van den Berg and Brits (1995) were the first to recognize the potentially high market demand for superior quality *Leucadendron* single-stem cut flowers as a separate product. They pointed out that it was almost impossible to find all the desirable cut flower combinations of attractive large flower heads, long flowering branches and a high yield, within a single species, and argued that interspecific crosses must be used to combine the desirable qualities from different species. It was, however, much earlier, in the early 1960s, that the first excellent, single stem cut flower cultivar 'Safari Sunset' was originated; it served as the role model for Brits' and van den Berg's 1986 research project (Bell 1988; Matthews and Carter 1983; van den Berg and Brits 1995; Matthews 2002). Heterosis (hybrid vigor) is often found in proteaceous hybrids (Brits 1983). In 1986 van den Berg and Brits (1995) started an extensive and systematic interspecies hybridization program with *Leucadendron*, intended partly to study both interspecific compatibility and heterosis in this genus. They found, surprisingly, a relatively high incidence of successful crosses, as well as high seed set, in the crosses, especially among the Alatosperma. Furthermore, among over 3000 hybrid seedlings produced from 36 interspecific crossing combinations, with average seed set approaching 50% of the pollinated florets, the majority showed strong hybrid vigor. This demonstrated the unusual potential for systematic interspecific breeding in *Leucadendron*.

In *The International Proteaceae Registrar* (including the register and the checklist, Sadie 2002) are listed over 110 names of *Leucadendron* cultivars; of these 38 are interspecific hybrids (Table 4.3, Sadie 2002). Most of the successful crosses are among species of the Section Alatosperma, Subsection Sunshine (Alata) con bushes, mainly between *L. laureolum* × *L. salignum*. However, there are reported hybrids between species belonging to different Subsections (*L. discolor* × *L. lanigerum*) and even between species belonging to different Sections (*L. elimense* × *L. laureolum*). The main species used for successful, interspecific hybridization are listed in Tables 4.3 and 4.4 (Sadie 2002). The first four cultivars of *Leucadendron* were developed in New Zealand during the 1960s. Sadie's Registrar lists eight cultivars developed in the 1970s, 42 during the 1980s, and 51 during the 1990s.

Table 4.3. Number of successful interspecific hybrid combinations as reported in “the International Protea Registrar” (Sadie 2002).

Species/ Species	*discolor*	*elimense*	*eucalypti-folium*	*grando-geri*	*lani-gerum*	*laure-olum*	*salig-num*	*spissi-folium*	*tinctum*	*uligino-sum*	*xantho-conus*	Total
conicum	1										1	2
coniferum			1								1	2
daphnoides									1	1	1	3
discolor				1	1	2	3			1		8
elimense						1						1
Eucalypti-folium						2	2					4
gandogeri								1				1
lanigerum							1	1				2
laureolum							14					14
salignum											1	1

The first intentional breeding of *Leucadendron* was done in New Zealand, in the early 1960s. The original breeding was done by Jean Stevens of Wanganui and was continued by her son-in-law Ian Bell (Bell 1988; Matthews and Carter 1983; Matthews 2002); they crossed *Leucadendron laureolum* with a red form of *L. salignum*, which was probably native to Langkloof, South Africa (FFTRI 1972; G. Brits, pers. commun., 2001). From this original cross emerged several selections, the best and most famous ones being *L*. 'Safari Sunset' and *L*. 'Red Gem'. The registrar (Sadie 2002) lists 14 additional cultivars based on the same cross combination; the most famous of these is *L*. 'Silvan Red', which was bred in Australia in 1992 (Sadie 2002).

It is difficult to select sufficiently superior cultivars just by selection within a species; therefore, crosses must be used to combine favorable qualities from different species. In the wild there are many "natural hybrids" between related species (for more information see *www.nbi.ac.za/protea* (protea information>protea ecology>hybrid relationships within proteas). It is more difficult to obtain viable crosses between taxonomically distant *Leucadendron* species (van den Berg and Brits 1995; Littlejohn 2001; Robyn and Littlejohn 2001). Genetic and breeding research has been accelerated in the last 5 to 10 years, especially by the very active programs at the ARC in South Africa (van den Berg and Brits 1995; Littlejohn 2001; Robyn and Littlejohn 2001) and more recently in Western Australia (Sedgley et al. 2001; Yan et al. 2001; Croxford et al. 2003).

Table 4.4. Classification of the main species used for interspecific hybridization in *Leucadendron* (Sadie 2002).

Section	Subsection	Species
Leucadendron	Sun	*daphnoides, tinctum*
	Crown	*elimense*
Alatosperma	Delta-seeds	*conicum, uliginosum*
	Clay	*lanigerum*
	Sunshine	*coniferum, discolor, eucalyptifolium, gandogeri, laureolum, salignum, spissifolium, xanthoconus*

The current range of *Leucadendron* cultivars includes: (1) clonal selections from within species, such as *L. salignum* cultivars 'Blush' or 'Yaeli' (Ackerman et al. 1997a); (2) interspecific hybrids of speculative parentage, such as the *L. laxum* hybrid cultivar 'Jubilee Crown'; and (3) interspecific hybrids of known parentage such as the *L. salignum* × *L. eucalyptifolium* cultivar 'Chameleon' or the *L. laureolum* × *L. elimense* cultivar 'Rosette' (Littlejohn et al. 1998; Littlejohn and Robyn 2000; Sadie 2002).

Controlled pollination in *Leucadendron* is relatively simple, because of dioecy (Brits 1983). A. Robyn (pers. commun., 2000) recognized three main steps in achieving controlled hybridization among *Leucadendron*s: (1) covering the female inflorescence to prevent uncontrolled pollination– a cone of the selected female parent is covered for two to four days with a greaseproof bag to prevent wind or insect pollination while the stigmas ripen; (2) pollination–ripe pollen from the selected male parent is applied to the ripe stigmas of the female florets, with a fine brush, and the pollinated cones are again covered with the greaseproof bags; and (3) seed maturation–the seeds in the successfully pollinated florets must ripen to full maturity on the plant during the following four to six months, before harvesting.

The following are the main aspects of a breeding program: (1) Pollen collection, storage, and viability assessment–since interspecific hybridization is a necessary approach to the development of superior new cultivars of *Leucadendron* (van den Berg and Brits 1995), and since different species flower at different times of the year, it is important to develop methods for storing pollen. Both investigating teams, in South Africa and in

Western Australia, studied pollen storage and assessment. Sedgley et al. (2001) recommended collecting male flower heads at anthesis: the cut stems, bearing many flower heads, are held at room temperature, and pollen can be separated from the flowering heads by removing the entire heads and sieving the pollen through a fine mesh sieve onto clean paper. The pollen is placed in open tubes within a sealed jar containing freshly dried silica gel at 4°C for 48 hr. The tubes should then be kept at either -20°C for short-term storage or at -80°C for long-term storage (Sedgley et al. 2001). Viability may be assessed by counting percentage pollen germination and pollen tube growth or by use of a fluorescent dye (Sedgley et al. 2001). (2) Hybridization compatibility–the main successful interspecific crosses in the genus *Leucadendron* are those between closely related species. Hybridization compatibility may be evaluated by scoring pollen-pistil interactions (Yan et al. 2001), or by estimating the percentage seed set (van den Berg and Brits 1995; Robyn and Littlejohn 2003). (3) Inheritance of important traits–relatively little is known about the genetics of *Leucadendron* and how important traits are inherited in these plants. Croxford et al. (2003) analyzed the inheritance of some important traits. (4) Survival at different trial sites–survival of hybrids was related to genotype, site, and the interaction between these two factors. Hybrid seedlings sometimes died because of incompatibility and delayed genetic incompatibility. The various sites had differing soil types and thus differed in the severity of infection from soil-borne pathogens, including *Phytophthora cinnamomi*. It has been observed that hybrids between pairs of parents chosen from *L. strobilinum, L. loureolum. L. gandogeri, L. eucalyptifolium, L. xanthoconus, L. uliginosum, L. salicifolium,* and *L. muirii* survived well in unfavorable sites, whereas when one of the above was crossed with *L. procerum* the tolerance of the resulting hybrids to those adverse sites was lost. (5) Juvenility–the length of the juvenile period was related to the parental combinations. Crosses having *L. muirii, L. discolor L. procerum, L. salignum, L. spissifolium, L. strobilinum*, or *L. gandogeri* as at least one parent produced hybrids with long juvenile periods, whereas crosses with species of the trigona subsection usually produced hybrids with shorter juvenile periods. (6) Flowering time–in general, the flowering time of hybrids is closely related to that of the parental species. Van den Berg and Brits (1995) found a wide variation of flowering times in their hybrid leucadendrons, ranging from June to September (Southern hemisphere). (7) Color of male flower heads–most male flower heads are yellow; however, two species, *L. discolor* and *L. procerum* can produce bright red male flower heads. When female plants from these species were crossed with other species, all the male offspring produced red flower heads. On the other hand, when a red *L. discolor* male was crossed with other species, only 70% of the male offspring were red. These results should be viewed as preliminary observations, indicating the beginning of understanding color inheritance in *Leucadendron*. (8) Bract (or more correctly "Involucre leaves") color–most *Leucadendron* species have yellow or green bracts, but some genotypes of *L. salignum* have red bracts or combinations of these colors. Some species have their own unique bract colors. Crosses between red-bract *L. salignum* and yellow-bract species often produced hybrids with red bracts. When the red-bract hybrid 'Red Gem' (an F1 hybrid between red *L. salignum* and yellow *L. laureolum*) was crossed with *L. laureolum* (yellow bracts), 50% of the offspring had yellow bracts and 50% red ones, indicating a simple single- gene inheritance of the red color. Hybridization with the 'Langkloof' forms of *L. salignum* seems to offer special potential, since these plants effectively have two distinct flowering seasons: in winter-spring, when flowering proper occurs, and in midsummer at the termination of elongation growth, when the fully expanded terminal bracts ('flower') turn bright red (usually). This latter stage may be the most lucrative for marketing the plant–as in the case of 'Safari Sunset' (van den Berg and Brits 1995). (9) Plant form–the leucadendrons most suitable for use as cut flower varieties have an upright form and an annual vegetative flush of long, straight stems, which may be single-head or multi-head. It has been observed that, in some species, the flowering stems of female plants tend to be single-head and those of male plants multi-head. In general, hybrids tended to combine form traits from both parents. (10) Regeneration from epicormic buds of the lignotuber–

the ability to regenerate new shoots from the base of the plant is an important quality for a good cut-flower cultivar. It seems that all the hybrids that result from a cross between a species with and one without a lignotuber have functional lignotubers, even though these may not be morphologically prominent (Brits et al. 1986). Second generation crosses of the above with a species with no epicormic trait produced hybrids that lacked this important trait. (11) Chromosome number–Croxford et al. (2003) counted the chromosomes of 25 genotypes from 15 different species and found that in all of them $2n = 26$. These counts agree with the findings of de Vos (1943).

Croxford et al. (2003) found neither aneuploidy nor euploidy in their counts. Littlejohn (1996c, 1997) evaluated *Leucadendron* selections according to the following traits: characteristics of the bush, the leaves, and the flower heads, flowering time, the ability to recover after harvesting of the flowers, and the yield. In many of these traits, she found great differences between closely related cultivars. For example, the average single-stem yields of various *L. salignum* clones ranged from eight per plant for the least productive to as high as 65 per plant for the most productive (at the third harvest).

B. Propagation

Malan (1992, 1995) reviewed the various propagation methods used for proteas. Here we outline some of these methods and add some accounts of practical experience reported by commercial propagators in Israel.

1. Seeds.

Seeds are used for propagating *Leucadendron* for two reasons. Firstly, many of the *Leucadendron* branches sold on the world market are still harvested from seed-propagated species. This is especially true in South Africa, where most of the production is based on broadcasting seeds on ripped ground (M. Middelmann, pers. commun. 2002) and not on vegetatively propagated cultivars. The second reason is that propagating from seeds is part of the process of breeding new cultivars. In general, proteas do not set abundant seeds, especially when they are grown outside their natural habitat, out of reach of their unique pollinators. In *Leucadendron*, cross pollination is obligatory since they are dioecious plants and is accomplished by insects, mainly beetles, or/and by the wind. The 10 most common wind-pollinated Proteas in southern Africa are all *Leucadendron* species (Rebelo 2001). Among southern African Proteaceae, the average percentage of florets that set seeds ranged from 77% in *Leucadendron* and 100% *Aulax*, to 8% in *Protea* and 15% in *Leucospermum* (Rebelo and Rourke 1986).

