

Smoke seed germination studies and a guide to seed propagation of plants from the major families of the Cape Floristic Region, South Africa

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Fynbos is the dominant vegetation of the Cape Floristic Region (CFR), one of world's richest regions in terms of its biodiversity and a region in which over two-thirds of the plant species and seven of the plant families are endemics. Many fynbos species from the major families such as the Proteaceae, Ericaceae, Asteraceae and Restionaceae are cultivated as ornamentals or are of importance as floricultural crops. Propagation of fynbos plants from seed is often difficult, as seeds of many species are dormant when shed and require very specific environmental 'messages' or cues before they will germinate. Fire provides the major cues for germination

in the wild and these cues have to be simulated when attempting to germinate wildflower seed in the laboratory and nursery. This study reports on the germination response to smoke of 283 species from 39 families of fynbos. In addition seeds of some of the species were subjected to other dormancy breaking treatments and these results, together with results of similar treatments reported in the literature, are included. Results from these germination trials have been used to provide new general guidelines or protocols for germinating fynbos seeds in the nursery or to update the previously published ones.

Introduction

The Cape Floristic Region (CFR) covers an area of 90 000 km² (35 000 sq miles) in the south western Cape, at the southern tip of Africa. This is less than four percent of the area of South Africa, yet it contains 9 000 plant species. It is one of world's richest regions in terms of its biodiversity and over two-thirds of the plant species and seven of the plant families are endemics (Goldblatt and Manning 2000a). Fynbos is the unique type of vegetation that is dominant in the CFR. It is a community of small shrubs, evergreen and herbaceous plants and bulbs and is exceptionally rich in species. It is perhaps best known as the home of the South African *Proteas* (sugarbushes, pincushions and conebushes), *Ericas* (Cape heaths) and *Helichrysums* (everlastings), and is also typified by the Restionaceae (Cape reeds or Cape grasses) (Brown *et al.* 1995, Goldblatt and Manning 2000a).

Many of the wildflowers from these families are cultivated as ornamentals in parks and gardens around the world or are of importance as floricultural crops. Propagation of fynbos plants from seed is often difficult, as seeds of many species are dormant when shed and require very specific environmental 'messages' or cues before they will germinate (Brown 1993a). The fynbos occurs in areas with a Mediterranean climate (winter rainfall) and the environment is characterised by a number of stress factors such as sum-

mer drought, low soil fertility and periodic fires. The fires have a frequency of 4–40 years and are a natural phenomenon in fynbos (Kruger 1983). Seeds of many wildflowers are adapted to germinate in response to one or more of the cues provided by fire. Heat from flames may fracture the impermeable seed coat of hard-seeded species (e.g. Fabaceae) resulting in the coats becoming permeable to water. Dry heat may also break dormancy by providing a heat-pulse that stimulates the embryo directly and results in germination (e.g. Restionaceae). Dry heat has also been reported to break seed dormancy of some South African *Leucospermums* (pincushions, family Proteaceae) by complete desiccation of their oxygen-impermeable seed coats. When rain falls the dry coats, which are permeable to water, split suddenly and the embryo then obtains sufficient oxygen for germination. Fires also provide chemical messages or cues, such as the gases of ethylene and ammonia, which stimulate germination in some species of *Erica*. In addition to the more obvious cues provided by heat, it was discovered by De Lange and Boucher (1990) that smoke from fynbos fires provides a major chemical cue that is responsible for stimulating the germination of seed of many fynbos species. The chemical cue has recently been identified by Flematti *et al.* (2004) and Van Staden *et al.* (2004). To date,

283 species from 39 families have been tested and 161 of these have given a positive response. Amongst those responding are the horticulturally important species of the Cape Reeds (*Restionaceae*), Everlastings (*Asteraceae*) and Brunias (*Bruniaceae*), (Brown 1993b, Van Staden *et al.* 1995). Fire may also have an indirect effect on germination by causing changes in the soil temperature regimes in the immediate post-fire environment (Brown 1993a). Fire thus provides the major cues for germination in the wild and these cues have to be simulated when attempting to germinate wildflower seed in the laboratory and nursery.

In a study of the effect of smoke in breaking dormancy one cannot ignore the fact that a smoke requirement for germination may be one of a number of factors (internal and external) imposing dormancy. For example, in situations where dormancy is partly coat-imposed, smoke stimulation may only occur once the coat is treated in some way to allow full uptake of water and oxygen and unhindered expansion of the embryo, (whichever process has been hindered by the intact seed coat). In the laboratory and plant nursery the known plant growth regulators (gibberellins, cytokinins and ethylene) are frequently applied to seeds to relieve embryo dormancy. Each may break embryo dormancy on its own or in combination with one or more other regulators. There is also the possibility that they may interact and have a synergistic effect with smoke (Thomas and Van Staden 1995).

The major emphasis of this study has been on studying the germination response of fynbos species to smoke. The framework for the presentation of results has been the degree of response to smoke, ranging from the very marked response of 1 000% or more increase in germination to a nil response. For selected species the effect of heat, scarification and growth regulators and their interaction with smoke has also been studied. This smoke and other germination data is summarised for each family studied and protocols have been drawn up as a guide to follow to obtain optimum germination for species in each family.

Materials and Methods

Collation of smoke germination data

Germination data presented in this study consist of new and unpublished data recently generated in laboratory and nursery trials, together with smoke germination data from previously published studies. Seeds used in the current study were collected from natural populations in the wild in various localities in the south western and southern Cape Province from a minimum of 100 (on average, 200–300) individual plants per species representative of the population. The new smoke germination data was generated using the methods outlined previously in Brown (1993a) and Brown *et al.* (1993). Data on seed mass was obtained by determining the mean air-dry seed mass of 10 samples of 100 seeds.

Data from the following published germination studies were included in the tables: De Lange and Boucher (1990), Brown (1993a, 1993b), Brown *et al.* (1993, 1994, 1995), Baxter *et al.* (1994), Pienaar (1995), Pierce *et al.* (1995), Keeley and Bond (1997) and Brown and Botha (1998, 2002).

Germination data from plant growth regulator trials

For selected species, germination data was recorded from experiments in which seeds were soaked in solutions of individual growth regulators for 24h. Seeds were then removed from the solutions and incubated under the same conditions as the smoke treated seeds. (Brown 1993a, Brown *et al.* 1993). Data from previously published trials by Brits (1986a, 1996), Brown and Drewes (1991), Small *et al.* (1982) and Van de Venter and Esterhuizen (1988) using growth regulators and other chemicals to break dormancy of fynbos seeds are included in tables of results.

Germination data from heat and scarification trials

For selected species, germination data was recorded from experiments in which seeds were either scarified lightly between two sheets of sandpaper or heated in an oven at 100°C for 10min, or placed in hot water at 100°C and then the water was allowed to cool. Seeds were then incubated under the same conditions as the smoke treated seeds. (Brown 1993a, Brown *et al.* 1993). Data from previously published heat trials on species of *Restionaceae* (Musil and De Witt 1981) and species of *Erica* (Van de Venter and Esterhuizen 1988) are included in the tables of results.

Format for presentation of germination results

Where available, actual germination results for dormancy breaking treatments and for controls are given in tables. In addition, figures for germination have been converted to a percentage improvement in response over the results for the water control treatments. For smoke treatments, these percentage responses were divided further into the following groups: percentage response greater than 1 000% and percentage response less than 1 000%. Where responses, but no actual germination percentages, are given in published texts, the abbreviation NGPG is used in tables.

Results and Discussion

Seed propagation protocols for some of the families of horticultural importance

Based on the germination results obtained in the smoke, plant growth regulator, heat and scarification trials, response groups of species, responding in a particular way, were identified in each family. Protocols for germinating seed were worked out for each response group. These protocols are for use as a general guide to the procedures to be followed for germinating seed of most species within that family. Families considered in some detail were the *Proteaceae*, *Restionaceae*, *Ericaceae*, *Asteraceae*, *Mesembryanthemaceae*, *Iridaceae*, *Rutaceae*, *Scrophulariaceae*, *Campanulaceae*, *Geraniaceae*, *Fabaceae* and *Bruniaceae*. Other families considered in less detail were *Brassicaceae*, *Haemodoraceae*, *Penaeaceae*, *Poaceae*, *Rhamnaceae*, *Sterculiaceae* and *Thymelaeaceae*.

When considering the germination requirements for a particular species, within a family, if it is listed under one of the response groups, then the detailed directions for that group

should be followed for best germination results. An example would be that if the species has been shown to germinate readily without any pre-treatment then time can be saved by incubating the seed immediately under suitable temperature conditions without any pre-treatment.

If the species is not listed, it should first be determined whether the seeds have any particular distinguishing features. For example: in Proteaceae, are seeds canopy-stored (serotinous) or are seeds shed and then stored in the soil? Or in Restionaceae, are seeds large and nut-like or are they small capsules and possibly winged? Once the response category has been ascertained, the general directions for germinating seed of the relevant group should be followed.

Alternatively, the species may be listed in a group where the species did not respond to smoke and gave generally low germination. These seeds potentially require special dormancy-breaking treatments (such as scarification, heat or soaking in promalin, $GA_4 + GA_7$ and/or ethrel) to improve germination. In this situation some experimentation with one or more of these treatments may be necessary to find a suitable dormancy breaking treatment or combination of treatments to maximise germination.

If the seed is listed in the group suggesting that seed could be non-viable, then a few seeds should be cut open to find out whether or not the seed embryos are fully-formed, and/or whether they are discoloured or show evidence of bacterial or fungal infection. (If available, a modified tetrazolium staining viability test (Brits and Van Niekerk 1976) could be done to determine the proportion of viable seeds.)

