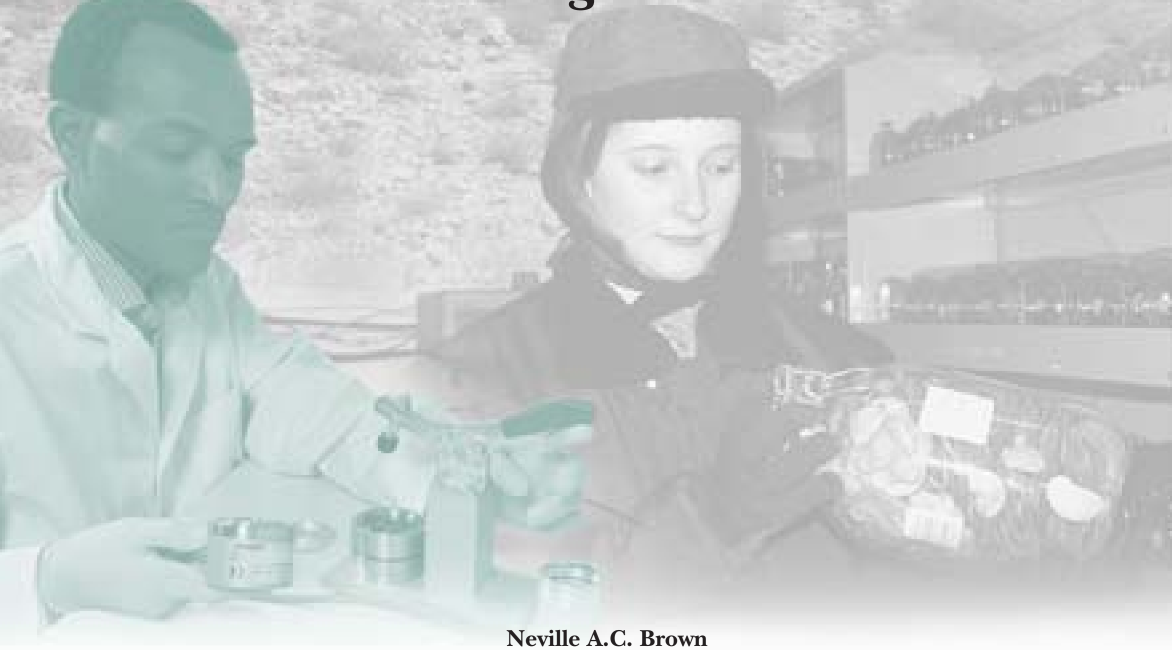
Chapter 31

# A Summary of Patterns in the Seed Germination Response to Smoke in Plants from the Cape Floral Region



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**Summary**

De Lange and Boucher (1990) discovered the germination enhancing effect of plant-derived smoke on seed of fynbos species. This finding has been applied to horticulturally important fynbos species and to date we have tested 221 species for a response to smoke. Germination in 120 (54%) of these was markedly improved by smoke treatment; the remaining 101 species showed no response.

The families showing a positive response include the horticulturally important families *Asteraceae* (Everlastings), *Bruniaceae* (Brunias), *Crassulaceae* (Crassulas), *Ericaceae* (Ericas), *Geraniaceae* (Pelargoniums), *Mesembryanthemaceae* (Mesembs), *Proteaceae* (Proteas) and *Restionaceae* (Restios). Amongst those families not responding were families of geophytes such as *Amaryllidaceae*, *Hyacinthaceae*, *Iridaceae* and *Haemodoraceae*. This latter finding highlighted the possibility of the smoke response being related to life-history traits.

Further analysis of the germination results using binary logistic regression showed that the growth form of geophytes was the only robust predictor of response to smoke; the geophytes exhibited no germination response to smoke. In addition, there was a suggestion that wind-dispersed species and herbaceous perennials were more likely to respond positively to smoke than other species.

## Introduction

Fynbos is a unique type of vegetation that is dominant in the Cape Floral Region (CFR) in the south western Cape, at the southern tip of Africa. The CFR covers an area of 90,000 km$^2$ (35,000 sq miles), which is less than four percent of the area of South Africa, yet it contains 8,600 plant species and is by far the richest temperate flora in the world. Over two-thirds of the Cape plant species and seven of the plant families are endemics. Fynbos, which is a community of small shrubs, evergreen and herbaceous plants and bulbs, is exceptionally rich in species and contributes most of the species to the flora of the CFR. 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).