Leucadendrons have two major types of seeds (strictly speaking, achenes): nut-like (6 being myrmecochorous–ant dispersed, and over 25 species are rodent dispersed) and serotinous (Bond 1985; Brits 1986b; Rebelo 2001). This biological dichotomy is common among the seeds of SA Proteaceae at the generic level with *Aulax* and *Protea* serotinous and the remaining genera being myrmecochorous. Rodent-dispersed seeds are only known in *Leucadendron*. The unique feature of *Leucadendron* to contain more than one seed type prompted Salisbury (in Knight 1809) to split the genus into several genera based on seed morphology–his groupings are now recognized at the subgeneric level. These seeds are rounded, nut or nutlet-like, and are relatively hard-shelled (Williams 1972; Brits 1986b). Myrmecochorous nutlets are covered with a fleshy skin–called the elaiosome–that attracts ants, which carry them away and store them in their nests. Serotinous seeds have a flattened, winged shape and are retained on the plant for long periods, in live (turgid) protective woody cones or seedheads that protect them from fire and predators. They are released and dispersed by a hygroscopic mechanism that is activated by dessication when the water supply to the seedheads stops as a result of fire or the death of the plant (Brits 1987; Rebelo 2001).

The seeds are ripe for harvesting 6-7 months after flowering, when the young flower heads on the tips of the new growth are already developing (Vogts et al. 1976). Serotinous seeds are common in species of the Section *Alatosperma* (Table 4.1).

With regard to dormancy and germinability, it is important to distinguish between two main types of seeds: the hard-coat nuts and the flat seeds (Brits 1986b). The first type is more difficult to germinate and should be handled similarly to other hard-coated proteaceous seeds; it includes *Leucospermum* (Van Staden and Brown 1977; Brits 1986b,c). Dormancy of hard-coated seeds can be overcome by mechanical or acid scarification, by hydrogen peroxide treatment (Brits 1986a,b; McLennan 1993; Brits et al. 1995), or by soaking the seeds in hot water (Harre 1988), although the last method may be an indirect form of scarification, which occurs when desiccated seeds are wetted (Brits et al. 1993).

Rourke (1994) stated that John Herschel studied the effect of heat on germination of *Leucadendron argenteum* as early as 1836. Herschel wrote: "*The seeds of protea argentea will be several years in the ground without germinating–but if the seeds be sown half an inch deep and then the ground burnt they come up at once.*" This reaction may in fact be induced indirectly by the desiccating effect of heat on the buried seeds, followed by watering (Brits et al. 1993): treating any well-desiccated fynbos nut-fruited Proteaceae seeds with free water may result in cracking of the seed coat, which amounts to mechanical scarification, and subsequent dormancy breaking, i.e., germination. However, scarification may also mechanically assist the embryo to emerge, which is probably a much lesser effect than that of oxygenation (van Staden and Brown 1977).

Van Staden and Brown (1973) and Brown and van Staden (1973b) in studies of the effects of oxygen on endogenous cytokinins levels and on germination of *Leucadendron daphnoides*, which has hard-coated seeds, found that scarification treatments and incubation of seeds in oxygen improved germination under alternating temperatures. The effect of high oxygen appears to be mediated by increased levels of endogenous cytokinins, since the latter condition is closely correlated with enhanced germination. Brits (1986b) showed that soaking in 1% H2O2 solution for 24 hr could be a practical way of oxygenating non-scarified, hard-coated proteaceous seeds. In *Leucadendron*, flat or winged seeds (alatosperma) appear not to need additional (artificial) oxygenation. The stimulating effect of elevated oxygen partial pressure within intact hard-coated seeds is consistent with the stimulating effect of scarification, which acts by breaking the impermeability of the intact seed coat to atmospheric oxygen, so that seeds are subsequently naturally oxygenated from the air (Brits et al. 1993). The effect of daily alternating temperature on germination of the hard, nut-like seeds of Cape Proteas has been studied thoroughly by Brits (1986c). It appears that all nut-like proteaceous seeds, including *Leucadendron*, require daily temperature variations between about 8°C-10°C night (16 hr) and 20°C day (8 hr) for optimal germination. There are also indications that some aqueous germination inhibitors may be present in seeds of *L. daphnoides* (Brown and van Staden 1971). There are many publications on dormancy and germination in proteas (Brown 1975; Brown and van Staden 1973a,b,c; van Staden and Brown 1977; Brown and Dix 1985), and recently Criley (1988) summarized all the methods being used for overcoming seed dormancy in hard-coated proteaceous seeds. In summary, all high quality *Leucadendron* seeds primarily need low temperature, preferably 10°C, with daily fluctuations to 20°C for successful germination; and non-scarified (intact) hard-coated seeds also need oxygenation (Brits 1986b; Brits et al. 1993).

After overcoming dormancy, the main cause for failure in propagating leucadendrons by seeds is death caused by fungi, and these deaths can occur both pre- and post-emergence. The development of damping off diseases is always accelerated by the presence of high levels of inocula in the germinating medium, and by excessive watering, insufficient aeration, and excessively high temperature (Harre 1988). Recently, Brown and Botha (2002) reported that seeds of *L. rubrum* and *L. tinctum* increased germination in response to smoke. The germination percentage also depends a great deal on the source of the seed and the species, i.e., on seed quality (Robyn and Littlejohn 2001).

There are several ways to sow the seeds: (1) broadcasting, is used mainly in South Africa. The mature cones are shredded and, without separating seeds from other components, the shredded material is broadcast onto ripped fields; (2) inserting brunches

with the matured cones in the ground. This is done with *L. platyspermum*, whose winged seeds may germinate before they emerge from the cones (Rourke 1998); (3) sowing in open beds; (4) sowing in shallow flats, which can be placed in the open or in a shade house and irrigated when necessary, or irrigated once and then stacked for 17-26 days at controlled temperatures (see recommended temperature regime above). When germination begins, the flats are removed from the stack and placed in an exposed location. Temperature fluctuations between 10°C (night) and 20°C (day) are essential for optimal germination (Brits 1986c); (5) seeds are spread between two layers of canvas and placed under mist in an unheated shade house, in autumn or mild winter. Seeds that are starting to germinate are collected every few days and placed in small pots; and (6) seeds are sown in individual plugs and a few days after germination the plugs with the germinated seeds are moved to a different location with a suitable irrigation regime.

Publications that address the seed ecology of Proteaceae include Bond (1988), Bond et al. (1995), and Bond and Maze (1999). Publications concerning seed germination under natural conditions were written by Brits (1987), Mustart and Cowling (1991), Lamont and Milberg (1997), and Musil et al. (1998).

2. Cuttings.

Most cultivars of *Leucadendron* are no longer considered difficult to root by means of standard techniques (Malan 1995). Jacobs (1981) indicated that the fall (March, April in the Southern hemisphere) is the best time for rooting leucadendrons. Nurserymen in Israel and New Zealand (Harre 1988) root leucadendrons all year round, provided that suitable wood is available and that there are proper facilities for rooting the cuttings. Terminal and sub-terminal cuttings can be used, which should not be "too soft" nor "too hard"; if too soft they will rot in the propagation bed, and if too hard they will root only after several months or not at all. It is best to use wood not more than 6 months old (R. Arlevsky, pers. commun. 2002). The cuttings, measuring 12 cm long by 8 mm diameter, should be taken from good healthy plants, grown under full sunlight, washed well, disinfected, e.g., with active chlorine solution, and kept under refrigeration until being inserted in the propagation bench.

Cuttings should be treated with rooting hormones; Malan (1995) gave a general recommendation of 4000 ppm IBA for proteas. Harre (1988) indicated an optimal level of 2000 ppm for *Leucadendron*, and recommended reducing this concentration to 1000 ppm for 'hairy-leaf' varieties. A 1-cm length at the base of the cuttings should be placed in the hormone solution for 10 seconds. The cuttings should be inserted in well drained and sterilized growth medium. Malan (1995) recommended sand: peat: polystyrene (1:1:1 v/v/v). In Israel it is common to use a mixture of finely ground polystyrene: medium-size peat (7:3 v/v) packed in "Ellepot" propagating plugs (Ellegard, Denmark).

The cuttings should be kept under a mist system in a protected and well-aerated greenhouse, with a light intensity of about 300 lux. Under Israeli conditions, in the summer the plastic cover of the propagation house is whitewashed and a 30% shade net is placed inside the house; in winter the whitewash is washed off by the rain and the 30% net is kept in position. In New Zealand, Harre (1988) recommended allowing full light intensity during the morning and evening, and cutting the 900-lux full light intensity at midday by 50%; higher light intensity could be maintained if it is possible to do so without elevating the temperature. The temperature at the base of the cuttings should be kept at a minimum of 18°C, and the air temperature should not exceed 26°C. The pad and fan cooling system is recommended. However, the high-humidity/high-temperature environment is excellent for the spread of diseases, against which a high level of phytosanitary conditions should be maintained. The house should be well aerated and the plants should be sprayed regularly against foliar diseases. To prevent root rots, the medium should be drained against *Pythium* and similar diseases with materials such as Dynon (propamocarb) or Rizolex (tolclofos-methyl). When all the recommendations are followed, good propagators achieve 85-95% well-rooted plants.

There have been several detailed studies that provide some additional information

on propagation by cuttings of leucadendrons: Rodriguez-Perez (1992) examined the possibility of using leaf-bud cuttings of *L*. 'Safari Sunset', and achieved a maximum rooting of 20%. The use of leafbud cuttings may be advantageous when the quantity of propagating wood is limited, but the low rate of rooting makes this method impracticable. Rodriguez-Perez et al. (1993) showed that wounding the base of the cuttings significantly improved the rooting percentage of *L*. 'Safari Sunset'. Perez-Frances et al. (2001a) studied the anatomy of adventitious root formation on wounded and unwounded cuttings of *L*. 'Safari Sunset' and *L. discolor*, and were able to show that adventitious root formation was initiated mainly in the wounded area, and at the basal cut surface of the cuttings. They also found that root primordia were present in the wounded areas as soon as 2 weeks from the time of inserting the cuttings. Perez-Frances et al. (2001a) cited MacKenzie et al. (1986) as claiming that wounding the bases of cuttings improved their rooting. Epstein et al. (1993) studied the metabolism of IBA in two cultivars of *L. discolor*–one early flowering and the other late flowering. He demonstrated that the early flowering rooted well, whereas the late flowering was difficult to root; 'early' also responded better to a 4000- ppm IBA treatment. Five weeks after inserting the cuttings, the rooting results were as follows: untreated 'early', 17%; hormone-treated 'early', 77%; untreated 'late', 0%; and hormone-treated 'late', 10%. Epstein et al. (1993) showed that these differences in rootability were related to IBA transport and metabolism in the cuttings. There were higher levels of IBA accumulation at the base of the 'early' rooting cultivar than in the 'late', difficult-to-root one.

Ben-Jaacov et al. (1995) studied the rooting of *L. linifolium* cuttings, produced outdoors *in vitro* conditions, found that NAA, CO2 enrichment, and sucrose all affected rooting. NAA had the greatest effect among the factors tested, but photosynthesis and sugar levels were also important. When the cuttings were treated with NAA, without adding either CO2 or sucrose, rooting was only 25%. When the atmosphere in the test tubes was enriched with CO2, rooting was increased to 41%, probably because of enhanced photosynthesis. When sugar was included in the medium, without CO2 enrichment, rooting was at a similar level of 43%. However, it is most interesting to note that when both sucrose and CO2 were used, rooting was increased to 70%. These results may have some important implications, both for rooting of cuttings and for propagation of *Leucadendron* in tissue culture.