Cape Proteaceae: a summary of past seed research and germination protocols

The seed biology of the family Proteaceae, with approximately 330 species, has been extensively researched over the years and the findings reviewed by Van Staden and Brown (1977), Brits *et al.* (1995) and Brits (1996). Species of the Cape Proteaceae have two distinct achene types. The one type is rounded (often ellipsoid), relatively hard and nut-like and stored in the soil. Germination is characterised by the splitting of the seed coat, due to cotyledon expansion, which is then followed by protrusion of the radicle. In the second type, the achene is winged, plumed or hairy (often flattened) and relatively soft. The latter type is produced mostly by serotinous species, i.e. species in which seeds are stored in the living plant canopy. In serotinous species, germination is first indicated by penetration of the seed coat by the radicle. Serotinous genera comprises *Protea*, *Aulax* and most of the *Leucadendron* spp. and make up approximately 37% of the Cape Proteaceae; with the remainder (excluding *Brabeium*) being nut-like. Nut-like and serotinous achenes show different germination patterns or syndromes (Brits 1996).

1. Proteaceae with nut-like achenes

These achenes do not germinate, or germinate poorly, in mature fynbos vegetation but seedlings recruit *en masse* during the first winter after fire. The breaking of dormancy in species with nut-like achenes is strongly dependent on moderately low seasonal air temperature. This is not a stratifica-

tion requirement, but the low temperature requirement is a mechanism to promote germination during the favourable cool, moist western Cape winter period. Diurnal high temperature is also required for maximal germination. A range of fluctuating temperatures is equally effective in stimulating germination, e.g. 4–10°C (night) and 20–28°C (day). Seed-coat-imposed dormancy by means of oxygen exclusion is a characteristic of most Proteaceae with nut-like fruits (10/14 species of three genera tested), but not of serotinous species (13/15 species of three genera tested). Germination of achenes of *Leucospermum* species can be improved by a single 24h treatment with relatively low concentrations (0.01–0.1%) of hydrogen peroxide. A relatively slight increase in the level of oxygen available to embryos is usually sufficient to initiate germination under suitable environmental conditions (Brits 1996).

2. Serotinous Proteaceae

Serotiny is an adaptive response to cyclical fire in fynbos. In nature, seeds are shed following a fire and germinate *en masse* only after fire. Seeds have a low temperature requirement for germination (1–11°C) which allows the avoidance of drought by synchronising germination to the first (wet) winter season following dispersal. In contrast to nut-fruited species, the seed coat in serotinous species apparently plays a lesser role in preventing oxygen diffusion to the embryo (Brits 1996).

Cape Proteaceae: recent seed germination results and revised germination protocols

An analysis of the germination results for the Proteaceae showed that species could be divided into the following response groups:

Group 1. Species that gave a statistically significant germination response to smoke treatment

Of the 44 species for which data were available, 10 (23%) gave a significant positive response to smoke. Of these species one gave a response greater than 1 000% (Table 1a) and nine species gave a response to smoke of less than 1 000% (Table 1b).

In both Tables 1a and 1b the effect of other dormancy breaking treatments show evidence of an interaction between smoke and other dormancy breaking agents such as promalin, ethrel, heat and scarification. This again suggesting a range of dormancy imposing factors (embryo and coat imposed) operating in different species.

In *Leucadendron tinctorum*, germination results for a smoke treatment combined with plant hormones showed that there was an interaction between smoke and promalin that gave a germination percentage greater than the individual treatments. Promalin and $GA_4 + GA_7$ alone each gave significantly higher germination than water controls. Thomas and Van Staden (1995) showed that dormancy in celery seeds was broken by a combination of plant derived smoke and BA and gibberellins $GA_4 + GA_7$. They suggested that smoke extracts act in a similar way to cytokinins, by enhancing gibberellin activity in the celery seed system. In addition, in *L.*

Table 1a: Species of Proteaceae that gave a statistically significant germination response to smoke treatment greater than 1 000%. S = Serotinous, NS = Non-serotinous

PROTEACEAE	S / NS	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	% Response to smoke	Effect of other dormancy-breaking treatments
<i>Leucadendron arcuatum</i>	NS	6	3	49	1 633	Germination improved by treatment with smoke + promalin 52% (response 1 733%); ethrel 29% (response 967%).

Table 1b: Species of Proteaceae which gave a statistically significant germination response to smoke treatment less than 1 000%

PROTEACEAE	S / NS	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	% Response to smoke	Effect of other dormancy-breaking treatments % Germination (% response)
<i>L. conicum</i>	S	79	59	80	136	
<i>L. coniferum</i>	S	95	79	98	124	
<i>L. daphnoides</i>	NS	5	10	14	140	Germination improved by scarification alone 23% (460%) and scarification + smoke 53% (1 060%) Germination improved significantly (**P = 0.01) by H ₂ O ₂ (Brits 1986b) Germination improved significantly (**P = 0.01) by promalin (Brown and Drewes 1991)
<i>L. rubrum</i>	S	40	20	61	305	
<i>L. salignum</i>	S	110	47	75	160	
<i>L. tinctum</i>	NS	4	13	38	292	
<i>L. tinctum</i>	NS	4	19	73	384	Germination improved significantly (**P = 0.01) by both promalin and GA ₄ + GA ₇ (Brown and Drewes 1991).
<i>L. tinctum</i>		4	21	83	390	Germination further improved by: heat + smoke 89% (423%)
<i>L. tinctum</i>	NS	4	12	54	450	Promalin and smoke 76% (140%); and ethrel 92% (767%).
<i>L. tinctum</i>	NS	4	12	45	375	Germination further improved by: heat + smoke 37% (308%); scarification + smoke 70% (583%). Germination improved significantly (**P = 0.01) by H ₂ O ₂ (Brits 1986b).
<i>Leucospermum prostratum</i>	NS	41	4	21	525	
<i>Protea compacta</i>	S	11	65	96	148	Germination improved by heat 74% (113%) and scarification 74% (113%).
<i>P. compacta</i>	S	11	68	88	129	Germination improved significantly (**P = 0.01) by both promalin and GA ₄ + GA ₇ (Brown and Drewes 1991)
<i>P. cordata</i>	S	38	68	74	109	
<i>Serruria villosa</i>	S	79	1	8	800	

tinctum, ethrel on its own also gave an higher percentage germination than smoke alone. In *L. spissifolium* subsp. *spissifolium* both ethrel alone and ethrel and smoke gave a higher germination percentage than smoke alone.

According to Brown and Van Staden (1997) although there appear to be an indication of an interaction of smoke extracts with seed hormones no clear-cut effects have emerged. Jäger *et al.* (1996) found that in 'Grand Rapids' lettuce seeds aqueous smoke in combination with ethylene showed a synergistic effect on germination at sub-optimal smoke concentrations.

Smoke and heat treatment significantly improved germination in *L. tinctum* over smoke treatment alone. Thomas *et*

al. (2003) showed that in some Australian species there was an independent and additive effect of smoke and heat.

Smoke and scarification also improved germination in *L. tinctum* above the effect of smoke alone. In *L. daphnoides* both scarification alone and smoke and scarification gave higher germination than smoke alone. In both these species of *Leucadendron* dormancy appears to be partially due to coat effects.

Group 2. Species that germinated without special treatment provided temperature was favourable

The second group of 10 species, given in Table 2, germinat-

ed without special treatment provided temperature was favourable. The temperatures in a shade house or open sun during autumn in the western Cape were optimal as were laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day). Reference to previous work on the effect of other dormancy breaking treatments does, however, suggest that some samples of the species may show degrees of embryo or coat-imposed dormancy and germination can be improved by applying one or more of the treatments referred to in the table.

Group 3. Species that did not respond to smoke and generally gave a low germination percentage

The third group of 11 species, given in Table 3, did not respond to smoke and generally gave low germination. *Leucospermum* species responded to 1% H₂O₂, scarification and oxygen (Brits 1986b, 1996) and should probably be treated to improve oxygen uptake before being tested for a smoke response. Other species in the table possibly require special embryo dormancy-breaking treatments such as soaking in promalin, GA₄ + GA₇ and/or ethrel to improve germination.

Table 2: Species of Proteaceae that germinated without special treatment provided temperature was favourable

PROTEACEAE	S / NS	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Aulax pallasia</i>	S	63	45	45	
<i>Leucadendron gandogerii</i>	S	50	87	93	
<i>L. muirii</i>	S	203	79	82	
<i>L. salicifolium</i>	S	50	72	68	
<i>L. sessile</i>	NS	5	76	71	Germination improved by scarification 86% (113%) Germination improved significantly (**P = 0.01) by H ₂ O ₂ (Brits 1986b)
<i>L. spissifolium</i> subsp. <i>spissifolium</i>	S	96	88	85	Germination improved by ethrel 92% (105%) and ethrel + smoke 93% (106%)
<i>L. xanthoconus</i>	S	84	35	36	
<i>L. xanthoconus</i>	S	84	81	86	
<i>Leucospermum cordifolium</i>	NS		76	54	Germination improved significantly (**P = 0.01) by H ₂ O ₂ (Brits 1986b). Germination improved significantly (***P = 0.001) by scarification + oxygen + promalin (Brits 1996). Germination improved significantly (**P = 0.01) by both promalin and GA ₄ + GA ₇ (Brown and Drewes 1991)
<i>Protea cynaroides</i>	S	30	44	41	
<i>P. eximia</i>	S	27	82	83	
<i>P. magnifica</i>	S	4	77	66	Germination improved by heat 91% (118%); promalin 87% (112%); and GA ₄ + GA ₇ 86% (111%) Germination improved significantly (**P = 0.01) by GA ₄ + GA ₇ (Brown and Drewes 1991)
<i>P. obtusifolia</i>	S	48	71	65	

Table 3: Species of Proteaceae that did not respond to smoke and generally gave a low germination percentage

PROTEACEAE	S / NS	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Leucospermum conocarpodendron</i>	NS		11	9	
<i>L. glabrum</i>	NS		21	22	Germination improved significantly (**P = 0.01) by H ₂ O ₂ (Brits 1986b). Germination improved significantly (***P = 0.001) by scarification + oxygen + promalin (Brits 1996).
<i>L. praecox</i>	NS		5	2	
<i>Mimetes argenteus</i>	NS		6	6	
<i>M. cucullatus</i>	NS		4	5	
<i>Protea acuminata</i>	S		14	17	
<i>P. longifolia</i>	S		18	22	
<i>P. punctata</i>	S		18	12	
<i>P. repens</i>	S		36	26	
<i>Serruria florida</i>	NS		17	20	

Group 4. Species that generally gave a low or nil germination percentage and where seeds were probably non-viable

The fourth group of species, given in Table 4, generally gave low or nil germination and seed samples tested were probably non-viable. Brits (1986b) found H_2O_2 to improve germination of the nut fruits of *Leucadendron pubescens* and it would be interesting to test this treatment together with a smoke treatment.