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 difficult, as seeds of many species are dormant when shed and require very specific environmental “messages” or cues before they will germinate (Brown, 1993a). Fynbos occurs in areas with a Mediterranean climate (winter rainfall) and the environment is characterised by a number of stress factors such as summer drought, low soil fertility and periodic fires. The fires have a frequency of 5 to 40 years and are a natural phenomenon in fynbos. 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. (Brown and van Staden, 1997; van Staden *et al.*, 2000).

The germination response to smoke can be interpreted as an adaptation to ensure germination occurs following fire, which guarantees germination occurs into vegetation free (high light) environments (Baskin and Baskin, 1998). Consequently, it might be expected that species requiring vegetation free patches for regeneration and that are dependent on seeds for regeneration would be most likely to respond to smoke, i.e., annuals and herbaceous perennials. Conversely, species that either avoid fire by aestivating (geophytes) or are able to exhibit at least some re-sprouting following fire (woody plants) may be less likely to respond to fire.

In this paper we examine the germination response of 221 fynbos species to smoke in an attempt to test if there are predicable patterns of responses associated with plant life-history traits, such as growth-form and seed dispersal agent.

## Materials and Methods

### 1. Seed Supplies

Fynbos taxa from fire-prone environments were selected for study. For convenience, all propagules whether they are fruits or seeds are referred to as "seeds". Seed was collected from the wild in various localities in the south-western and southern Cape.

### 2. Effects of Smoke Treatments on Germination.

In a series of experiments, seeds were sown in trays containing dry, unsterilized fynbos soil. Half the trays were smoke-treated and half were left untreated as controls. The trays were smoked in a polythene tent according to the method of de Lange and Boucher (1990). Bellows were used to blow the smoke through a polythene pipe into the tent for 30 min. The system allowed the smoke to cool before it entered the tent. Trays were left in the smoke tent for 2 h. All trays were subsequently irrigated with distilled water and then incubated in a covered shade house. The criterion for germination was the emergence of a healthy seedling. Results were recorded weekly for eight weeks.

### 3. Effects of Smoke Extracts on Germination.

Aqueous extracts of plant-derived smoke were obtained using the method of de Lange and Boucher (1990). Smoke was bubbled through a glass column containing 2.5 l distilled water, for 30 min. This concentrated smoke extract was diluted using distilled water, and the effect on germination of each of a range of dilutions was investigated. In laboratory trials, seed was germinated on disks of Whatman No. 3 filter paper in 70 mm diameter plastic Petri dishes. Distilled water (2.5 ml/dish) was added to controls. In trials, 2.5 ml of smoke extract solution was added to the filter paper in each Petri dish, and seeds were incubated on the smoke solutions. Seeds were incubated in a germination cabinet in the light at alternating temperatures of 10°C for 16 h followed by 20°C for 8 h. Germination counts were taken twice weekly and the emergence of a radicle 2 mm in length was taken as the criterion of germination.

### 4. Statistical Analysis

An extensive literature study was undertaken of growth form, fire survival strategy, and seed dispersal mode for the species occurring in the Cape Floral Region. This information was only obtainable for 169 species and was used to determine whether there were predictable patterns of smoke response between different plant groupings. For each plant species, the probability that it would not exhibit a positive germination response to smoke was examined with respect to (1) seed dispersal mode (two categories: wind/passive dispersal (0) or animal/bird dispersal (1)) (2) post-fire regeneration strategy (two categories: predominately dependent on regeneration from seed (0) and predominantly dependent on re-sprouting (1)) and (3) growth form (four categories, annual, geophyte, herbaceous perennial and woody) using the binary logistic regression analysis procedure of Minitab 13 (Minitab Inc. PA, USA). Because there is no defined order to the three variables for growth form, three dichotomous variables were created. Thus growth form(1) was coded 1 if the growth form was annual and 0 if otherwise, growth form(2) was coded 1 if geophyte and 0 otherwise and growth form(3) was coded 1 if herbaceous perennial and 0 if otherwise. Woody plants were identified by 0 on all three dichotomous variables (Tabachnick and Fiddell, 2001). To evaluate the contribution of each main factor to the full logistic model containing all five terms, the logistic regression analysis was repeated for all possible four-term reduced models followed by likelihood ratio tests, where $G = 2[\log L_{full} - \log L_{reduced}]$, and $G$ is distributed as $\chi^2$ with 1 *d.f.*, to determine the significance of the change in log-likelihood after removal of each term (Tabachnick and Fidell, 2001).