3. Grafting.

The aim of plant breeding is to make genetic improvements, especially those that lead to better quality and higher yield. It is, however, a long and expensive process. To make breeding more efficient, it is possible to breed the scion and the rootstock separately. Grafting is a common technique that is practiced in fruit trees, ornamentals, and vegetables (Gardner 1958; Elliot and Jones 1982; Hartmann et al. 1990; Lee and Oda 2003), and its use had already been suggested in the early days of protea cultivation (Rousseau 1966; Anonymous 1971; Vogts et al. 1976). Many of the Australian proteaceous plants are often grafted (Elliot and Jones 1982; Barth and Benell 1986; Crossen 1991). A comprehensive study of grafting of *Leucospermum* was carried out from 1976 to 1980 by Brits (1979; 1990a,b). Moffatt and Turnbull (1994) carried out a wide ranging study on grafting, which covered many *Protea*, *Leucospermum*, and *Leucadendron* species, and presented the following reasons for grafting proteas: to overcome soil-borne diseases, especially phytophthora and nematodes; to enhance soil adaptability; to propagate hard-toroot clones; to achieve rapid increase of genetic stock; and to preserve endangered selections. However, their studies, and those of Brits, were mainly intended to enable the cultivation of proteas in phytophthorainfested areas of Eastern Australia (Turnbull 1991; Moffatt and Turnbull 1994) and South Africa (Brits 1990a, 1990b). At about the same time, Ben-Jaacov et al. (1989a, 1991a, 1991b) and Ackerman et al. (1997b) demonstrated the beneficial effect of using *L*. 'Orot' (a local selection of *L. coniferum*) rootstock on the growth of *L*. 'Safari Sunset' and *L. discolor* in extremely high pH soils in Israel. This demonstration and publications in the local trade

journals stimulated local nurseries to produce commercial quantities of grafted *Leucadendron* plants that were planted in all parts of the country, in all types of soils, and in artificial growth media (Ben-Jaacov et al. 1991b; Ackerman et al. 1997b).

Grafting efficiency was greatly improved with the development of the "cutting-graft" method (Burke 1989; Gibian and Gibian 1989; Ackerman et al. 1997b). This simultaneous rooting-grafting method, designated as "stenting" by Van de Pol et al. (1986), is frequently used for propagating roses. Most of the commercial *Leucadendron* grafting in Israel is done by "cutting-grafts". Wedge-grafting is used and tying is done with Parafilm strips (Ackerman et al. 1997b). The nurseryman R. Arlevsky (pers. commun., 2002), recognized that *L. galpinii* might serve as a good rootstock for *Leucadendron*. Field observations of *L*. 'Safari Sunset' plants grafted on *L. galpinii* and on *L*. 'Orot' showed differing behavior of these rootstocks in different soils. It is well known that different species of *Leucadendron* have differing degrees of adaptability to different soil conditions (Eliovson 1983); also, different cultivars respond differently to differing phosphorus regimes (Silber et al. 2000b). Recent studies of water requirements of grafted and non-grafted *L*. 'Safari Sunset' indicated that there were interactions between the rootstock and the water requirements: grafted *L*. 'Safari Sunset' on *L*. 'Orot' produced higher yields of flowers under lower levels of irrigation than *L*. 'Safari Sunset' on its own roots. On the other hand, the grafted plants were more sensitive to soil-borne diseases under a high-watering regime (Silber et al. 2003). All the information reported above suggests that further studies are needed of the suitability of rootstocks to specific cultivars, specific soils, and specific cultivation technologies.

Grafting compatibility has never been studied methodically: Van der Merwe (1985) tried to understand the intergeneric relationships among the Proteaceae by comparing grafting compatibility between the genera. In general, it seems that grafting compatibility between species in *Leucadendron* is wider than their hybridization compatibility (Ben-Jaacov et al. 1991b; Moffatt and Turnbull 1994; R. Arlevsky, pers. commun., 2002). Table 4.5 (modified from Moffatt and Turnbull 1994) summarizes leucadendrons grafting. The rootstocks used all belonged to the section *Alatosperma*. Of the scions used, six were species belonging to the section *Leucadendron*, and nine to *Alatosperma*. When the first group (*Leucadendron* on *Alatosperma*) was used, 37% of the grafting combinations were 100% successful and 37% gave a success rate below 50%. When the second group (*Alatosperma* on *Alatosperma*) was used, 32% of the grafting combinations were 100% successful and 12% gave a success rate below 50%. The conclusion from these data is that there was no correlation in grafting compatibility within the sections or between the sections. The same conclusion may be drawn, regarding grafting compatibility between or within the sub-sections. Two species predominate as rootstocks in Israel: *L. galpinii* and *L*. 'Orot' (a local selection of *L. coniferum*). Successful (i.e., the plants stayed alive for at least 5 years) grafting of the following species and cultivars on these rootstocks has been achieved: *L. discolor*, *L*. 'Safari Sunset', *L*. 'Yaeli', and *L. argenteum* (R. Arlevsky, pers. commun., 2002).

4. Tissue Culture.

Success rates (*in vitro* multiplication) varied greatly among members of the Proteaceae (Perez-Frances et al. 2001b). Research on in vitro propagation has been done with most of the commercially grown proteas (Ben-Jaacov and Jacobs 1986), but at present, commercially grown cultures are available only of some Grevilleas, and a few cultivars of *Telopea*. Since *Leucadendron* can be easily propagated by cuttings, there has been little effort to propagate them in vitro. Perez-Frances et al. (2001b) reported successful establishment of *L. discolor* in vitro; they used spring-grown nodal and shoot-tip explants, and treated them with polyvinyl-pyrrolidone to prevent oxidation. Shoots grew and proliferated on half-strength MS medium containing 3% sucrose, 0.7% agar, and benzyl adenine at 0.5 mg L^{-1}. The multiplication rate was low, and it declined with sub-culturing. Earlier attempts to propagate *L*. 'Safari Sunset' in vitro failed because of the very low multiplication rate (Perez-Frances et al. 1995). Recently, Ferreira et al.

(2003) reported an efficient method for in vitro propagation of *L*. 'Safari Sunset': a modified MS medium containing ascorbic acid (15 mg L^{-1}) and 2% sucrose, amended with BAP at 2 mg L^{-1} and GA3 at 2 mg L^{-1}, and obtained seven 19-mm-long shoots from each explant. They cut off these shoots, dipped their basal ends in auxin solution (IBA 1 g L^{-1}) for 5 min and for rooting placed them on solid medium or Sorbarods plugs saturated with basal liquid medium, without growth regulators. In both cases, 83% of the shoots showed root formation. The small rooted plantlets exhibited cytological and morphological modifications that might be responsible for their incapacity to survive ex vitro.

C. Site Selection and Environmental Responses

Leucadendrons and other Proteas are commercially cultivated, very successfully in many places, under very different environmental conditions from those found in their natural habitats (Veld and Flora 1984). Ben-Jaacov (1986) used revised versions of the Climatic Diagrams of Walter and Helmut (1976) to illustrate the climates of the main protea production areas around the world. All books about Proteas emphasize the importance of proper site selection for their cultivation, including that of leucadendrons. Most of these recommendations, however, are based on the various authors' experience and the environments and soils found in their own areas, and are therefore not always relevant to other places. Matthews (2002) describes 32 species and cultivars of *Leucadendron*, 28 of which are suitable for use as cut flowers or/and cut foliage. He discussed the hardiness of each, and indicated that most of them are hardy and sustain midwinter frosts of -3°C to -6°C. The plants can probably sustain these temperatures, but flowers of at least some of these species and cultivars (e.g., *L. discolor*) can be damaged even in lighter frosts. Eliovson (1983) indicated that *L. album*, *L. arcuatum*, and *L. rubrum* grow above the snowline or at high altitudes in the Cape mountains, and should tolerate cold conditions.

Leucadendrons are evergreen, but the degree of their activity depends on the location of their cultivation. Vegetative growth of *L*. 'Silvan Red' in South Australia commenced between October and November (spring) and ceased by March (fall). During the summer peak growth season, the average elongation was about 12 cm per month and the average increase in diameter was 0.63 mm (Barth et al. 1996). At high elevation in Ecuador (0 degrees latitude), growth and flowering of *L*. 'Safari Sunset' continues year round (S. Pollack, pers. commun. 2004).

Table 4.5. Grafting compatibility among leucadendrons belonging to various subsections (Source: Moffatt and Turnbull 1994).

	Delta-seeds CB (Alatosperma)		Sunshine CB (Alatosperma)				
Scion/Rootstock	*floridum*	*macowanii*	*eucalyptifolium*	*gandogeri*	Safari Sunset	*salicifolium*	*xanthoconus*
Leucadendron							
galpinii (Sandveld)[z]	-	-	66 (26)	33 (28)	-	100 (27)	-
arcuatum (Arid)	33 (20)[y]	-	100 (26)	-	-	100 (20)	-
nervosum (Jonaskop silver)	-	-	100 (8)	-	-	-	-
album (Silver)	0	-	100 (13)	-	-	90 (8)	57 (7)
orientale (Sun)		16 (10)	50 (27)	0	-	100 (47)	57 (18)
elimense (Crown)	-	-	28 (12)	-	-	100 (27)	16 (5)
Alatosperma							
floridum (Delta-Seed)		--	100 (15)	-	-	100 (28)	-
macowanii (Delta-Seed)	-	-	-	33 (28)	-	-	-
uliginosum (Delta-Seed)	-	83 (27)	66 (30)	-	-	37 (17)	-
stelligerum (Clay)	-	-	0	-	-	-	-
discolor (Sunshine)	-	100 (27)	83 (27)	-	-	66 (33)	77 (29)
gandogeri (Sunshine)	-	-	77 (26)	-	-	100 (27)	71 (19)
laureolum (Sunshine)	-	-	83 (14)	-	-	90 (27)	83 (12)
procerum (Sunshine)	-	-	100 (29)	-	91 (41)	66 (27)	100 (29)
'Safari Sunset' (Sunshine)	-	100 (27)	66 (21)	-	-	100 (33)	66 (15)

[z]Cone bush

[y]Successful grafts (%), in brackets: age of oldest grafts (months).

D. Cultural Practices

1. Specific Requirements of Species and Cultivars.

Methods of cultivation vary among species planted as seedlings and vegetatively propagated plants as well as among the cultivars themselves, and specialized publications supply information on the cultivation and post-harvest treatment of specific cultivars, e.g., *L*. 'Rosette', *L*. 'Chameleon', *L*. 'Flash', and *L*. 'Asteroid' (Littlejohn 1994a, 1994b, 1996a, 1996b). In Israel, most of the publications intended to inform farmers are specific for *L*. 'Safari Sunset', the main protea produced in Israel (Shtaynmetz 1998; Shtaynmetz et al. 2002, 2004a), but there are also publications that deal specifically with other cultivars (Shtaynmetz et al. 2000).

2. Spacing.

Distances between plants and between rows vary according to the cultivar, methods of production, and traditions around the world: Barth et al. (1996), reporting the yield of fully producing, 6-year-old *L*. 'Silvan Red', indicated that the bushes were 1.0-1.5 m wide and 1.5-2.0 m tall; Cecil et al. (1995) indicated that in Australia, the planting density is generally 2600 plants per hectare. In Israel, *L*. 'Safari Sunset' is planted with spacings of 2 m between rows and 0.8 m within rows, i.e., 6250 plants per hectare, and some growers plant even more densely (Shtaynmetz et al. 2004a). It is recommended to leave a wider space between rows every 50 m, to allow the passage of harvesting vehicles (Shtaynmetz et al. 2004a). With smaller cultivars, such as *L*. 'Yaeli', the distance between rows can be reduced to 1.8 m (Shtaynmetz 1998; Shtaynmetz et al. 2000).

3. Nutrition of *Leucadendron.*

The Effect of P Application. Proteaceae originated in Australia and South Africa, where most species grow on leached soils, which are poor in available minerals (Handreck 1997; Richards et al. 1997a). Purnell (1960) described proteoid roots as "clusters of rootlets of limited growth which form lateral root", are widespread in the Proteaceae. Similar root structures have been described in several other families, and Lamont (1982) described them as "root clusters". Dinkelaker and Marschner (1995) divided the root clusters into: (1) proteoid-like root clusters, including (1a) proteoid roots of the Proteaceae, and (1b) other non-root clusters of the genera: *Casaurina, Acacia, Lupinus, Kennedia, Viminaria, Myrica,* and *Ficus*; and (2) non-proteoid-like root clusters, including dauciform, capilarroid, and stalagmiform roots of the Cyperaceae and Restionaceae, and of the genus *Eucalyptus*. The function of proteoid roots has been investigated since the early 1960s, but their specific role in uptake of nutritional elements, especially phosphorus P, was poorly understood. Jeffrey (1967) observed that the proteoid roots of *Banksia ornata* were very efficient in adsorbing P, and related this beneficial property to their high surface area rather than to a metabolic factor. Lamont (1983) and Lamont et al. (1984) too attributed the higher P uptake of proteoid roots to the greater soil volume they exploited, and found that, compared with non-proteoid roots, proteoid roots in *Leucadendron laureolum* had a 15x greater specific surface area ($mm2\ mg^{-1}$) and exploited a 33x greater specific soil volume ($mm3\ mg^{-1}$). Jeffrey (1967) suggested that low P status in a plant induces the formation of proteoid roots and Lamont (1972) extended this idea to include deficiency levels of other nutrients, especially N. Several investigations demonstrated that a proper nutrient regime induced decreased formation of proteoid roots, and at the same time improved shoot growth (Lamont 1972; Groves and Keraitis 1976; Thomas 1981). Idealized relationships between soil nutrient availability and proteoid roots, non-proteoid roots, and shoot production are presented in Fig. 4.1. However, despite the clear evidences that adequate nutrition may be beneficial to shoot growth even in the absence of proteoid roots, Lamont (1986) stated that "*There can be no denying that the presence of abundant proteoid roots is a sign of a healthy plant*".