Revised general germination protocol for seeds of Proteaceae

When working out a general protocol for germination it is necessary to consider into which group the seed of each species falls and whether the seeds are serotinous or non-serotinous.

Protocol for non-serotinous Proteaceae

In species of *Leucospermum* and some species of *Leucadendron* (Section *Leucadendron*) seed dormancy is imposed primarily by the intact seed coat (Brits 1986b). The coat is readily permeable to water but poorly permeable to oxygen. To improve oxygenation, soak achenes in 1% H_2O_2 before making commercial sowings in seedbeds. In the laboratory, achenes could be hand-scarified, using sandpaper in order to improve oxygen penetration or they could be incubated in oxygen. (Following scarification seeds could be smoke-treated.) The outer gelatinous coat in species of *Leucospermum* appears to cut down oxygen supply to the seed embryo and should be removed following seed soaking.

1. For species responding to smoke seeds may be soaked in aqueous smoke extract or one of the commercial smoke seed primers (several of which have growth regulators added) for 24h before sowing; or alternatively, seeds may be smoked once sown in trays. Some growers combine H_2O_2 treatment with commercial smoke seed primer by eluting each smoke primer paper with 50ml 1% H_2O_2 and soaking seeds in this solution for 24h (Brits 2004, pers. comm.).
2. Seed germination is strongly dependent on seasonal low temperature. Therefore, sow seeds in seedbeds during autumn or early winter. In the laboratory incubate seeds at an optimum low temperature of between 8°C and 10°C.

3. High temperature is also required for germination and should be alternated with low temperature on a daily basis. Commercial seedbeds should thus be constructed in full sun. In the laboratory the optimum high temperature of 18°C to 23°C should be maintained for 8h per day followed by a period of low night temperature (16h).
4. Seeds should be given a light dusting with a fungicide dressing to prevent pre- and post-emergence seedling infection

Protocol for serotinous Proteaceae

Serotiny is an adaptive response to cyclical fire in fynbos. In nature, seeds are shed following a fire and germinate *en masse* only after fire. Seeds have a low temperature requirement for germination (1–11°C) which allows the avoidance of drought by synchronising germination with the first (wet) winter season following dispersal. In contrast to nut-fruited species, the seed coat in serotinous species apparently plays a lesser role in preventing oxygen diffusion to the embryo.

1. Use freshly harvested seed, as seeds lose viability with age.
2. Species showing a response to smoke seeds may be pre-soaked in aqueous smoke extract or a commercial smoke seed primer for 24h before sowing; or alternatively, seeds may be smoked once sown in trays.
3. Germinate seeds at temperatures below 20°C, preferably between 1°C and 11°C.
4. Sow seeds in a well-aerated, well-drained, sandy soil and avoid waterlogging.
5. Seeds should be given a light dusting with a fungicide dressing to prevent pre- and post-emergence seedling infection (Brown *et al.* 1996).

Cape Restionaceae: a summary of past seed research and germination protocols

The Restionaceae is a family of evergreen, rush-like plants which is almost restricted to the Southern Hemisphere. There are about 320 species in Africa (300 in the Western Cape), and 100 in Australia. The African Restionaceae are relatively diverse in their seed dispersal mechanisms, which could be implicated in the survival of seeds during or after fires. The modes are (i) wind dispersal of unilocular, indehiscent ovaries with a persistent perianth, which acts as a

Table 4: Species of Proteaceae that generally gave low or nil germination and where seeds were probably non-viable

PROTEACEAE	S / NS	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Leucadendron dubium</i>	NS	17	0	0	Germination improved significantly (**P = 0.01) by H_2O_2 (Brits 1986b)
<i>L. glaberrimum</i>	NS	9	0	0	
<i>L. pubescens</i>	NS	7	0	0	
<i>Paranomus reflexus</i>	NS	16	0	0	
<i>Serruria adscendens</i>	NS		0	0	
<i>S. glomerata</i>	NS	118	0	0	
<i>Spatalla curvifolia</i>	NS	248	0	0	

wing for the fruit (e.g. *Thamnochortus*, *Staberhoa* and *Calopsis*); (ii) myrmecochory of fruits containing elaisomes. The ovary is unilocular and indehiscent, and the ovary wall is heavily lignified (e.g. the 'nut-fruited' restiads: *Anthocortus*, *Mastersiella*, *Hypodiscus*, *Willdenowia*, *Ceratocaryum* and *Cannomois*). These seeds are also serotinous and are retained on the plant until the next season's seed crop is mature; and (iii) the so-called 'basic' condition, showing dehiscent ovaries, with 1–3 locules. Here the seed is released from the ovary after maturation, but it is not known how it is dispersed after release (*Restio*, *Ischyrolepis*, *Askidiosperma*, *Chondropetalum*, *Dovea*, *Nevillea* and *Rhodocoma*) (Linder 1991, 2001, Brown *et al.* 1994).

Restios are wind pollinated and many flower during spring or late summer, producing seed after a period of 6–11 months. The seed varies from very fine seed like *Chondropetalum tectorum*, with about 10 000 seeds per gram to the large nut-like seeds of *Cannomois virgata* which are 8mm in diameter and have a mass of 248mg seed⁻¹. Seed collection is fraught with difficulties, as there is very little information available for individual species on the season of flowering, on the period required for seed maturation and on the timing of seed drop. Seeds of many species look ripe from the outside but on dissection are found to be green and immature (Brown *et al.* 1998b).

Factors of importance in germination

The poor germination achieved with seed of many species has been attributed to the limited seed set of some species and the difficulty in determining when seeds are mature and ready for harvest (1) Heat treatment of seeds at 120°C for 3min gave a significant improvement in the germination of seeds of some species (Musil and De Witt 1991). (2) In common with many other fynbos species, most restios require alternating high and low diurnal autumn temperatures as a cue for germination. (3) Germination is stimulated by plant-derived smoke and aqueous smoke extracts (Brown and Van Staden 1997). Brown *et al.* (1994) conducted a major

study, in which seed of 32 species was screened to obtain an indication of how important the smoke cue is for germination in this family. The results of this study represented the first occasion that comparative germination data for South African species of this family had ever been obtained. Twenty-five of the 32 species tested showed a statistically significant improvement in germination following smoke treatment. Germination percentages ranging between 0.1–2.0% were obtained from untreated seeds of 18 of the species responding to smoke. These germination figures showed that seed from these species exhibited a high degree of dormancy. The results suggested that under natural conditions smoke from fynbos fires provided an important cue for triggering seed germination in many species in this family. The four species that did not germinate were all myrmecochorous, nut-fruited species, which possibly require a different or additional heat cue for germination.

Cape Restionaceae: recent seed germination results and revised germination protocols

An analysis of the germination results for the Restionaceae showed that species could be divided into the following response groups:

Group 1. Species that gave a significant germination response to smoke treatment

Of the 67 species for which data were available, 42 (63%) gave a significant positive response to smoke. Of these species 15 gave a response of 1 000% or greater (suggesting that smoke is the overriding cue for germination) and 30 gave a response less than 1 000% (suggesting that smoke is possibly one of a number of germination cues of importance). The species in the two response categories are listed in Tables 5a–5b. In *Chondropetalum mucronatum*, germination results for smoke treatments combined with plant hormones showed that there is an interaction between smoke and ethrel and smoke and benzyl adenine (BA), both of

Table 5a: Species of Restionaceae that gave a significant germination response to smoke treatment of 1 000% or greater

RESTIONACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Chondropetalum hookerianum</i>	833	1	61	6 100	Germination improved by smoke + promalin 24% (2 400%)
<i>C. tectorum</i>	8 620	0.1	2.1	2 100	
<i>Dovea macrocarpa</i>	90	2	77	3 850	
<i>Elegia persistens</i>	909	1	15	1 500	
<i>Ischyrolepis sieberi</i>	383	1	69	6 900	
<i>I. subverticillata</i>	538	5	64	1 280	
<i>Restio tetragonus</i>		2	97	4 850	
<i>Rhodocoma capensis</i>	5 263	0.2	50.6	25 300	
<i>Staberoha aemula</i>	602	1	62	6 200	
<i>S. banksii</i>	240	4	42	1 050	
<i>S. cernua</i>	911	1	43	4 300	
<i>Thamnochortus bachmannii</i>	9 090	0.1	7.9	7 900	
<i>T. cinereus</i>	1 010	1.1	20.3	1 845	
<i>T. pellucidus</i>	350	0.3	7.9	2 633	
<i>T. punctatus</i>		0.5	2.2	4 400	