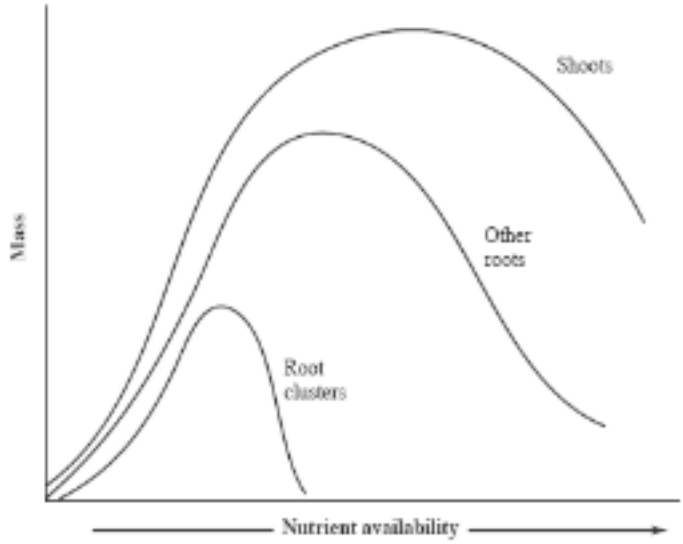

Fig. 4.1. Idealized relationships between nutrients availability and production of root clusters, other roots and shoots (copied from Lamont 2003, adapted from Lamont 1982).

Nutritional problems gave the impression of being the greatest single cause of difficulties in the nursery culture of proteaceous plants (Thomas 1974). During the 1970s and the 1980s, studies conducted in Australia, Hawaii, New Zealand, and South Africa focused on the nutritional demands of pot-grown Proteaceae (Specht and Groves 1966; Thomas 1974; Groves and Keraitis 1976; Nichols et al. 1979; Thomas 1980, 1981; Nichols and Beardsell 1981a,b; Goodwin 1983; Dennis 1985; Dennis and Prasad 1986; Claassens 1986; Heinsohn and Pammenter 1986; Parvin 1986; Prasad and Dennis 1986; Grose 1989; Buining and Cresswell 1993). It was found that P application to pot-grown plants induced growth impairment, leaf chlorosis and necrosis, and abscission of mature leaves (Thomas 1974; Groves and Keraitis 1976; Nichols et al. 1979; Thomas 1980, 1981; Nichols and Beardsell 1981a,b; Goodwin 1983), therefore, P levels that generally applied for agricultural crops were regarded as toxic for the Proteaceae (Grose 1989). The problem introduced by Nichols et al. (1979), of why P levels that are essential for most other plants are toxic to the Proteaceae, remained unsolved.

Elucidation of the problem posed by Nichols et al. (1979), regarding the effect of P nutrition on the development of Proteaceae, gained a breakthrough as a result of the excellent research conducted by Gardner on the legume white lupin (*Lupinus albus* L.). Gardner et al. (1982a,b, 1983) demonstrated that the availability of P and metal ions in the root environment of white lupin was improved as a result of excretion of citrate and protons from the proteoid roots. Furthermore, the activity of proteoid roots was primarily influenced by the P status in the plant, and their formation was depressed at high rhizosphere-P levels. High P levels and low proteoid root activity in turn reduced manganese uptake (Gardner et al. 1982b). Subsequently, numerous investigations using *Lupinus albus* as a plant model established a comprehensive knowledge on the interactions between P status in the plant and the formation and functions of proteoid roots (Dinkelaker et al. 1989; Dinkelaker and Marschner 1992; Gerke et al. 1994; Dinkelaker and Marschner 1995; Johnson et al. 1994, 1996a,b; Keerthisinghe et al. 1998; Watt and Evans 1999; Neumann et al. 2000).

Recent and up-to-date reviews on these topics have been collected by Lambers and Poot (2003). It is generally accepted that the primary role of proteoid roots is associated with modification of the root environment, i.e., by exudation of organic acids

(mainly citric) that enhance P mobilization towards the plant root. It seems that under intensive cultivation conditions, when all nutrient elements are supplied according to plant needs, the specific role of the proteoid roots is limited.

In light of the recently accumulated knowledge, it is suggested that high rates of P application to proteaceous plants could reduce the availability of micronutrients, especially Fe, Mn, and Zn, because of: (1) precipitation of metal-P compounds; (2) enhancement of specific adsorption of metal ions on the charged surfaces of oxides and hydroxides in the soil following increases in negative charges; and (3) a decrease in solubilization of metal ions following the decrease in excretion of organic acids. It is possible, therefore, that the symptoms of growth impairment, leaf chlorosis, necrosis, and abscission of mature leaves that characteristically affect proteaceous plants following P application, and which in the past were attributed to P toxicity, actually derive from deficiency of metal ions. Thus, it may be correct to extend the term "P-induced zinc deficiency" introduced by Cakmak and Marschner (1986, 1987), to Fe, Mn, and/or any other metal micro-nutrient. This suggestion is supported by Handreck's (1991) observations that iron deficiency was the main visible effect of P excess on the shoot of *Banksia ericifolia*, that its severity increased as the P supply increased, and that classic symptoms of P toxicity appeared in plants exposed to high levels of P and low Fe supplementation.

Nutritional Demand of Leucadendron. The nutritional demands of *Leucadendron* 'Safari Sunset', the most important cultivar in the protea industry, have been extensively investigated during the last two decades (Silber et al. 1998, 2000a,b,c, 2003). The objective of the research was to assess the response of *L*. 'Safari Sunset' to nutritional management, especially that of phosphate, and all their findings showed that adding fertilizer to the irrigation water resulted in increased biomass production compared with that of tap-water-irrigated plants. The nutritional treatments affected the development of proteoid roots, and root clusters were present mostly in tap-water-irrigated plants. Some proteoid roots developed on plants irrigated with nutrient solution when P was omitted, but none developed in any of the other treatments. Increasing the P concentration up to 20 mg L^{-1} significantly improved *L*. 'Safari Sunset' growth and there was no indication of toxic symptoms that could be attributed to an excess of P. These results are consistent with the conclusions of Prasad and Dennis (1986) that realistic levels of soil-P concentration (below 40 mg kg^{-1} as assessed by bicarbonate extraction) are not toxic to *L*. 'Safari Sunset'.

A significant quadratic regression was obtained between the number of marketable branches and leaf-P concentration of *L*. 'Safari Sunset' plants exposed to various nutrient application rates (Silber et al. 2000a), and similar relationships were obtained for the fresh and dry weights of shoots (not presented). According to the quadratic equation presented in Fig. 4.2, the maximum number of marketable branches was achieved when leaf-P concentration approached 3.4 g kg^{-1} DW, similar to what has been reported for many plants (Marschner 1995). These results indicate that *L*. 'Safari Sunset' plants are not susceptible to P toxicity at normal P application rates. Fig. 4.2 also includes added data from a further experiment, carried out 5 years later, in which *L*. 'Safari Sunset' plants were grown in several different soils (Silber et al. 2003). The plants in the later experiment were grown under the same nutritional regime but were planted in four soils that differed in their buffering capacity and their native pH, and so induced differing P availability in the root environment. The effect of plant-P status on *L*. 'Safari Sunset' growth is highlighted by the similarity between results attained under two different growth conditions: (1) plants grown in 40-cm deep holes, dug in sandy soil and filled with volcanic material, which were exposed to various nutrient application rates (Silber et al. 2000a); and (2) plants grown under an equivalent nutritional regime in soils that differed in their chemical properties (Silber et al. 2003). Furthermore, these findings indicate that leaf-P concentration may be used to monitor the P nutritional regime.

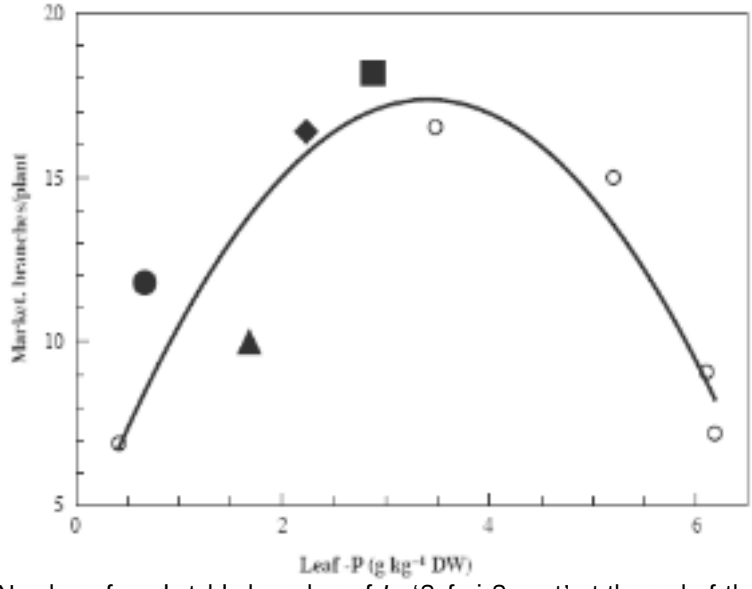

Fig. 4.2. Number of marketable branches of *L*. 'Safari Sunset' at the end of the 2nd year as a function of leaf-P concentration. The solid line was calculated from the data (open circles) of *L*. 'Safari Sunset' grown in Bet Dagan, Israel, during 1994-1995 and exposed to different nutrient rates in the irrigation water (detailed in Silber et al. 2000a). The solid symbols represent data from a different experiment in which *L*. 'Safari Sunset' plants were grown during 1999-2000 under an identical nutritional regime but were planted in four soils that differed in their buffer capacity and the native pH, which induced differing P availability in the root environment (Silber et al. 2003).

The response of two other *Leucadendron* cultivars (clonal selections of *L. coniferum* and *L. muirii*) to different P level was also tested by Silber et al. (2000b). The development of *L. coniferum* (*L*. 'Orot') plants under P deficiency (no P added in the irrigation water) was significantly superior to that of *L*. 'Safari Sunset' and *L. muirii* cultivars, but as P application increased to 20 mg L^{-1}, the growth of *L*. 'Safari Sunset' became quite similar to that of *L. coniferum*. No symptoms of P toxicity were observed even at the highest P level (20 mg L^{-1}) in any of the cultivars tested. Shoot dry weight of *L. coniferum* plants irrigated with tap water was almost three times that of *L*. 'Safari Sunset' under the same conditions. Nevertheless, the response of *L. coniferum* to nutrient addition was lower and less significant than that of *L*. 'Safari Sunset'. Thus, the dry weight (shoots and roots) production of *L*. 'Safari Sunset' fed with an adequate P level (20 mg L^{-1}) was quite similar to that of *L. coniferum* plants under the same conditions. The dry weight production (shoots plus roots) of *L. muirii* plants and their response to the fertilization treatments were the lowest (Silber et al. 2000b).

Higher water-N and -P concentrations led to enhanced leaf nutrient status and associated increased photosynthesis rates and stomatal conductance in four *Leucadendron* species: *L. xanthoconus*, *L. laureolum*, *L. coniferum*, and *L. meridianum* (Midgley et al. 1999). Increased nitrogen application up to 100 mg L^{-1} progressively increased the yield of *L*. 'Safari Sunset' but further nitrogen increases reduced it (Silber et al. 1998; 2000a). The NH4-N:NO3-N ratio in the irrigation water is an important factor in 'Safari Sunset' growth: the yield of NO3-fed plants was low, their leaves were small and their stem elongation was inhibited, with a "little-leaf" appearance, compared with those of NH4-fed plants (Silber et al. 2000a). These results are consistent with the data of Heinsohn and

Pammenter (1986) for *L. salignum* grown in water culture. However, in an aero-hydroponic system at two fixed pHs (5.5 and 7.5) *L*. 'Safari Sunset' growth was not inhibited at a low NH4-N:NO3-N ratio (Silber et al. 2000c). The results obtained at fixed pH may indicate that the main detrimental effect of a low NH4:NO3 ratio is indirect, e.g., via the pH in the root environment (Silber et al. 2000a).

The potassium concentration in the leaves of *L*. 'Safari Sunset' was found to be very low (Cecil et al. 1995; Silber et al. 1998, 2000a,b,c) and below the values considered necessary for other ornamental plants (Jones et al. 1991). Sodium concentrations were high and exceeded on a molar basis those of K (Silber et al. 1998). The low K requirement of the Proteaceae may be attributed to an adaptation to the low-K soils on which they originated (Parks et al. 1996; Walters et al. 1991) and that Na may partially substitute for K as suggested by Walters et al. (1991).

Effect of pH on L. 'Safari Sunset' Growth. The pH in the rhizosphere is an important factor affecting the growth of *L*. 'Safari Sunset' (Ganmore- Neumann et al. 1997; Silber et al. 1998, 2000a,c). Silber et al. (2000a) achieved the maximum number of marketable branches when the rhizosphere pH was approximately 6.0; below this value, release of toxic Mn and Al from soil constituents (Silber et al. 1999) impaired plant development, and above it the availability of micro-nutrients was probably too low to provide adequate nutrition. Despite the use of chelates, Fe, Zn, and Mn concentrations in the leaves of plants grown in high pHs were lower than those in plants grown in acidic pHs, and the incidence of "little leaf" attributed to Zn deficiency increased (Silber et al. 2000a,c). Whether pH affects the plants directly through physiological mechanisms or indirectly through its effects on nutrient availability is not clear.

Effects of Various Nutritional Regimes on the Growth of Leucadendron Species and on Leaf-Nutrient Concentrations. The optimal nutritional regime for a *Leucadendron* plant depends on the nutrient availability in the soil, on the one hand, and on the desired or expected yield (number and quality of marketable stems, and the amount of nutrients removed by the crop), on the other hand. Most *Leucadendron* species are not grown in commercial fields and data are scarce, but information is available for two cultivars of *L. salignum* × *L. laureolum*: 'Safari Sunset' in South Australia (Cecil et al. 1995) and in Israel (Silber et al. 2003; Shtaynmetz et al. 2004a), and 'Silvan Red' in South Australia (Barth et al. 1994, 1996; Cecil et al. 1995). *Leucadendron* is grown in South Australia on various soil types, including clay, sandy loam and highly leached sands, with pH values between 4.8 and 7.0 (Barth et al. 1996; Cecil et al. 1995). *Leucadendron* is grown in Israel on sandy soils in the coastal plain or in volcanic clayey soils in the north of the country (Silber et al. 2003; Shtaynmetz et al. 2004a). The climates of both countries are Mediterranean, with cool, wet winters and dry, warm summers. Planting in Australia is at a stand of 2600 plants ha^{-1}, whereas in Israel a much higher stand is used: 6000-6500 plants ha^{-1}. Yields and nutrient removal rates by the crops in the two countries are summarized in Table 4.6.

Monitoring nutrient concentrations in plant organs, especially in the leaves, may be a useful means of surveying plant growth and optimizing the nutritional regime. However, caution is advised when trying to translate analysis data from leaves (or any other organ) into agricultural recommendations, because of seasonal variations in the chemical composition of leaves (Cecil et al. 1995) and in growth conditions. Two groups of published data are available for nutrient values in leaves of *Leucadendron* plants (Table 4.7): (1) data from commercial fields in Australia (Barth et al. 1994, 1996; Cecil et al. 1995); and (2) data from nutritional experiments in Israel (Silber et al. 1998, 2000a, 2000b, 2000c, 2003), Australia (Parks et al. 1996), and South Africa (Heinsohn and Pammenter 1986). In addition, the recommendations of the Israeli Extension Service (Shtaynmetz et al. 2004a) are included in Table 4.7. Data obtained from commercial fields provide useful information on nutrient contents of field-grown plants, but the growth conditions are rarely well defined or controlled; therefore, the interpretations and the comparison with other data obtained under different conditions may be problematic. On the other hand, data obtained from nutritional experiments representing only small

numbers of plants may provide valuable information on nutrient status under well-controlled conditions in which only a single parameter is varied. Leaf-nutrient concentration data from several sources under wide ranges of nutritional regimes and growth conditions, including plant ages, are presented in Table 4.7.

Table 4.6. Accumulation of dry weight and annual nutrient removal per plant or ha basis for *Leucadendron* 'Safari Sunset' and 'Silvan Red' in South Australia and in Israel.

		Nutrient								
Cultivar	DW	N	P	K	Na	Ca	Mg	Fe	Zn	Mn
	kg plant^{-1}			**g plant^{-1}**				**mg plant^{-1}**		
Silvan Red[z]	5	19	2.8	10	25	19	11	450	50	450
Safari Sunset[z]	5	28	2.8	14	19	26	9	220	100	500
Safari Sunset[y]	2.2	19	5	10	9	6	2	82	10	380
				kg ha^{-1}				**g ha^{-1}**		
Silvan Red[z]	1300	4.9	0.7	2.6	6.5	4.9	2.9	117	13	117
Safari Sunset[z]	1300	7.3	0.7	3.6	4.9	6.8	2.3	57	26	130
Safari Sunset[y]	1360	11.8	3.1	6.2	5.6	3.7	1.2	51	6	99

[z]Cecil et al. (1995).
[y]Silber et al. (2003).

4. Response of *L*. 'Safari Sunset' to Irrigation Regime.

The effect of irrigation regime on the growth of *Leucadendron* species has been examined solely for *L*. 'Safari Sunset' in Israel, where there is a Mediterranean climate, with cool, wet winters and dry, warm summers. The harvest period of *L*. 'Safari Sunset' in Israel extends from the middle of September (autumn) to the end of April (spring), but usually the majority of the yield (80%) is harvested between early October and the end of December. The plants are pruned during the winter, and the new vegetation appears as the weather becomes warmer around the end of March. Water doses should be adjusted according to weather conditions and plant growth; therefore, the recommendations to the Israeli growers regarding water application are based on pan evaporation data and plant conditions (Shtaynmetz et al. 2004a). The pan coefficient (Kp) for the class A pan according to Shtaynmetz et al. (2004a) for adult *L*. 'Safari Sunset' plants is 0.3 (i.e., 2-4 litres per plant per day) in early April (spring), and it increases progressively to 0.9 (12-14 litres per plant per day) at the end of July (summer), and then decreases to 0.6-0.8 (6-10 litres per plant per day) in September-October (fall). Usually, water supply *via* precipitation during the winter (November-February) provides sufficient water for plant demands and irrigation ceases.

Table 4.7. Nutrient concentrations in leaves (Young = youngest leaves on the top of the stem; YFEL = youngest fully expanded leaves; Mature = leaves at the bottom of the stem; All = all the leaves of several *Leucadendron* species).

	Macronutrient removal (g kg^{-1} DW)						Micronutrient removal (µg g^{-1} DW)		
Leaf	N	P	K	Na	Ca	Mg	Fe	Zn	Mn
Safari Sunset									
Young[z]	9-12	1.2-1.5	5-7	5-7	5-6	2-3	70-100	30-90	150-350
Young[y]	10-12	1.0-1.3	3-5	nd	7-10	3-10	60-100	17-25	150-250
YFEL[x]	4-12	0.3-1.3	1-4	2-7	2-5	2-3	26-59	11-61	105-313
Mature[l]	12-15	0.5-3.5	6-10	7-11	7-10	1-2	100-	10-90	300-400

							350		
All[z]	10-11	2.2-3.5	5-6	6-7	7-8	2-3	80-200	15-70	150-500
All[x]	6	0.6	3	4	5	2	42	19	95
All[w]	15	3.5	6	nd	14	7	250	120	280
Silvan Red									
YFEL[x]	3-7	0.3-1.3	1-3	3-7	3-6	2-3	22-46	7-34	60-146
All[x]	3	0.3	1-2	4-5	3-4	1-2	50-199	8-11	65-75
L. coniferum									
('Orot') All[v]	18	9.1	7	nd	10	5	nd	nd	nd
Sundance									
Mature[u]	10-22	0.5-1.1	6-10	nd	nd	nd	nd	nd	nd
L. salignum									
All[t]	20-30	0.6	7-12	nd	nd	nd	nd	nd	nd

[z]Silber et al. (2003)
[y]Shtaynmetz et al. (2004a)
[x]Cecil et al. (1995)
[w]Silber et al. (2000a)
[v]Silber et al. (2000b)
[u]Parks et al. (1996)
[t]Heinsohn and Pammenter (1986)

Silber et al. (2003) examined the effect of irrigation dose and frequency on *L.* 'Safari Sunset' grown in clayey soil of volcanic origin in the Golan Heights. The daily global irradiance and pan evaporation data (calculated per plant) from the experimental site are presented in Fig. 4.3. The maximum water application rate (100%) was defined as the water dose required to fulfill plant demands without any stress, and was monitored with tensiometers located around the plants at various distances and with phytomonitors. It was found that young plants (1-3 years after planting) responded positively to increased irrigation doses, and significant linear regressions were obtained between the biomass production of the shoots, on the one hand, and the water dose applied and the soil water content, on the other hand (Fig. 4.4). The positive effect of increased water amount on biomass production of *L. xanthoconus* was reported by Davis, Flynn, and Midgley (1992). However, in the fourth year, after the space between plants had been covered entirely (6200 plants ha^{-1}), the irradiation became the limiting factor for shoot growth, and the yield was no better under the highest water doses (100%) than under a lower rate (70%). Irrigation dose did not affect the number of marketable stems but significantly affected their quality. The diameter of the "flower heads" of plants exposed to low irrigation doses was small, and it increased progressively as the irrigation dose increased (Fig. 4.5). From the marketing point of view, this effect is extremely important in light of the dominant role of the 'flower head' dimension on the price of *L.* 'Safari Sunset' stems in the cut flower markets.

5. Overcoming Soil Problems in Cultivating *L.* 'Safari Sunset' in Israel.

The two parents of *Leucadendron* 'Safari Sunset' are native to South African soils that have low pH. However, in Israel, despite the suitable climate, growers of proteas have encountered problems because of unfavorable soil characteristics, such as high pH and high free-lime content. Two agro-technical methods are feasible for overcoming these soil limitations (Silber and Ben-Jaacov 2001): (1) improvement of the rhizosphere conditions; and (2) grafting sensitive cultivars onto resistant rootstocks.

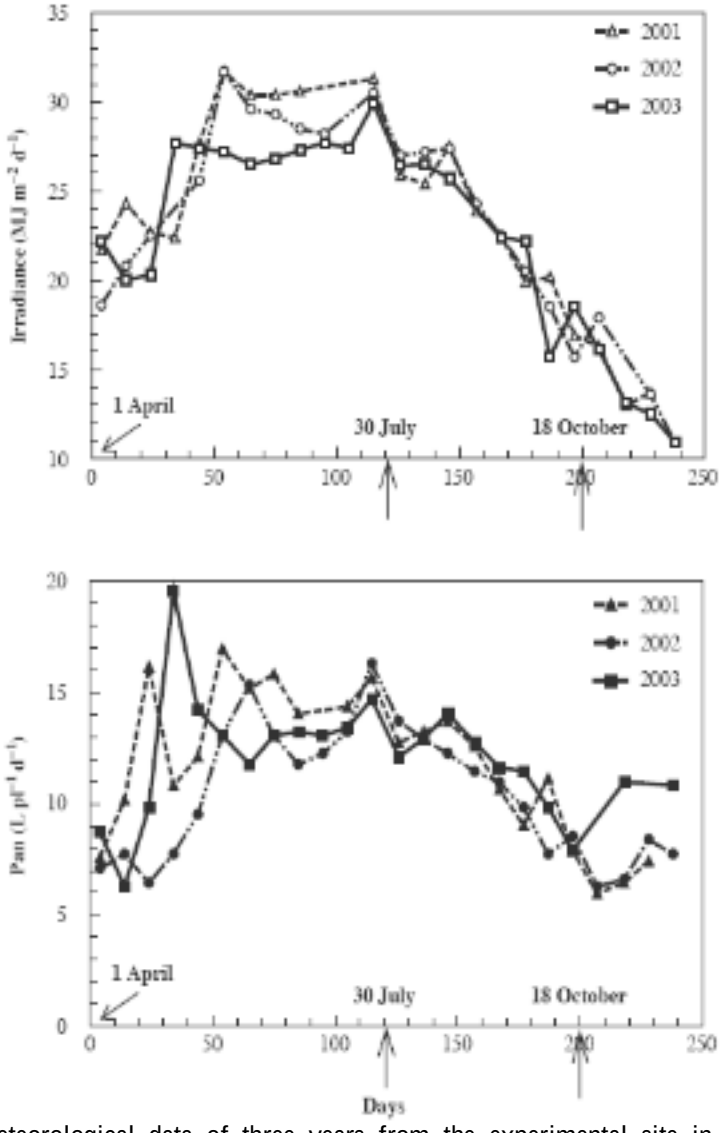

Fig. 4.3. Meteorological data of three years from the experimental site in the Golan Heights: (top) global irradiation, and (bottom) pan evaporation calculated for single plant (6200 plants ha^{-1}).