Table 5b: Species of Restionaceae that gave a significant germination response to smoke treatment of less than 1 000%

RESTIONACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Askidiosperma andreaeaeum</i>		6	42	700	
<i>A. paniculatum</i>	373	53	67	126	
<i>Cannomois virgata</i>	4	2	18	900	Germination improved by storage and incubation at alternating temperatures of 18°C/28°C
<i>C. virgata</i>	4	12	42	350	
<i>Chondropetalum ebracteatum</i>	794	66	85	128	
<i>C. hookerianum</i>	859	2	10	500	
<i>C. mucronatum</i>	248	14	86	614	
<i>C. mucronatum</i>	248	35	90	257	Germination also improved by GA ₃ 78% (223%); GA ₃ + smoke 89% (254%); GA ₄ + GA ₇ 73% (208%); GA ₄ + GA ₇ + smoke 90% (257%); promalin 65% (185%); promalin + smoke 87% (249%); ethrel 86% (246%) ethrel + smoke 92% (263%) benzyl adenine 50% (143%) benzyl adenine + smoke 96% (274%)
<i>Elegia capensis</i>	2 010	0.3	1.0	333	
<i>Elegia cuspidata</i>	706	2.4	5.2	216	
<i>E. equisetacea</i>	1 250	3	14	466	
<i>E. fenestrata</i>		11.3	21.1	366	
<i>E. filacea</i>	2 200	16	32	200	
<i>E. grandis</i>	64	24	43	170	
<i>E. spathacea</i>	1 912	13	54	415	
<i>Hypodiscus</i> sp.	568	0	7	700	nut-fruited
<i>Ischyrolepis ocreata</i>	460	10	47	470	
<i>Restio brachiatus</i>	2 000	53	76	143	
<i>Restio bifarius</i>	364	30	45	150	
<i>R. dispar</i>	290	12	61	508	
<i>R. dispar</i>	290	26	37	142	
<i>R. dispar</i>	290	80	88	110	Germination also improved by: GA ₃ 90% (113%); GA ₃ + smoke 92% (115%); GA ₄ + GA ₇ 94% (118%); GA ₄ + GA ₇ + smoke 98% (123%).
<i>R. festuciformis</i>	4 147	9.0	13.2	146	
<i>R. similis</i>	10 000	13	44	338	
<i>R. triticeus</i>	1 136	37	94	254	
<i>Rhodocoma arida</i>	1 149	19	54	284	
<i>R. fruticosa</i>	961	68	97	142	
<i>R. gigantea</i>	725	23	79	343	
<i>Staberhoa distachyos</i>		6	32	533	Germination significantly improved (**P = 0.01) with 120°C heat treatment (Musil and De Witt 1991)
<i>Staberhoa vaginata</i>	568	1	8	800	
<i>Thamnochortus insignis</i>	795	10	28	280	
<i>Thamnochortus platypteris</i>	408	1	4	400	
<i>T. spicigerus</i>	385	0.4	3.7	925	
<i>T. sporadicus</i>		1	4	400	
<i>Willdenowia incurvata</i>	8	2	6	300	Germination improved to 40% (2 000%) by storage at alternating temperatures of 18°C/28°C for 8 weeks followed by smoke treatment and incubation at alternating temperatures of 10°C/20°C

which gave germination greater than smoke alone. In *Restio dispar*, GA₄ + GA₇ alone and smoke and GA₄ + GA₇ both gave higher germination than smoke alone. Thomas and Van Staden (1995) showed that dormancy in celery seeds was broken by a combination of plant derived smoke and BA

and gibberellins GA₄ + GA₇. They suggested that smoke extracts act in a similar way to cytokinins, by enhancing gibberellin activity in the celery seed system. According to Brown and Van Staden (1997), although there appears to be an indication of an interaction of smoke extracts with seed

hormones, no clear-cut effects have emerged. Jäger *et al.* (1996) found that in 'Grand Rapids' lettuce seeds aqueous smoke in combination with ethylene showed a synergistic effect on germination at sub-optimal smoke concentrations.

Smoke treatment significantly improved germination in *Staberhoa distachyos*, as did a heat treatment of 120°C (Musil and De Witt 1991). Thomas *et al.* (2003) showed that in some Australian species there was an independent and additive effect of smoke and heat. It would be interesting to test for this effect in seeds of *Staberhoa distachyos*.

Group 2. Species that germinated without special treatment provided temperature was favourable

The second group of nine species is shown in Table 6. These germinated without special treatment provided temperature was favourable. The temperatures in a shade house or open sun during autumn in the Western Cape are optimal as are laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day).

Group 3. Species that generally gave a low or nil germination percentage

The eight species shown in Table 7 generally gave a low or nil germination percentage. Seeds of some of these species were probably non-viable. Most of the nut-fruited species, however, are thought to require another (as yet undiscovered?) germination cue.

Revised general germination protocol for seeds of Restionaceae

1. Use fresh, mature seed.

2. Seeds may be pre-soaked in aqueous smoke extract or one of the commercial smoke seed primers for 24h before sowing; or seeds may be smoked once sown in trays. Fill trays with a sand/loam/bark mixture that is well drained.
3. Incubate seeds under alternating night/day temperatures of 8°C (16h) to 23°C (8h) for optimum germination.
4. Nut-fruited species remain difficult (often seemingly impossible) to germinate in the nursery or laboratory. One suggested dormancy-breaking treatment is to heat fruits to 120°C for 3min (Musil and De Witt 1991) prior to pre-soaking in aqueous smoke extract or pre-soaking in a commercial smoke seed primer for 24h. In some nut-fruited species a pre-germination storage treatment at 18–28°C for several weeks gives improved germination and others will germinate if incubated moist at 18–28°C. In general, germination cues for nut-fruited restios require further study (Brown *et al.* 1996). Results of some recent experiments also suggest that more attention needs to be paid to the role of light in restio seed germination (Van Staden *et al.* 2000).

In the nursery seeds may be sown in trays using a sowing medium consisting of loam, composted milled pine bark and industrial sand in a proportion of 1:2:2. Seeds should be covered with a thin layer of milled bark (Brown *et al.* 1998b).

Cape Ericaceae: A summary of past seed research and germination protocols

Seed germination studies in this family were reviewed by Brown *et al.* (1993). Ninety-five percent of the c. 860 species are confined to the southern tip of Africa (Goldblatt and Manning 2000a) and many are of importance in horticulture and floristry. The fruit is mostly a loculicidal capsule, but sometimes an indehiscent capsule, drupe, achene or berry.

Table 6: Species of Restionaceae that germinated without special smoke treatment provided temperature was favourable

RESTIONACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Askidiosperma chartaceum</i>	632	52	58
<i>A. esterhuyseniae</i>	1 219	23	23
<i>Calopsis paniculata</i>	3 333	24	24
<i>Chondropetalum tectorum</i>	10 550	36	34
<i>Restio pachystachyus</i>	340	76	78
<i>R. praeacutus</i>		40	58
<i>Thamnochortus rigidus</i>	714	10	10

Table 7: Species of Restionaceae that generally gave a low or nil germination percentage

RESTIONACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Seed Type / Comments
<i>Cannomois parviflora</i>	27	0	0	nut-fruited
<i>C. taylorii</i>		0	0	nut-fruited
<i>Ceratocaryum argenteum</i>	9	0	0	nut-fruited
<i>Elegia caespitosa</i>	529	0	2	probably low viability
<i>E. capensis</i>	2 010	0.3	1.0	probably low viability
<i>Hypodiscus neesii</i>	21	0	0	nut-fruited
<i>H. striatus</i>	22	0	0	nut-fruited
<i>Mastersiella digitata</i>	181	1	2	nut-fruited

Seeds are mostly ellipsoid or variously angled; testa is thick or almost non-existent; embryo embedded in copious endosperm (Oliver 2000). In the wild, fire is very important in the ecology of the Ericaceae and the vast majority of species regenerate from seed only after a veld fire. Seeds are very small and, in all but one species, are shed when ripe. Serotiny is rare in this family and is found only in *Erica sessiliflora*.

Factors of importance in germination

1. Dry heat and the gases ethylene and ammonia stimulate germination of some species (Van der Venter and Esterhuizen 1988).
2. Germination is stimulated by soaking seeds in GA₃ (Small *et al.* 1982) and GA₄ + GA₇ (Brown *et al.* 1998a).
3. Alternating day/night temperatures, as occur in autumn/winter in burnt fynbos, are important as a cue for germination.
4. Germination is stimulated by plant-derived smoke and aqueous smoke extracts (Brown and Van Staden 1997). In the first major germination study in this family, Brown *et al.* (1993), screened seed of 40 species to obtain an indication of how important the smoke cue was for germination. The improved germination following smoke treatment shown by 26 of the 40 species tested, suggested that under natural conditions smoke from fynbos fires provided an important cue for triggering seed germination in this family. Amongst the species responding to smoke treatment were a number of species of particular horticultural importance. The smoke treatment ensures a much greater efficiency when propagating from seed and this is of importance in plant-breeding programmes. Its use has resulted in many more plants of these species becoming available to the horticulture industry.