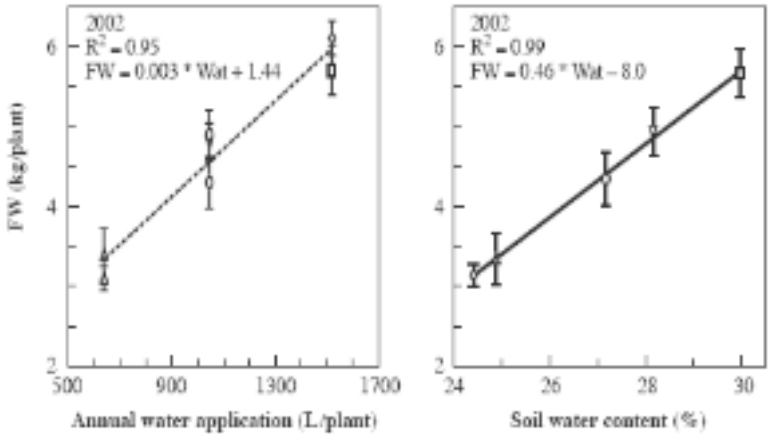

Fig. 4.4. Total fresh weight production (not including roots) of 'Safari Sunset' plants (3 years after planting) as a function of: (left) annual water application (L/plant), and (right) soil water content (mL g^{-1} soil) * 100.

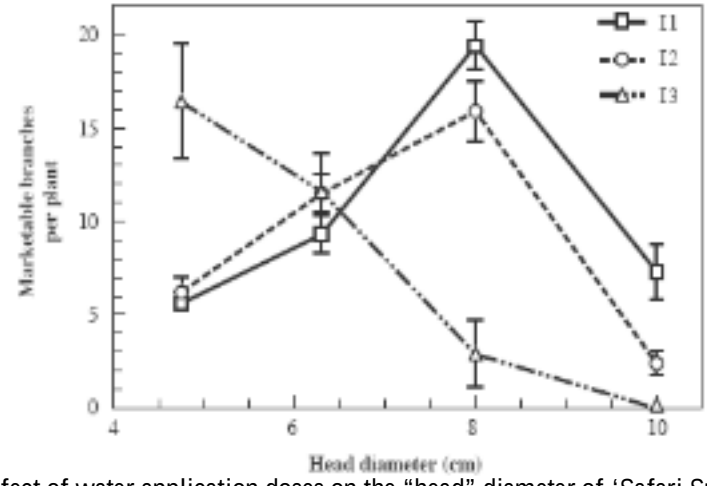

Fig. 4.5. Effect of water application doses on the "head" diameter of 'Safari Sunset' plants (3 years after planting). I1: irrigation doses that fulfill all plant demands during the season, without any stress; I2: 70% of I1; and I3: 40% of I1 (from Silber et al. 2003).

Improvement of the Rhizosphere Conditions. The common horticultural practice in Israel is to improve the rhizosphere conditions in a restricted volume of the root zone by using a small volume (30-50 litres) of artificial substrate and/or by employing nutritional management that reduces the pH. *Leucadendron* 'Safari Sunset' is often planted in tuff (volcanic material), which is placed in holes dug in the native soil, or on the soil as a small pile. Usually, there are no barriers to the free extension of roots from the tuff into the native soil, and the roots develop under two different environments: (1) a predetermined volume (usually 30-50 L) in the vicinity of the plant, where the tuff properties ensure suitable drainage and pH conditions for plant growth; and (2) the surrounding native soil, where air deficiency or high pH may restrict plant development.

Examination of roots at the end of the second year of *L*. 'Safari Sunset' growth

demonstrated that at least 80% of the root system was located in the tuff (Silber et al. 2000a). The root system in the tuff was healthy and white with good branching, whereas that in the soil was restricted and brown with poor branching. The use of artificial substrates and of modern irrigation and fertilization equipment enables the appropriate conditions to be provided for plant growth and facilitates control of the rhizosphere pH. Reducing the soil pH through addition of acids via the irrigating solution is almost ineffective and is not recommended, whereas an indirect approach, such as modifying the rhizosphere pH by choice of the N source is more likely to succeed. The nitrogen source affects the rhizosphere pH via three mechanisms (Marschner 1995; Marschner and Romheld 1996): (1) displacement of H+/OH- adsorbed on the solid phase; (2) nitrification/denitrification reactions; and (3) release/uptake of H+ by roots in response to NH4/NO3 uptake. Mechanisms 1 and 2 are not associated with any plant activity, and affect the whole volume of the fertigated soil, but mechanism 3 is directly related to the uptake of nutritional elements and may be very effective because it affects a limited volume of soil in the immediate vicinity of the roots. Obviously, in addition to the above indirect effect, the nature and concentration of the irrigation-N source may have direct effects on plant growth, on chlorophyll content in leaves, and on chlorosis incidence (Mengel and Kirkby 1987; Marschner 1995). Use of a high NH4:NO3 ratio and appropriate nutritional management are common means for achieving desirable pH and ion concentrations in the tuff medium (Fig. 4.6), and hence for improving *L*. 'Safari Sunset' growth (Silber et al. 1998).

Grafting Sensitive Cultivars onto Resistant Rootstocks. The use of rootstocks in cultivating Proteaceae was suggested as early as 1966 by Rousseau (1966), but has been commercially adopted only during the last two decades (Ben-Jaacov et al. 1992). Some species, native to highpH soils in South Africa, were studied as potential rootstocks in Israel in the late 1980s. As a result of these studies, several clones and species were selected and the best results were achieved by using a clonal selection of *L. coniferum*, which was named 'Orot', and by propagating *L. galpinii*. The possibility of improving plant production by using the two alternatives simultaneously, i.e., growing *L*. 'Safari Sunset' grafted on a resistant rootstock in a tuff medium under optimal nutritional management, was proposed as the most promising method. Several studies have shown that the growth of grafted plants was significantly superior to that of ungrafted plants, and that this advantage was more significant under conditions of nutrient deficiency and non-optimal pH.

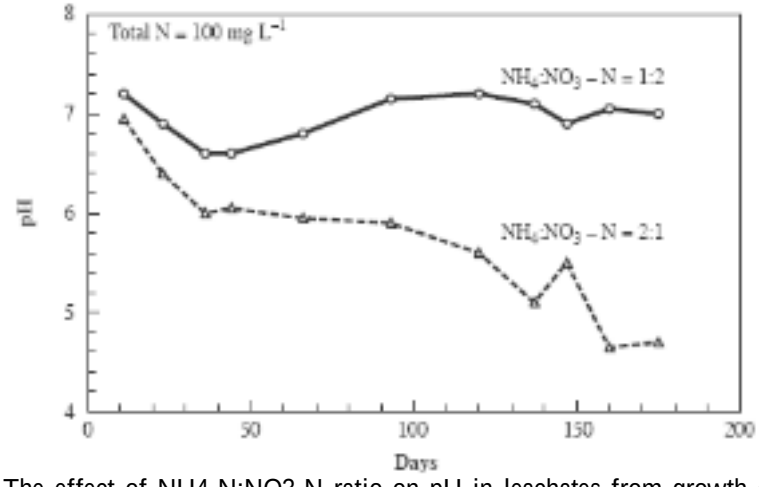

Fig. 4.6. The effect of NH4-N:NO3-N ratio on pH in leachates from growth containers with 'Safari Sunset' plants (adapted from Silber et al. 2000a).

6. Control of Growth and Flowering - Pruning and Pinching.

Efficient pruning to maximize yield is essential, and is a specialized operation in *Leucadendron*. Brits et al. (1986) first attempted to give systematic, general guidelines for commercial pruning of proteas, including *Leucadendron*. The growth cycle of leucadendrons depends on the season.

They sprout in the spring, slow down their growth through the summer, and then initiate flowers. The reason for the cessation of growth, for flower induction, and for the development of the colorful involucre leaves is unknown. Pruning in done mainly by picking the flowers at harvesting time (Mathews 1982; Brits et al. 1986). Leucadendrons will take heavy pruning; therefore, the shrubs can be kept tidy and shaped to any particular need. Ben-Jaacov and Kadman-Zahavi (1988) showed that the imposition of long days at the end of the summer delayed flower development in *Leucadendron discolors*. At high elevation in Ecuador (latitude 0°), growth and flowering of *L*. 'Safari Sunset' continue year round (S. Pollack, pers. commun. 2004).

Like other proteas, leucadendrons may be divided into two groups; sprouters and seeders. The sprouters, which have a lignotuber, will recover easily after heavy pruning, whereas seeders, if pruned heavily, i.e., down to heavy wood that has already lost its leaves, will not sprout (Brits et al. 1986). Most leucadendrons are shrubs, but the silver tree (*L. argenteum*) is a tree and if allowed to grow straight up it will reach a height of 10 m. It can, however, be restricted to a height of 4-6 m if tip pruned in the first, second, or third year, and it will then cover a diameter of 4-5 m (Mathews 1982). However, if this tree is pruned down to old branches that lack foliage, it will not sprout.

The yield and seasonal growth flushing of *Leucadendron* 'Silvan Red', in South Australia, were studied by Barth et al. (1996). They indicated that in South Australia *L*. 'Silvan Red' produces two types of products: in fall stems that terminate in red "flower heads" are harvested, but stems can remain on the bush to be harvested in the winter with tricolor (yellow-red-green) "flower heads." The use of soft pinch in the springtime doubled or even tripled production, by the growth of two to four more branches on each pinched stem. It is important to pinch only stems that are at least 10 mm in diameter at the base (Wolfson et al. 2001). When pinching is done later in the summer, some of the branches develop into good-quality multi-headed stems, but most of the stems originating in the middle of the summer are of poor quality, many of them of the "little leaf" type (see E2, Wallerstein et al. 1989; Wolfson et al. 2001). Lahav et al. (1997) indicated that the last date for soft pinch of *L*. 'Safari Sunset' grown in the coastal region of Israel is at the end of May or beginning of June. The current recommendation for *L*. 'Safari Sunset' in Israel is to prune heavily in the first two years in order to branch the young plants. Later the commercial pruning is done by harvesting and corrective pruning in the early spring (Shtaynmetz et al. 2004a).

E. Plant Protection

1. Diseases.

In the recent book by Crous et al (2004) there is excellent information regarding *Leucadendron* diseases. In addition there are 2 booklets devoted entirely to protea diseases (von Broembsen 1989; Forsberg 1993). In addition, Swart (undated) of the Fynbos Unit in South Africa compiled information on the main Protea diseases in South Africa, including the following diseases that attack *Leucadendron: Phytophthora cinnamomi* (Pc) commonly called "root rot", "crown rot" or "collar rot", *Fusarium oxysporum* commonly called "wilt", *Elisinoe* spp. commonly called, "scab" or "corky bark", *Botryts cinerea* commonly called "flower head blight", *Coleroa senniana* commonly called "coleroa leaf spot", *Batcheloromyces proteae* and *B. leucadendri* commonly called "batcheloromyces leaf spot", *Cerostigmina protearum* var. *protearum*, and *C. protearum* var. *leucadendri* commonly called "stigmina leaf spot", and *Vizella interrupta* commonly called "five o'clock shadow disease". In much of the literature, leucadendron diseases are addressed together with diseases of other genera of proteas.