Cape Ericaceae: Recent research results and revised germination protocols

An analysis of the germination results for the Ericaceae showed that species could be divided into the following response groups:

Group 1. Species giving a significant germination response to smoke treatment

Of the 53 species for which data were available, 33 (62%) gave a significant positive response to smoke. Of these species eight gave a response of 1 000% or greater (suggesting that smoke is the overriding cue for germination) and 25 gave a response less than 1 000% (suggesting that smoke is possibly one of a number of germination cues of importance). The species in the two response categories are listed in Tables 8a and 8b.

Group 2. Species which germinated without special smoke treatment provided temperature was favourable

The second group of 10 species is shown in Table 9. These species germinate without special smoke treatment provid-

ed temperature is favourable. The temperatures in a shade house or open sun during autumn in the western Cape are optimal as are laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day).

Group 3. Species which generally gave a low or nil germination percentage

Two species shown in Table 10 generally gave a low or nil germination percentage and were probably non-viable or may require another germination promoting treatment such as GA₃ (Small *et al.* 1982) or GA₄ + GA₇ (Brown *et al.* 1998a).

Revised general germination protocol for seeds of Ericaceae

1. Use fresh mature opaque seed.
2. Soak seeds in aqueous smoke extract or one of the commercial smoke seed primers for 24h before sowing; or 'smoke' seeds sown in seed trays. The trays should have a sand/loam/bark mixture and be well drained.
3. Alternatively, seeds may be pre-soaked in GA₃ or GA₄ + GA₇ solution prior to sowing.
4. Fine gauze bags or coffee strainers are very useful for handling the extremely small seeds.
5. Incubate seeds under autumn/winter conditions such as alternating night/day temperatures, e.g. 10°C (16h-night); 15–25°C (8h-day) (Brown *et al.* 1996).

Cape Asteraceae: A summary of past research and germination protocols

The Asteraceae, usually the largest family in floras of arid to semi-arid regions, is also the family with the most species (1 036, including 655 endemics) in the Cape flora (Goldblatt and Manning 2000a). Many of the 1 036 species within this family are of horticultural importance. Amongst these are the so-called 'everlastings'. These species produce colourful inflorescences or flower heads which are harvested and dried and are of importance to the dried wild flower industry.

Factors of importance for germination

Achenes (one-seeded fruits), hereafter called seeds, are produced from the fertile flowers at the centre of the flower heads, the sterile flowers on the periphery provide the colourful papery bracts. The seed biology of some of the most attractive of the everlastings with horticultural potential was studied in a nursery trial by Brown (1993b) and Brown and Botha (1998). These everlastings were (i) *Syncarpha vestita* (Cape Everlasting, Sewējaartjie); (ii) *S. speciosissima* (Cape Everlasting); (iii) *Syncarpha eximia* (Strawberry Everlasting); (iv) *Edmondia sesamoides* (Strawflowers); (v) *Helichrysum patulum*; (vi) *H. foetidum* (Yellow Everlasting); and (vii) *Phaenocoma prolifera* (Red Everlasting).

In nature these wildflowers act as fire ephemerals. Seeds are dormant and germinate in response to the smoke of a veld fire, and a large numbers of seedlings then appear. The plants then gradually die out, until a flush of germination occurs after the next fire.

Table 8a: Species of Ericaceae which gave a significant germination response to smoke treatment of 1 000% or greater

ERICACEAE	No. of seeds g ⁻¹	% Germination or Seedlings g ⁻¹ Water control	% Germination or Seedlings g ⁻¹ Smoke	Response 1 000% or greater
<i>Erica clavispala</i>		4g ⁻¹	324g ⁻¹	8 100
<i>E. glauca</i> var. <i>glauca</i>	9 000	0.16g ⁻¹	11.8g ⁻¹	7 571
<i>E. glomiflora</i>	15 700	0.15%	2.6%	1 675
<i>E. grata</i>		404g ⁻¹	4 250g ⁻¹	1 052
<i>E. nudiflora</i>		2g ⁻¹	20g ⁻¹	1 000
<i>E. phyllifolia</i>		26g ⁻¹	296g ⁻¹	1 138
<i>E. plukenettii</i>	14 285	18g ⁻¹	316g ⁻¹	1 755
<i>E. sphaeroidea</i>		0.9%	11.3%	1 259
<i>E. tumida</i>	11 111	2g ⁻¹	20g ⁻¹	1 000

Table 8b: Species of Ericaceae that gave a significant germination response to smoke treatment of less than 1 000%

ERICACEAE	No. of seeds g ⁻¹	% Germination or Seedlings g ⁻¹ Water control	% Germination or Seedlings g ⁻¹ Smoke	Response 1 000% or greater	Effect of other dormancy breaking treatments
<i>Erica baccans</i>	13 280	9%	37%	411	Germination improved significantly with heat treatment; ammonia and ethylene (Van de Venter and Esterhuizen 1988)
<i>E. canaliculata</i>		528g ⁻¹	3 540g ⁻¹	670	
<i>E. capensis</i>		56g ⁻¹	104g ⁻¹	186	
<i>E. curvirostris</i>	3 050	470g ⁻¹	990g ⁻¹	210	
<i>E. deflexa</i>		168g ⁻¹	266g ⁻¹	158	
<i>E. discolor</i>	7 297	2.2%	3.6%	164	
<i>E. ericoides</i>		1 552g ⁻¹	2 524g ⁻¹	166	
<i>E. formosa</i>	50 857	3.8%	8.6%	227	
<i>E. hebecalyx</i>	10 560	1 370g ⁻¹	2 410g ⁻¹	175	
<i>E. lateralis</i>	40 210	1.7%	10.8%	620	
<i>E. longifolia</i>	10 260	350g ⁻¹	2 580g ⁻¹	737	
<i>E. oatesii</i>		408g ⁻¹	1 604g ⁻¹	393	
<i>E. perlata</i>		10 800	33 940	314	
<i>E. pinea</i>	6 000	3.1%	6.5%	210	
<i>E. sessiliflora</i>	5 181	39%	72%	184	
<i>E. simulans</i>		26%	54%	207	
<i>E. sitiens</i>	16 120	0.9%	6.5%	743	
<i>E. spectabilis</i>	16 666	1 120g ⁻¹	2 060g ⁻¹	184	
<i>E. taxifolia</i>	17 110	110g ⁻¹	180g ⁻¹	164	
<i>E. thomae</i>		298g ⁻¹	1 326g ⁻¹	445	
<i>E. versicolor</i>	10 610	1%	3%	300	
<i>E. vestita</i>	12 500	300g ⁻¹	800g ⁻¹	267	

Table 9: Species of Ericaceae that germinated without special smoke treatment provided temperature was favourable

ERICACEAE	No. of seeds g ⁻¹	% Germination or Seedlings g ⁻¹ Water control	% Germination or Seedlings g ⁻¹ Smoke
<i>Erica brachialis</i>	10 000	11%	12%
<i>E. capitata</i>		1 968g ⁻¹	3 100g ⁻¹
<i>E. cerinthoides</i>	1 000	11%	10%
<i>E. cruenta</i>	33 333	4 260g ⁻¹	4 380g ⁻¹
<i>E. halicacaba</i>		3 100g ⁻¹	2 750g ⁻¹
<i>E. oblongiflora</i>		131 g ⁻¹	196g ⁻¹
<i>E. patersonii</i>	7 970	88 g ⁻¹	86g ⁻¹
<i>E. peziza</i>	4 000	2 108g ⁻¹	2 480g ⁻¹
<i>E. pillansii</i>	25 000	22g ⁻¹	16g ⁻¹
<i>E. turgida</i>		20g ⁻¹	28g ⁻¹

Table 10: Species of Ericaceae which generally gave a low or nil germination percentage

ERICACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Effect of other dormancy-breaking treatments
<i>Erica junonia</i> var. <i>minor</i>	20 000	6	10	Germination improved significantly with GA ₃ (Small <i>et al.</i> 1982)
<i>Erica perspicua</i>	8 333	0	0	
<i>E. porteri</i>	1 250	1	1	

Asteraceae

An analysis of the germination results for the Asteraceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the 53 species for which data were available, 20 (38%) gave a significant positive response to smoke. Of these, two species gave a response of 1 000% or greater (suggesting that smoke is the overriding cue for germination) and 18 gave a response less than 1 000% (suggesting that smoke is possibly one of a number of germination cues of importance). The species in these two response categories are listed in Tables 11a and 11b.

Group 2. Species that germinated without special smoke treatment provided temperature was favourable

A group of 22 species, shown in Table 12, germinated without special smoke treatment provided temperature was favourable. The temperatures in a shade house or open sun during autumn in W. Cape are optimal as are laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day). Some of the species germinated, but germination percentages for both treatments were low, suggesting that seed viability of these samples was also low.

Group 3. Species which gave generally low or nil germination

Table 13 shows 12 species of Asteraceae which gave low or nil germination from some samples where seeds were obviously non-viable. In some cases other samples from different collections of the same species gave greater germination percentages (see figures in brackets).

Revised general germination protocol for seeds of Asteraceae

1. Use only mature, plump, fully formed seeds. In most species these are darker in colour than the immature ones.
2. Pre-soak seeds in aqueous smoke extract or one of the commercial smoke seed primers for 24h; or smoke seed trays after sowing.
3. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
4. Sow seeds in a sandy, well-drained soil medium.

5. Incubate in full sun under autumn/winter temperature conditions, e.g., alternating 10°C (16h-night) x 20°C (8h-day).
6. Seeds of some species are sensitive to light. Light may either promote or inhibit germination. There is also an interaction between the effect of light and the germination response to smoke.