Leucadendrons are often infected with fungal diseases of the stems and roots as well as several post-harvest diseases, which are generally caused by widespread fungi with little host specificity. On the other hand, diseases of the leaves are generally caused by *Leucadendron*-specific pathogens, many of which originated in South Africa. Protea pathogens in South Africa are fairly well documented (Knox-Davies et al. 1986, 1987, 1988) but little is known about pathogens of South African Proteas cultivated elsewhere in the world. Taylor (2001) has recently surveyed all such pathogens in Australia, South Africa, U.S.A., and Zimbabwe, in light of the recent changes in the phytosanitary regulations, ratified by the World Trade Organization (World Trade Organization 1994). Taylor concluded that many of the pathogens that originated in South Africa are already widespread and have varying degrees of importance in other countries. However, other pathogens have been recorded only in South Africa, and measures must be taken to prevent their spread. Different pathogens assume greater or smaller importance in some countries or regions than in others.

South African proteas and especially leucadendrons originated in areas of winter rainfall, and when planted in wet and humid parts of the world, where summer rainfall prevails, they are very susceptible to many fungal diseases. Phytophthora root and collar disease, caused by the fungus *Phytophthora cinnamomi* (Pc), is probably the most serious soil-borne disease of *Leucadendron* (Von Broembsen and Brits 1985). Pc has an extremely wide host range and has a worldwide distribution (Von Broembsen and Kruger 1985) but, nevertheless, the economic pressure of this fungus on the commercial production of *Leucadendron* as cut flowers varies greatly with the location. For instance, Forsberg (1993) pointed out that Proteas grown in Queensland are more susceptible to this fungus than those grown in southern states of Australia. This variability may occur because the pressure of this disease is greater in summer rainfall areas (Zentmyer et al. 1994; Zentmyer 1980), or because the type of *Phytophthora* (A2 type) that is dominant in Australia is more virulent than the type (A1) that affects proteas in South Africa (Forsberg 1993). A survey of wild flower farms in the south-west of Western Australia identified two other species of *Phytophthora* that attack Leucadendrons: *P. citricola* and *P. cactorum* (Boersma et al. 2000).

Phytophthora cinnamomi has been rarely identified on *Leucadendron*- infected plants in Israel. Several other soil-borne fungi: *Fusarium solani* and *Pythium* Sp. were identified as causing death of *Leucadendron* plants (Ben-Yephet et al. 1999). The difficulties in identifying the exact cause of a sudden death of mature *Leucadendron* plants can be seen in a report from New Zealand: Soteros and Dennis (undated) described two wilt disorders that caused concern to leucadendron growers in some areas of the southern parts of New Zealand's North Island; both are commonly called "wiri wiri" wilt by growers. One disorder was indeed root rot disease, caused by Pc; it was reported to be active mainly when soil conditions were warm and moist. The other disease, which they called "waitara" wilt, initially displayed similar leaf symptoms to the root rot disease caused by Pc, but as Soteros and Dennis (undated) indicated, it is a different disease, which affected only the cultivars 'Safari Sunset', 'Red Gem', and *L. laureolum*; it does not affect the root system and is evident mainly during production of the bracts, from autumn to winter. Although chemical spray reduced the spread of the disease, the cause of the disorder has not been identified. Phytophthora dieback, or as it called in Western Australia "protea sudden death", is still a major problem and is, therefore, currently being investigated in many places (Dieback Working Group 2000; Duncan and Dunne 2000).

The occurrence of Pc on silver trees was reported as early as 1973 (Van-Wyk 1973).The occurrence of Pc on indigenous (Von Broembsen and Kruger 1985) and exotic hosts in South Africa has been reported by Von Broembsen (1984). There are four main ways to avoid or overcome sudden death (Pc) of *Leucadendron* (Brits and von Broembsen 1978; von Broembsen and Brits 1986): (1) plant only on well-drained soil and avoiding over-watering; (2) sanitation: prevent the presence of the fungi in the nursery, in the soil of the plantation, and in the water used for irrigation; (3) use of chemical (Turnbull and Crees 1995; Marks and Smith 1990, 1992), biological (Turnbull et al. 1989), and

biofumigant (Duncan and Dunne 2000) methods to control the disease; and (4) use of resistant plant material and/or grafting the desired cultivar on a resistant rootstock. Von Broembsen and Brits (1985) found that *L. argenteum* and *L. salignum* were very sensitive to Pc, whereas *L. nervosum* and *L. uliginosum* were resistant. Turnbull (1991) and Moffatt and Turnbull (1994) found that *L. eucalyptifolium* and *L. xanthoconus* were resistant, whereas *L. procerum* and *L*. 'Silvan Red' were very sensitive. Cultivars and rootstocks can be evaluated for resistance to Pc by several methods, such as stem inoculation techniques (Denman and Sadie 2001). In irrigation experiments conducted in Israel, Silber et al. (2003) observed that under intensive watering treatments more *L*. 'Safari Sunset' grafted on *L*. 'Orot' died from soil-borne diseases than those grown on their own roots.

Although Pc, when present, is the main killer of *Leucadendron*, many other fungi are often found on dying plants, on rooting cuttings, and on young seedlings in the nursery. Among these are: Armillaria (Forsberg 1993), *Fusarium solani*, and *Pythium* spp. (Ben-Yephet et al. 1999), and *Fusarium oxysporum* (Benic 1986). Anthracnose, caused by *Colletotrichum gloesporioides*, is known in *Protea* and *Leucospermum*, but *Leucadendron* was recorded as being resistant to this disease (Knox- Davies et al. 1986). Moura and Rodrigues (2001) reported that *Rosellinea necatrix* was the "most frequent" soil fungus found on roots of *Leucadendron* in the Madeira Islands and indicated that the cultivars 'Safari Sunset', 'Long Tom', 'Inca Gold', and 'Wilson Wonder' are very susceptible to the disease, whereas 'Pisa', 'Silvan Red', and 'Rising Sun' seem to be more tolerant. They also identified *Fusarium solani* and *Rhizoctonia solani* among the root diseases present in *Leucadendron* in Madeira Island. Dunne et al. (2003) surveyed 28 protea plantations in southwest parts of Western Australia and were able to isolate Pc in 11 of them. In other plantations, Protea death and decline were attributed to other fungal pathogens, including *Fusarium*, *Botryosphaeria*, and *Pestalotiopsis*, as well as to nutritional disorders and physical factors. Leaf and shoot diseases are very common on proteas (Doidge and Bottomley 1931) and are less common on *Leucadendron* (Doidge 1950).

Schizophyllum commune has been reported to cause "trunk rot" in *Leucadendron argenteum* (Doidge 1950), and Van-Wyk (1973) reported that *Botrryosphaeria ribis* caused branch die-back on *L. argenteum*. The scab disease caused by *Elsinoe* is a very serious disease of *Leucospermum* (Forsberg 1993), however it has been reported also on several *Leucadendron* species (Forsberg 1993). In 1985 Van-Wyk et al. (1985a) reported the identification of *Helicosingula* as a new genus of fungi that attacks *Leucadendron tinctum*, and they found *Batcheloromyces leucadendri* on other *Leucadendron* spp. (Van-Wyk et al. 1985b) in South Africa. In humid climates, Botrytis blight (*B. cinerea*) has been reported to damage leucadendrons (Serfontein and Knox-Davies 1990; Forsberg 1993; Moura and Rodrigues 2001). Silver leaf caused by the fungus *Chondrostereum purpureum* has been reported from New Zealand but has not been detected on *Leucadendron* in Australia (Forsberg 1993). *Lasidiplodia*, *Botyodiplodia*, *Phomopsis*, and *Botryosphaeria* may cause rotting, mainly of wounded or weak branches (Forsberg 1993). Moura and Rodrigues (2001) isolated *Pestalotia guepini*, *Phoma glomerata*, and *Stemphylium botryosum* from *Leucadendron* in Madeira. The only fungi that were reported to cause leaf and stem diseases on *L*. 'Safari Sunset' in Israel are *Lasidodiplodia* (known in Israel as diplodia), which mainly attacks wounded and weak stems, and *Alternaria*, which has been reported as a storage disease (Shtaynmetz et al. 2004b). In Australia, several leaf and shoot diseases have been reported to attack leucadendrons (Crous and Palm 1999; Crous et al. 2000). Elsinoe scab causes substantial economic losses to proteas including leucadendrons in Australia; a survey showed the most severely affected species and cultivars to be (in descending order): *Leucadendron* 'Silvan Red', *L*. 'Safari Sunset', *Leucospermum cordifolium*, *Leucadendron laureolum*, *Leucospermum tottum* 'Firewheel', *Leucadendron* 'Inca Gold', *Leucadendron* 'Red Gem', and *Serruria florida* (Pascoe et al. 1995)

2. Physiological Disorders.

The "little-leaves" phenomenon in *L*. 'Safari Sunset' is well known in Israel (Lahav et al. 1997; Wallerstein et al. 1989; Wolfson et al. 2001; Silber et al. 2003), although this physiological disorder has not been described in the international literature. The leaves along the shoot are small, most of the buds situated at the axes of these leaves are somewhat elongated, and in the autumn the ends of the stems terminate in small involucre leaves without real flower heads. The exact cause of this phenomenon is not well known, but it is enhanced by one or several stress conditions: pruning or pinching in the middle of the summer (Lahav et al. 1997; Wolfson et al. 2001), high soil pH (Silber et al. 2000a), insufficient irrigation (Silber et al. 2003), and insufficient light (Wallerstein et al. 1989). This phenomenon could have been a result of Zn deficiency as hypothesize by Silber et al (2000a), however direct evidence is missing.

3. Insects.

Insects are a relatively minor problem in *Leucadendron* cultivation. Most publications related to insects as pests of Proteaceae address the subject in general and are not specific for *Leucadendron* (Coetzee et al. 1997; Zachariades and Midgley 1999; Leandro et al. 2003; Wright 2003). Wright (2003) reviewed pests that attack Proteaceae around the world (Table 4.8). It is clear that the greatest problems with insects are in South Africa, so it is very important to try to prevent the entry of these insect into other Protea-producing countries. Leandro et al. (2003) were more specific, and indicated the insects they found on leucadendrons grown in southwest Portugal: *Helicoverpa armigera* and *Cacoecimorpha pronubana* were found on shoots and flowers; *Sesamia nonagrioides* attacked the stems of young plants; scales and mealybugs damaged stems and leaves; and aphids attacked shoots of leucadendrons. Wright (undated) described the following insects that attack leucadendrons in South Africa: *Epichoristodes acerbella* (*Lepidoptera: Tortricidae*), commonly known as "Carnation worm" and *Phyllocnistis* spp. (*Lepidoptera: Phyllocnistidae*), commonly known as "Channel leaf miner".

Table 4.8. Major pest groups found on South African proteaceous species, grown in different countries.

Pest group	S. Africa	Australia	New Zealand	USA (Calif.)	USA (Hawaii)	Zimbabwe
Bud borers	xx[z]					x
Stem borers	xx	x	x			x
Root borers	x					
Leaf minors	xx	x	x			x
Leaf chewers	x		x	x	x	
Scale insects	xx	x	x		x	x
Mealybugs	xx				x	
Thrips	x			x	x	

[z]xx = severe pest, x = occasional/moderate pest (Revised from Wright 2003).

4. Nematodes.

Root knot nematodes can be a major problem with some proteas under certain climatic and soil conditions (Cho and Apt 1977). These works screened several species of proteas, leucospermums, and leucadendrons for resistance to the nematode *Meloidogyne incognita*, and found that, in general, *Leucadendron* is more resistant than the other two genera. Among leucadendrons, *L. argenteum* and *L. discolor* were resistant to the nematode, whereas *L. laureolum* and *L. uliginosum* were more susceptible.

5. Weeds.

Uncontrolled weeds in *Leucadendron* plantations are harmful. Weed control is important, since Leucadendrons have shallow roots that can be easily damaged by hand-hoeing. Therefore, it is recommended to install woven ground cover in the planting rows. Between the rows, mechanical weed control may be applied, whether the ground is tilled or untilled. If it is untilled, the weeds may be mowed (a common practice in New Zealand), or they can be controlled chemically (DeFrank and Easton-Smith 1990). It is recommended for *L*. 'Safari Sunset' in Israel to spray in the fall, using Goal (oxyfluorfen) at 1000 g/ha + Simazine at 2000 g/ha, against winter weeds, and to use nonselective weed killers in the summer (Shtaynmetz 1998).

F. Post Harvest Studies

1. Handling and Storage.

In general, Leucadendrons have very long shelf lives. Storage, if done properly, can be continued for long periods without any reduction in the shelf life of the flowers. For these reasons, there have been relatively few attempts to improve their storage or vase life. With the increased importance of sea transport, several studies were done, in attempts to improve vase life after long periods of dry storage. Jones and Faragher (1991) and Jones (1991) reported that *L*. 'Silvan Red' maintained a commercially acceptable vase life of 19 days even after 49 days of storage. Pulsing *L*. 'Silvan Red' stems with sucrose solutions at a concentration of 200 g L^{-1} (20%) or higher for 24 h at 1°C prevented leaf desiccation during 42 days of dry storage at 1°C (Jones 1995). Street and Sedgley (1990) showed that water stress was the main factor that reduced the vase life of *L*. 'Silvan Red'.

In the last few years, the Israeli growers have been sending about 75% of their yearly 30 million *L*. 'Safari Sunset' stems to Europe by sea (Gazit 2002). The duration of the transport is 10 days, from the producers' packing house to the Aalsmeer Auction floor. Meir et al. (2000) were able to store *L*. 'Safari Sunset' successfully even for 6.5 weeks. The post harvest procedure for sea transport, as recommended by the Israeli Research and Extension Service (S. Philosoph-Hadas and S. Meir, pers. commun., 2002; Shtaynmetz et al. 2002, 2004b), includes the following steps and precautions: (1) harvest and ship only ripe and lignified, healthy and undamaged stems; (2) place the stems in water containing organic chlorine or simply hydrochlorite; (3) cool the stems at 2-5°C for 24 hr; (4) after sorting the stems, pulse them with 0.5% TOG 4 (containing 8-HQC, citric acid and surfactants) or 0.1% TOG 3 (containing 8-HQC, TBZ, glycolic acid and surfactants); (5) cool the stems in the above solution for 12-24 hr; and (6) dry the foliage and the stems well before placing them in the shipping boxes.

However, even when the above procedure is used, problems have occurred from time to time (un-predicted and irregular), involving dry or rotting stems (sometimes only a few in a bunch). The main causes for these problems were identified as diseases, mainly *Alternaria* but sometimes *Clodosporium*, *Fusarium*, or *Diplodia*; physiological stresses; and physical injuries that stimulate the diseases. After a humid summer, the damage caused by *Alternaria* was the most serious. To overcome the above fungal diseases, it was recommended to apply preventive sprays in the plantations and/or in the packing house, to fumigate the cut stems in the cold rooms, and to remove all physically damaged tissues. Physiological stresses may be caused by freezing and/or by overheating if stems are not cooled down sufficiently before putting them in the shipping boxes or in case of a failure in the cooling chain. The main conclusion was that careful observance of the above recommendation would eliminate the arrival of damaged stems to the markets (Shtaynmetz et al. 2002, 2004a,b).

Prolonged storage may be needed not only for sea shipping, but also to regulate the market and to ensure uniformity of the product over a long time. The involucral leaves of the Israeli *L. salignum* selection 'Yaeli' turn yellow about one month before Easter, and in order to be able to market the yellow flowering stems during Easter, (S. Meir pers.

commun., 2002) stored the yellow flowering stems for one month. At the end of the storage period, the stored stems bore nice yellow involucral leaves, whereas the stems harvested during Easter carried less attractive, green involucral leaves (Shtaynmetz et al. 2000; S. Meir, pers. commun., 2002).

2. Insect Eradication.

Leucadendrons are produced in open field plantations, therefore it is difficult to achieve 100% control of insects, especially if the production is under wild or semi-wild conditions, so that it is sometimes necessary to eradicate insects from the harvested cut branches after harvesting and before marketing. This can be done by chemical treatments or by hot-air disinfestation. In a recent study, it was found possible to achieve control of quarantine pests, including thrips and armored scales, with a hot-air treatment (Hara et al. 2003). The following protocol was recommended for cut branches of *Leucadendron* 'Safari Sunset': increasing the temperature gradually, starting at 39°C for 15 min and at 41°C for 15 min, both at RH of 60-75%, then the eradication treatment at 44°C and RH 60% for 1 hr. This treatment controlled the insects, did not damage the foliage, and did not impair shelf life (Hara et al. 2003).

G. *Leucadendron* as a Pot Plant

Woody flowering plants have potential for use as flowering pot plants (Ben-Jaacov et al. 1989b). There is a continuous introduction and development of new woody flowering pot plants (Tal et al. 1994). There is no problem in being able to produce large flowering plants in large pots or tubs, but transport and marketing considerations make the production of such plants uneconomical, and the production and marketing of small (in pots up to 15 cm in diameter) woody flowering pot plants present a challenge. Of all the proteas, plants from only three genera are currently being marketed as small flowering pot plants; they are *Serruria* (Brits 1995), *Leucospermum* (Criley 1998), and *Grevillea* (Tal and Ben-Jaacov 1988). There have been only a few attempts to study and produce small flowering pot plants of *Leucadendron*. To overcome the difficulties in inducing flowers on young *Leucadendron* plants in small pots, Ben- Jaacov et al. (1986) attempted to use the "Rapid Production System", which involves the rooting of induced, large, and branched cuttings. This system, which had been suggested several years earlier by Jacobs, Brits and others, was finally developed for *Leucospermum* by Ackerman and Brits (1991), and Ackerman et al. (1995), who found it possible to root large, branched, and induced cuttings of *Leucadendron discolor*. The best flowering occurred on cuttings taken between Nov. 21 and Dec. 25 (in the Northern hemisphere). In cuttings taken earlier, the percentage of flowering terminals was low; some did not initiate flowers and many of the flowers that were initiated aborted or reverted to vegetative growth. The stress placed on the plants during the rooting period resulted in the production of low-quality potted plants (Ben-Jaacov et al. 1986).

Tal and Ben-Jaacov (1988) attempted to produce *L. discolor* and *L.* 'Safari Sunset' as flowering pot plants in small (10 cm diameter) pots by using conventional methods of production. They planted 3-month-old rooted cuttings in 10-cm pots, and studied the effects of the growth retardants paclobutrazol and diaminozide in retarding shoot elongation. Two weeks after planting, all the shoots were cut back to two-bud branches. After a further two weeks, when the new growth had reached about 1 cm, the young plants were sprayed or drenched with the growth retardants. Both chemicals and methods of application were effective in dwarfing the plants. However, since the plants never flowered in the small pots, the project was terminated.

V. CROP POTENTIAL AND RESEARCH NEEDS

Leucadendron is probably one of the best decorative foliage plants available in the flower market. Its product characteristics (Coetzee and Littlejohn 2001) are excellent, branches have a very long shelf life, measured in weeks; it can be easily shipped by sea and can travel for at least 10 days; and its stems are straight, making it very easy to pack efficiently. Many of the species and cultivars are sold as foliage and can be marketed almost the year round. The color of the foliage ranges from bronze-red through yellow to various shades of green and silvery gray. Some of the species and cultivars present greater difficulties than others in marketing, especially male cultivars that are marketed at their flowering time, for example, male *L. discolor*, characterized by rapid flower senescence leading to very short shelf life. However, the selection of early, mid-season, and late cultivars could extend the production and marketing period of this beautiful flower.

The production characteristics of *Leucadendron* (Coetzee and Littlejohn 2001) are also almost perfect: the yield is much higher than that of any other protea; most species and cultivars have very vigorous growth; production starts from a young age, and the plantations can have a fairly long life. Most species and cultivars are tolerant of low and high temperatures, and if planted under suitable conditions the plants are relatively resistant to diseases and pests. Nevertheless, growers and researchers can do much to further the prosperity and continued expansion of the leucadendron industry. Aspects worthy of attention include: genetic improvement; diversification of leucadendrons; continuous development and improvement of the agro-technology; and increased public awareness of this wonderful flower. We should conserve all the available genetic variability to ensure the possibility of future improvement (Littlejohn et al. 2000). Genetic improvement may be achieved through advances in breeding technology and through the use of a wider range of interspecific hybrids, and also by mutation breeding. Sub-clonal selections have already led to the development of some excellent cultivars, e.g., the variegated *L*. 'Safari Sunset' named 'Jester' (Sadie 2002), and the Israeli improved *L*. 'Safari Sunset' named 'Petra' (S. Kadosh, pers. commun., 2003). Increasing the selection of leucadendrons available in the market is an important way to increase the total sales volume. There is a need to develop cultivars specifically suited for the production of potted plants, and research is needed for the development of the appropriate technology.

There is very little knowledge of the mechanisms of flower induction and development, and greater knowledge of how to control growth and flowering is needed for many reasons. In modern intensive production of *L*. 'Safari Sunset', an excess of shoot length is produced, which is wasted. This is because the achievement of high-quality, large flower heads in this cultivar demands a high level of irrigation, which also leads to excessively long shoots (Silber et al. 2003). Thus, the question is how to produce the large flower heads without producing excessively long stems. For better and more profitable marketing, it is important to improve selling standards. There is an attempt in Israel to sort and market *L*. 'Safari Sunset' according to the size of the "flower head". Growers and machinery manufacturers are now working on the development of a sorting machine based on photographic image processing (S. Kadosh, pers. commun. 2004). It is hoped that this machine will help to ensure the marketing of more uniformly high-quality flowers in an efficient way. There is a need to increase leucadendron production efficiency, and there is now a joint effort in Israel to develop a pruningharvesting machine (Lev et al. 2004). Production and marketing technology of *L*. 'Safari Sunset' is already advanced, and it is important to extend this production technology to other *Leucadendron* cultivars.

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Plate 4.I

1. 'Safari Sunset' (*Leucodendron salignum* x *L. laureolum*): (a) flower head; (b) typical commercial branches (Photograph courtesy of S. Kadosh).
2. 'Yaeli' (selection of *L. salignum*): (a) flower head; (b) typical commercial branches. (Photograph courtesy of S. Kadosh).
3. 'Jester', a variegated mutant of 'Safari Sunset': (a) flower head; (b) typical commercial branches. (Photograph courtesy of S. Kadosh).
4. Spray branches of *L.* 'Gold Strike' (*L. salignum* x *L. laureolum*) (Photograph courtesy of S. Kadosh).
5. Spray branches of *L. procerum* (Photograph courtesy of S. Kadosh).
6. Spray branches of 'Inca Gold' (*L. salignum* x *L. laureolum*) (Photograph courtesy of S. Kadosh).

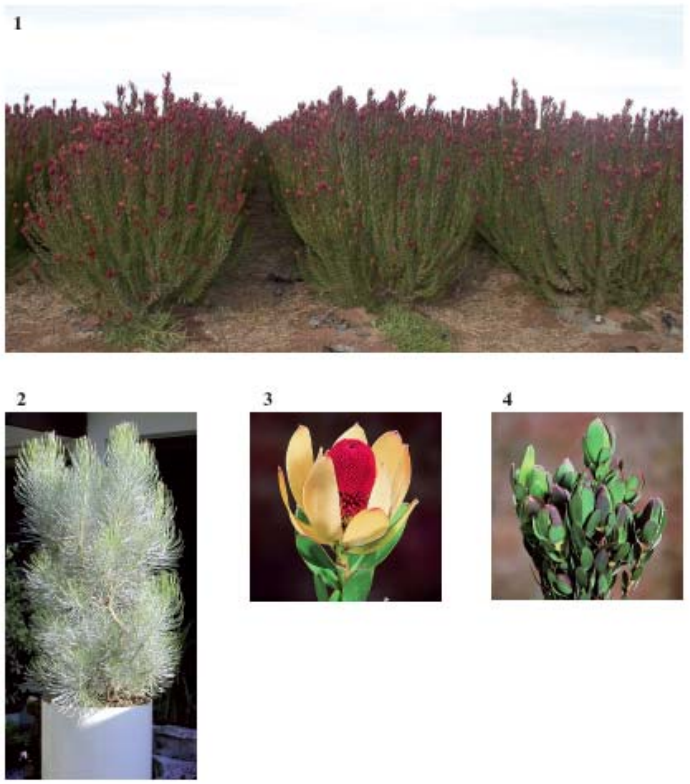

Plate 4.II

1. 'Safari Sunset' field before harvest. (Photograph courtesy of Y. Stienmetz).
2. Pot plant of *L. album* (Photograph courtesy of J. Ben-Jaacov).
3. Male flower head of *L. discolor* 'Red Discolor'.
4. Foliage of *L. discolor* 'Green Discolor'.

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