Mesembryanthemaceae

There are 660 species (including 525 endemics) in this family, making it the fourth largest family in the Cape flora (Goldblatt and Manning 2000a). This is a family of succulent plants with usually showy flowers, often forming brilliant sheets of colour when grown in mass. It contains many popular garden plants. The fruit is a capsule splitting open when dry or mostly fleshy and indehiscent. Seeds are reniform, glossy to rugose or papillate and rough, black to brown to pale cream: embryo curved around perisperm (Chesselet *et al.* 2000).

An analysis of the germination results for the Mesembryanthemaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the 21 species for which data were available, nine (43%) gave a significant positive response to smoke. Of these species six gave a response of 1 000% (suggesting that smoke is the overriding cue for germination) and three gave a response less than 1 000% (suggesting that smoke is possibly one of a number of germination cues of importance). The species in the two response categories are listed in Tables 14a and 14b.

Group 2. Species which germinated without special smoke treatment provided temperature was favourable

A group of nine species, shown in Table 15, germinated without special smoke treatment provided temperature was favourable. The temperatures in a shade house or open sun during autumn in the western Cape are optimal as are laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day).

Group 3. Species which gave generally low germination

Three species shown in Table 16 gave generally low germination and were probably largely non-viable or might require another germination cue.

Table 11a: Species of Asteraceae which gave a significant germination response to smoke treatment of 1 000% or greater

ASTERACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater
<i>Metalsia densa</i>		1	14	1 400
<i>Syncarpha vestita</i>	1 826	6	88	1 466

Table 11b: Species of Asteraceae that gave a significant germination response to smoke treatment of less than 1 000%

ASTERACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000%
<i>Arctotis stoechadifolia</i>	148	4	23	575
<i>Corymbium laxum</i> subsp. <i>Bolusii</i>	157	14	22	157
<i>Dimorphotheca nudicaulis</i> (Syn. <i>Castalis nudicaulis</i>)	113	4	9	225
<i>Edmondia sesamoides</i>	5 025	11	98	890
<i>Euryops linearis</i>	855	31	73	235
<i>E. speciosissimus</i>	139	24	64	267
<i>E. virgineus</i>	925	6	31	516
<i>Felicia aethiopica</i> subsp. <i>aethiopica</i>	1 540	18	30	167
<i>F. heterophylla</i>	583	22	46	209
<i>Helichrysum patulum</i>	10 000	24	98	408
<i>Oedera capensis</i>	2 128	5	20	400
<i>Othonna quinqueidentata</i>		44	63	143
<i>Phaenocoma prolifera</i>	511	59	97	164
<i>Senecio rigidus</i>		80	90	113
<i>S. umbellatus</i>	3 704	56	79	141
<i>Syncarpha eximia</i>		19	80	421
<i>S. speciosissima</i>	122	17	30	176

Table 12: Species of Asteraceae that germinated without special smoke treatment provided temperature was favourable

ASTERACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Arctotis acaulis</i>	131	27	29
<i>Chrysocoma coma-aurea</i>	3 161	10	10
<i>Cotula turbinata</i>	7 692	57	55
<i>D. nudicaulis</i> (Syn. <i>Castalis nudicaulis</i>)	113	96	78
<i>Hirpicium alienatum</i>		54	72
<i>Hymenolepis parviflora</i>	405	34	32
<i>Oedera capensis</i>	2 128	47	48
<i>Oncosiphon grandiflorum</i>		47	45
<i>O. suffruticosum</i>		46	45
<i>Osteospermum fruticosum</i>	58	31	36
(Syn. <i>Dimorphotheca fruticosa</i> <i>Pentzia grandiflora</i>)	10 000	44	45
<i>Plecostachys serpyllifolia</i>	28 571	13	10
<i>Senecio halimifolius</i>	4 630	37	34
<i>S. pinifolius</i>	300	30	25
<i>S. umbellatus</i>	3 704	99	99
<i>Syncarpha eximia</i>		96	92
<i>Trypteris sinuata</i>		64	56
<i>Ursinia sericea</i>	769	15	16
<i>U. tenuifolia</i>	1 837	53	44
<i>U. tenuifolia</i>	1 837	67	64

General germination protocol for seeds of Mesembrythemaceae

1. Use only mature, plump, fully-formed seeds.
2. Pre-soak seeds in aqueous smoke extract or one of the commercial smoke seed primers for 24h; or smoke seed

trays after sowing.

3. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
4. Sow seeds in a sandy, well-drained soil medium.
5. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

Table 13: Species of Asteraceae that gave low or nil germination in some samples

ASTERACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Disparago ericoides</i>	1 538	0	0
<i>Edmondia fasciculata</i>		0	0
<i>Euryops abrotanifolius</i>	428	0	0
<i>E. speciosissimus</i>	139	0 (27)	0 (64)
<i>Felicia aethiopica</i>	1 456	0	0
<i>F. filifolia</i>	2 164	0	0
<i>Helichrysum dasyanthum</i>	11 900	0	0
<i>H. pandurifolium</i>	6 667	0	0
<i>H. patulum</i>		0 (24)	0 (98)
<i>Phaenocoma prolifera</i>	511	0 (59)	0 (97)
<i>Senecio halimifolius</i>	4 630	0 (37)	0 (34)
<i>S. umbellatus</i>		0 (99)	0 (99)

Table 14a: Species of Mesembryanthemaceae that gave a germination response to smoke treatment of 1 000% or more

MESEMBRYANTHEMACEAE	No. of seeds g ⁻¹	% Germination or Seedlings g ⁻¹ Water control	% Germination or Seedlings g ⁻¹ Smoke	Response 1 000% or greater
<i>Amphibolia hutchinsonii</i>	2	27		1 350
<i>Drosanthemum speciosum</i>	12 500	2	48	2 400
<i>D. thudichumii</i>		10g ⁻¹	10 000g ⁻¹	1 000
<i>Erepsia anceps</i>	1	10		1 000
<i>Lampranthus multiradiatus</i>	3 170	0	21	2 100
<i>Ruschia carolii</i>	2 174	7	70	1 000

Table 14b: Species of Mesembryanthemaceae that gave a germination response to smoke treatment of less than 1 000%

MESEMBRYANTHEMACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000%
<i>Lampranthus aureus</i>	3 448	2	19	950
<i>L. haworthii</i>	901	3	10	333
<i>Ruschia multiflora</i>	1 308	5	23	460

Table 15: Species of Mesembryanthemaceae that germinated without special smoke treatment provided temperature was favourable

MESEMBRYANTHEMACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Carpanthea pomeridiana</i>	820	13	10
<i>Caryotophora skiatophytoides</i>	109	13	15
<i>Conicosia pugioniformis</i>	1 639	10	19
<i>Drosanthemum bellum</i>	9 500	27	30
<i>D. bicolor</i>	13 514	29	30
<i>D. stokoei</i>	7 692	75	77
<i>Leipoldtia schultzei</i>		91	92
<i>Oscularia deltoides</i>	7 142	10	17
<i>Ruschia macowanii</i>	3 846	43	49

Table 16: Species of Mesembryanthemaceae that gave generally low germination

MESEMBRYANTHEMACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Erepsia aspera</i>	1 639	4	11
<i>Lampranthus austricolus</i>	3 623	7	9
<i>L. bicolor</i>		2	4

Iridaceae

The Iridaceae is the third largest family in the Cape flora with 661 species (including 520 endemics). This remarkable number of species is particularly striking as nowhere else in the world does this family provide more than a small proportion of the total species. It is predominantly a family of herbaceous, seasonal geophytes (Goldblatt and Manning 2000a), many of which are of horticultural value. The fruit is a capsule, rarely indehiscent, firm to cartilaginous, occasionally woody. The seeds are globose to angular or discoid, sometimes broadly winged, usually dry, rarely seed coat fleshy or an aril present, rugulose or smooth, shiny or matte; endosperm hard, with reserves of hemicellulose, oil and protein; embryo small (Goldblatt and Manning 2000b).

An analysis of germination results for the Iridaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the 15 species for which data were available, only two (13%) gave a significant positive response to smoke. Both of these species gave a response of less than 1 000%. The species are listed in Table 17. These results are in agreement with those of Brown *et al.* (2003) who showed that geophytes exhibited a very low germination response to smoke.

Group 2. Species which germinated without special smoke treatment provided temperature was favourable

A group of 11 species, shown in Table 18, germinated without special smoke treatment provided temperature was favourable. The temperatures in a shade house or open sun during autumn in the western Cape are optimal, as are laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day).

Group 3. Species which gave generally low or nil germination

Table 19 lists three species that gave generally low or nil germination and where seeds were possibly of low viability.

General germination protocol for seeds of Iridaceae

1. Use only mature, fully-formed seeds.
2. Seeds of the majority of species do not require a pre-treatment before germination. Those species shown to respond to smoke should be pre-soaked in aqueous smoke extract or one of the commercial seed primers for 24h; or seed trays may be smoked after seed sowing.
3. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
4. Sow seeds in a sandy, well-drained soil medium.
5. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

Rutaceae

The Rutaceae is the ninth largest family in the Cape flora with 273 species and 258 endemics. Many of the species are of importance as sources of volatile oils for the industries producing perfumes, cosmetics, soap and food colourants (Goldblatt and Manning 2000a, Powrie 1998). Fruits are variable, mostly schizocarps, drupes or berries. The seeds are often black, sometimes with an aril; embryo is large, straight or bent, endosperm present and fleshy or absent (Victor 2000).

An analysis of the germination results for the Rutaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the five species for which data were available, one (20%) gave a significant positive response to smoke. This species gave a response of less than 1 000%. The species is shown in Table 20.

Group 2. Species which gave generally low or nil germination

Table 21 shows a group of six species which gave low or nil germination and where seeds were probably of poor viability or they potentially require special dormancy-breaking treatments such as seed coat softening, promalin, GA₄ + GA₇ and/or ethrel to improve germination.

A general germination protocol for seeds of Rutaceae

1. Use only mature, fully-formed seeds.
2. The seed coat is woody and seeds should be pre-treated by placing them in hot water at 100°C to soften the coat.
3. Then pre-soak seeds in one of the commercial smoke seed primers for 24h.
4. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
5. Sow seeds in a sandy, well-drained soil medium.
6. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

Scrophulariaceae

There are 418 species and 297 endemics in the Scrophulariaceae in the Cape flora, making it the sixth largest family (Goldblatt and Manning 2000a). Several genera provide attractive garden ornamentals. The fruit is usually a dry capsule with various types of dehiscence. If indehiscent, the fruit is either dry or succulent. The fruit is occasionally a berry and rarely a fleshy drupe. The seeds are small to minute. One-many per locule, variously shaped, pitted, furrowed, ridged, ribbed or winged, rarely smooth; embryo straight to weakly curved; endosperm oily (Smithies 2000).

An analysis of the germination results for the Scrophulariaceae showed that species could be divided into the following response groups:

Table 17: Species of Iridaceae which gave a significant germination response to smoke treatment

IRIDACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke Smoke	Response less than 1 000%
<i>Aristea africana</i>	840	23	46	200
<i>A. racemosa</i>	226	68	90	132

Table 18: Species of Iridaceae that germinated without special smoke treatment provided temperature was favourable

IRIDACEAE	No. of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Aristea major</i>	225	73	73
<i>Bobartia gladiata</i>	131	62	56
<i>B. gladiata</i> subsp. <i>gladiata</i>	136	74	80
<i>Geissorhiza</i> sp.	2 000	74	60
<i>Moraea ramosissima</i>	181	83	86
<i>Pillansia templemanii</i>	17	81	81
<i>Tritoniopsis parviflora</i>	77	74	74
<i>T. triticea</i>	184	72	66
<i>Watsonia borbonica</i>	60	61	61/47
<i>W. tabularis</i>	75	75	75/71

Table 19: Species of Iridaceae that gave generally low or nil germination

IRIDACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Moraea ochroleuca</i>	580	18	17
<i>Nivenia stokoei</i>		0	0
<i>Romulea</i> sp.	350	2	6

Table 20: Species of Rutaceae that gave a significant germination response to smoke treatment of less than 1 000%

RUTACEAE	% Germination Water control	% Germination Smoke	Response less than 1 000%
<i>Agathosma ovata</i>	4	10	250

Table 21: A group of six species of Rutaceae that gave low or nil germination

RUTACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Agathosma betulina</i>	47	0	0
<i>A. crenulata</i>	101	0.15	0.20
<i>A. tabularis</i>	639	8	11
<i>A. tabularis</i>	639	0	0
<i>Coleonema album</i>	571	0.10	0.15
<i>Diosma acmaeophylla</i>		1	1

Group 1. Species which gave a significant germination response to smoke treatment

Of the 13 species for which data were available, 10 (79%) gave a significant positive response to smoke. Of these species three gave a response of 1 000% or greater (Table 22a) and seven gave a response less than 1 000% or actual % germination response data was not available (Table 22b). The species in the two response categories are listed

in the tables.

Group 2. Species which gave nil germination

Table 23 shows the germination results for the three species where seeds were probably of poor viability or, less likely, they might require special dormancy-breaking treatments such as promalin, GA₄ + GA₇ and/or ethrel to improve germination.

Table 22a: Species of Scrophulariaceae that gave a response to smoke of 1 000% or greater

SCROPHULARIACEAE	No of seed g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Manulea cheiranthus</i>		2	32	1 600	
<i>Nemesia versicolor</i> cv. Blue Bird		0			smoke + promalin 12 (1 200%)
<i>Zaluzianskya villosa</i>	20 000	1	23	2 300	

Table 22b: Species of Scrophulariaceae that gave a response less than 1 000% or that gave a significant germination response to smoke but where actual % germination data was not given in reference (GPNG)

SCROPHULARIACEAE	% Germination Water control	% Germination Smoke	Response less than 1 000%
<i>Chenopodiopsis chenopodioides</i>			GPNG
<i>C. hirta</i>			GPNG
<i>Dischisma capitatum</i>	8	20	250
<i>Hebenstreitia paarlensis</i>			GPNG
<i>Nemesia lucida</i>	12	24	200
<i>N. versicolor</i>			GPNG
<i>Selago</i> sp.			GPNG

Table 23: Species of Scrophulariaceae that gave generally low or nil germination

SCROPHULARIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Nemesia strumosa</i>	4 167	0	0
<i>Pseudoselago serrata</i>	5 587	0	0
<i>P. spuria</i>	4 545	0	0

Campanulaceae

The Campanulaceae has 184 species, including 140 endemics and is the fourteenth largest family of the Cape Flora (Goldblatt and Manning 2000a). It contains mostly herbs, but rarely shrubs or undershrubs. The fruit is a capsule or, rarely, a berry; variously dehiscent, rarely indehiscent. Seeds are often small, smooth or reticulate-rugose (Welman 2000).

An analysis of the germination results for the Campanulaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the nine species for which data were available, seven (70%) gave a significant positive response to smoke. Of these species one gave a response of 1 000% or greater (Table 24a) and six gave a response less than 1 000% or actual % germination response data was not available (Table 24b). The species in the two response categories are listed in the tables.

Group 2. Species which gave nil germination

One species tested gave nil germination (Table 25). Seeds were probably of poor viability or, alternatively, they required

special dormancy-breaking treatments such as promalin, GA₄ + GA₇ and/or ethrel to improve germination.

Geraniaceae

The Geraniaceae contains 155 species, including 91 endemics, and is the sixteenth largest family in the Cape flora (Goldblatt and Manning 2000a). The fruit is a three- to five-lobed, rarely eight-lobed schizocarp, breaking up from the base of the beak into 1(2)-seeded mericarps, usually with persistent elastic styles as long awns twisting spirally. Seeds usually have a curved embryo and endosperm is absent or sparse (Dreyer and Makwarela 2000).

An analysis of the germination results for the Geraniaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the 10 species for which data were available, three (30%) gave a significant positive response to smoke. These species gave a response of less than 1 000%. The species are listed in Table 26. Two additional treatments, the first, where seeds were soaked in hot water and the second, where seeds were soaked in hot water and then smoked, both gave better germination than smoke treatment alone. These results suggest that dormancy may be partially coat-imposed.

Table 24a: Species of Campanulaceae that gave a response to smoke of 1 000% or greater

CAMPANULACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater
<i>Roella triflora</i>	5 555	5	50	1 000

Table 24b: Species of Campanulaceae that gave a response to smoke of less than 1000%

CAMPANULACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000% than 1 000%
<i>Lobelia coronopifolia</i>	9 804	1	5	500
<i>L. linearis</i>	5 556	2	8	400
<i>L. sp.</i>	8 853	0	9	900
<i>Monopsis lutea</i>	10 152	10	35	350
<i>Roella ciliata</i>	6 780	32	92	283

Table 25: Species of Campanulaceae that gave nil germination

CAMPANULACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Lobelia pinifolia</i>	2 519	0	0

Table 26: Species of Geraniaceae that gave a significant response to smoke of less than 1 000%

GERANIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000%	Effect of other dormancy-breaking treatments % Germination (% response)
<i>Geranium incanum</i>		60	85	142	
<i>Pelargonium crithmifolium</i>		40	80	200	
<i>P. cucullatum</i>		8	15	187	hot water (100°C) gave germination of 59% (738%); hot water + smoke gave germination 46% (575%)

Group 2. Species which germinated without special smoke provided temperature was favourable

Table 27 shows the results for six species that germinated without smoke treatment provided temperatures were favourable (e.g. shade house or open sun during autumn in the Western Cape or laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day)). Germination results for most of the species were very low and it would have been interesting to determine whether hot water treatment would have improved germination.

Germination protocol

1. Use mature, fully-formed seeds.
2. Place seeds in hot water at 100°C and then allow them to soak for 10h.
3. Then soak in aqueous smoke extract or one of the commercial smoke seed primers for 24h, or smoke seed trays after sowing.
4. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
5. Sow seeds in a sandy, well-drained soil medium.

6. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

Fabaceae

The Fabaceae is the second largest family in the Cape flora and contains 760 species, including 627 endemics (Goldblatt and Manning 2000a). Fruits are generally two-valved dehiscent pods, rarely fleshy and sometimes indehiscent and occasionally breaking into segments. Seeds are variously without or with very little endosperm (Germishuizen 2000). Seeds of many of the species are hard-seeded and require fracturing by means of hot water or dry heat treatment or acid or mechanical scarification for water to be absorbed (Jeffrey *et al.* 1988).

An analysis of the germination results for the Fabaceae showed that species could be divided into the following response groups:

Group 1. Species which gave a significant germination response to smoke treatment

Of the eight species for which data were available, two

(25%) gave a significant positive response to smoke. Of these species one gave a response of 1 000% or greater (Table 28a) and for one there was a significant response to smoke but actual % germination data was not available (Table 28b). The species in the two response categories are listed in the tables.

Group 2. Species that did not show a response to smoke but responded to hot water treatments

Four species did not show a response to smoke but gave a significant response to hot water treatment (Table 29).

Germination protocol

1. Use mature, fully-formed seeds.
2. Place seeds in hot water at 100°C and then allow them to soak for 10h.
3. Then soak in aqueous smoke extract or one of the commercial smoke seed primers for 24h; or smoke seed trays after sowing.

4. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
5. Sow seeds in a sandy, well-drained soil medium.
6. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

Bruniaceae

The Bruniaceae is one of the distinctive families of the Cape flora and is almost endemic. It has an estimated 64 species in 11 genera and only three species extend outside the confines of the Cape Region (Goldblatt and Manning 2000a). The fruits are indehiscent to dehiscent. The seeds are fleshy with a thin testa (Hall 2000). The first report of improved seed germination following smoke treatment was for seeds of *Audouinia capitata*, (which belongs to the Bruniaceae) scarified in the soil by soil micro-organisms (De Lange and Boucher 1990).

An analysis of the germination results for the Bruniaceae showed that species could be divided into the following response groups:

Table 27: Species of Geraniaceae that germinated without special treatment provided temperature was favourable

GERANIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Pelargonium auritum</i>		80	84
<i>P. capitatum</i>	234	8	8
<i>P. cucullatum</i>	225	4	4
<i>P. peltatum</i>	80	4	4
<i>P. quercifolium</i>	210	4	4
<i>P. suburbanum</i>	110	16	16

Table 28a: Species of Fabaceae that gave a response to smoke of 1 000% or greater

FABACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response 1 000% or greater
<i>Otholobium fruiticans</i>	291	4	65	1 625

Table 28b: Species of Fabaceae that gave a response to smoke but actual % germination data was not available

FABACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000% than 1 000%
<i>Cyclopia intermedia</i>				GPNG

Table 29: Species of Fabaceae did not show a response to smoke but gave a significant response to hot water treatment

FABACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Additional effective dormancy breaking treatments
<i>Indigofera filifolia</i>	100	3	1	hot water (100°C) gave a response of 42% (1 400%); and hot water + smoke gave (39%) (1 300%)
<i>Podalyria sericea</i>	40	5	12	hot water 70% (1 400%); and hot water + smoke 62% (1 240%)
<i>Psoralea pinnata</i>	123	10	12	hot water 72% (720%)
<i>Virgilia divaricata</i>	16	3	5	hot water 20% (667%); and hot water + smoke 15% (300%)

Group 1. Species that gave a significant germination response to smoke treatment

Of the seven species for which data were available, three (43%) gave a significant positive response to smoke. All these species gave a response of less than 1 000% (Table 30).

Group 2. Species that germinated without special smoke treatment provided temperature was favourable

One species of Bruniaceae germinated without special smoke treatment provided temperature was favourable (e.g. Shade house or open sun during autumn in the western Cape or laboratory controlled-temperature conditions of 10°C (16h-night) alternating with 20°C (8h-day)) (Table 31).

Group 3. Species that gave generally low or nil germination

Four species of Bruniaceae gave generally low or nil germination and seeds were probably of poor viability. A less likely possibility is that they require special dormancy-breaking treatments such as promalin, GA₄ + GA₇ and/or ethrel to improve germination (Table 32).

Brassicaceae, Haemodoraceae, Penaeaceae, Poaceae, Rhamnaceae, Sterculiaceae and Thymelaeaceae

Germination in a range of species selected from a number of other fynbos families has also been studied previously by Brown *et al.* (1998). Those species which showed a germination response to smoke included: *Endonema retzioides* (Penaeaceae), *Themeda triandra* (Poaceae) and *Passerina vulgaris* and *P. ericoides* (Thymelaeaceae).

Brassicaceae

In the Brassicaceae, the fruit is basically a capsule, divided into two locules by a persistent septum to which seeds are attached. Seeds are discoid to globose, often winged, seed coat often mucilaginous, embryo folded double with radicle lying against sides or backs of cotyledons. Cotyledons are linear to circular, variously folded or rolled. Endosperm is absent or present in a small amount (Dreyer and Jordaan 2000).

Haemodoraceae

In the Haemodoraceae the fruit is a capsule and seeds are solitary to many in each capsule (Archer 2000).

Penaeaceae

In Penaeaceae the fruit is a four-valved loculicidal capsule, often with valves awned with the persistent base of the style. Seeds by abortion are one or two in each locule (Bredenkamp 2000a).

Poaceae

In Poaceae the fruit is mostly a caryopsis with the thin pericarp adnate to the seed, sometimes the pericarp is free, sometimes an achene, nut or berry; the caryopsis is commonly combined with various parts of the spikelet, or less often inflorescence, to form a false fruit (Fish 2000).

Rhamnaceae

In the Rhamnaceae the fruit is a drupe or a capsule, partly or wholly enclosed by a persistent calyx tube. The seed is

Table 30: Species of Bruniaceae that gave a significant positive response to smoke of less than 1 000%

BRUNIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	Response less than 1 000%
<i>Audouinia capitata</i>		4	14	397
<i>Brunia albiflora</i>	170	1	9	900
<i>B. laevis</i>	321	1	6	600

Table 31: Species of Bruniaceae that germinated without special smoke treatment provided temperature was favourable

BRUNIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Brunia albiflora</i>	170	17	20

Table 32: Species of Bruniaceae that gave generally low or nil germination

BRUNIACEAE	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke
<i>Berzelia abrotanoides</i>	877	0	0
<i>B. galpinii</i>	1 205	4	5
<i>B. lanuginosa</i>	1 923	2	6
<i>Staavia radiata</i>	1 080	0	0

solitary in each capsule (Bredenkamp 2000b).

Sterculiaceae

In the Sterculiaceae the fruit is a capsule, usually dry, sometimes fleshy, dehiscent or indehiscent. Seeds with embryo straight or curved; endosperm is usually present (Bredenkamp 2000c).

Thymelaeaceae

In the Thymelaeaceae the fruit is an achene, nut, drupe or loculicidal capsule, sometimes fleshy, usually enclosed in the base of a persistent calyx tube. Seeds usually with a caruncle-like appendage. Outer coat thin or crustaceous, usually black with or without endosperm; embryo straight; cotyledons flat or thickened, narrow or broad (Bredenkamp and Beyers 2000).

Germination results for the present study are shown in Table 33. Details of the germination response to smoke are given in the final column on the right hand side of the table.

Germination protocol

1. Use mature, fully-formed seeds.
2. Seeds of many of the species do not require a pre-treatment before germination. Those species shown to respond to smoke should be pre-soaked in aqueous smoke extract or one of the commercial seed primers for 24h, or seed trays may be smoked after seed sowing.
3. Seeds should be given a light dusting with a fungicide dressing to prevent post-emergence seedling infection.
4. Sow seeds in a sandy, well-drained soil medium.
5. Incubate in full sun under autumn/winter temperature conditions, e.g. alternating 10°C (16h-night) x 20°C (8h-day).

General significance of fynbos seed propagation studies

Research has led to more knowledge of germination cues, particularly those related to fire viz. heat, smoke and alternating temperatures. A considerable amount of Information has also been accumulated regarding the potential use of growth regulators to break dormancy and improve germination of seeds in the Proteaceae, Restionaceae and

Table 33: Germination response of species from Brassicaceae, Haemodoraceae, Penaeaceae, Poaceae, Rhamnaceae, Sterculiaceae and Thymelaeaceae

	No of seeds g ⁻¹	% Germination Water control	% Germination Smoke	% Response to smoke
BRASSICACEAE				
<i>Heliophila coronopifolia</i>	1 923	92	93	Germinates without smoke
<i>Heliophila macowaniana</i>		GPNG		No response
<i>Heliophila pinnata</i>		68	62	Germinates without smoke
<i>Heliophila</i> sp.		GPNG		Response to smoke less than 1 000%
<i>Brachycarpaea juncea</i>	71	0	0	No germination Impenetrable seed coat
HAEMODORACEAE				
<i>Dilatrix pillansii</i>	126	0	0	No germination
<i>Wachendorfia paniculata</i>	190	41	37	Germinates without smoke
<i>Wachendorfia paniculata</i>	190	60	78	130
<i>Wachendorfia thyrsiflora</i>	70	15	40	267
PENAEACEAE				
<i>Endonema retziodes</i>		36	86	238
POACEAE				
<i>Pentachistis colorata</i>		0	24	2 400
<i>Pseudopentameris macrantha</i>	231	5	26	520
<i>Themeda triandra</i>		6	36	600
RHAMNACEAE				
<i>Phylica buxifolia</i>		1	1	No response
<i>Phylica ericoides</i>		8	9	No response
<i>Phylica pubescens</i>	52	28	24	No response
STERCULIACEAE				
<i>Hermannia alnifolia</i>		0	1	No response
<i>Hermannia hyssopifolia</i>		2	0	No response
<i>Hermannia rudis</i>		2	2	No response
<i>Hermannia scabra</i>		GPNG		No response
<i>Hermannia</i> sp.		GPNG		No response
THYMELAEACEAE				
<i>Gnidia pinifolia</i>	282	2	5	250
<i>Passerina vulgaris</i>	1 961	GPNG		Significant response
<i>P. ericoides</i>				
<i>Struthiola myrsinites</i>	658	10	33	330

Ericaceae. Research results have led to:

1. Greater efficiency in germinating fynbos seeds and thus more plants obtained from seed samples.
2. A marked increase in the range of fynbos species available for cultivation by the horticultural industry.
3. Guaranteed germination for many rare threatened and endangered species, which has contributed to their conservation.
4. Improved germination of hybrid seed in plant breeding and plant improvement programmes involving native species.
5. The smoke research results have been applied in Australia, USA, Europe and other parts of the world and have made a major contribution to native plant propagation and utilisation projects. Also benefiting have been programmes of vegetation rehabilitation following activities such as strip mining and road building.

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