# Results and Discussion

## 1. Smoke as a Germination Cue

In addition to the more obvious cues provided by heat, smoke from fires provides as yet unidentified, chemical message(s), which, independently of the heat produced in a fire, can stimulate seed germination of many fynbos species. De Lange and Boucher (1990) were the first to report this effect. They showed that germination of *Audouinia capitata* was significantly enhanced by treatment with plant-derived smoke or with aqueous extracts of smoke. Subsequently, we have screened 221 species for a response to smoke. A summary of the results showed that germination of 54% of these species was significantly enhanced by smoke (Brown, 1993a; Brown, unpublished). Similar studies have been carried out on Western Australian species and lists of those species that responded positively to smoke or smoke extracts have been published. (Dixon and Roche, 1995; Dixon *et al.*, 1995; Tieu *et al.*, 1999). Baskin and Baskin (1998) summarised all the available information on matorral species and compiled an extensive list of species in which seed germination was stimulated by smoke and/or smoke extracts.

## 2. Patterns in Response to Smoke Shown by Different Plant Families

Table 31.1 shows a list of the families to which test species belonged and whether the family contained species that showed improved germination with smoke treatment. The families showing a positive response include the horticulturally important families *Asteraceae* (everlastings), *Bruniaceae* (brunias), *Crassulaceae* (crassulas), *Ericaceae* (ericas), *Geraniaceae* (pelargoniums), *Mesembryanthemaceae* (mesembs), *Proteaceae* (proteas) and *Restionaceae* (restios). Amongst those families not responding were families of geophytes such as *Amaryllidaceae* (*Cyrtanthus*), *Hyacinthaceae* (*Albuca*), *Iridaceae* (*Bobartia, Geissorhiza, Moraea, Romulea*) and *Haemodoraceae* (*Wachendorfia*). This latter finding highlighted the possibility of the smoke response being related to life-history traits.

## 3. Ecological Patterns in the Germination Response to Smoke

This and other studies have found that the smoke response is phylogenetically widespread in the fynbos (De Lange and Boucher, 1993b; Brown 1993a; Brown *et al.*, 1993; Brown *et al.*, 1995), in chaparral (Keeley and Fotheringham 1998) and in the Western Australian plant communities (Roche *et al.*, 1997b). However, although a positive germination response to smoke is found in a wide range of families within fynbos vegetation, not all the species within a family or genus exhibit the same smoke response. For example, despite having similar life-history strategies, 64% of the *Erica* species investigated (30 of 47) responded to smoke;

**Table 31.1 Plant families tested for a germination response to smoke**

| | |
|---|---|
| ✔ *Aizoaceae* | ✖ *Haemodoraceae* |
| ✖ *Amaryllidaceae* | ✖ *Hyacinthaceae* |
| ✖ *Anacardiaceae* | ✖ *Iridaceae* |
| ✖ *Asphodelaceae* | ✔ *Mesembryanthemaceae* |
| ✔ *Asteraceae* | ✖ *Montiniaceae* |
| ✔ *Brassicaceae* | ✔ *Penaeaceae* |
| ✔ *Bruniaceae* | ✔ *Poaceae* |
| ✔ *Campanulaceae* | ✔ *Proteaceae* |
| ✔ *Caryophyllaceae* | ✔ *Restionaceae* |
| ✔ *Crassulaceae* | ✖ *Rhamnaceae* |
| ✖ *Cupressaceae* | ✔ *Rosaceae* |
| ✖ *Cyperaceae* | ✖ *Rubiaceae* |
| ✔ *Ericaceae* | ✔ *Scrophulariaceae* |
| ✔ *Fabaceae* | ✖ *Sterculiaceae* |
| ✔ *Geraniaceae* | ✔ *Thymelaeaceae* |

✔ = Germination improved significantly in some species.
✖ = No improvement in germination for any of the species tested.

the remaining 36% did not. This may reflect adaptation for regeneration in very specific micro-sites or may indicate that there is little adaptive significance in responding to smoke. However, this remains to be tested.

Smoke-enhanced germination in fynbos has been recorded for a wide range of plant species showing a variety of life-history traits, i.e., in both regeneration strategies (annual seeders and long-lived resprouters), in both dispersal modes (wind/passive or animal) (Figure 31.1) and in all growth forms from annuals to trees (except geophytes) (Figure 31.2). The logistic regression analysis indicated that only seed dispersal mode and growth form had a significant effect on the likelihood of a species not responding to smoke (Table 31.2). Thus, in fynbos, species that respond to smoke are most likely to be herbaceous perennials or species with seeds that are passively or wind dispersed (Figure 31.1 and 31.2) although the significance of this result was low ($P < 0.05$; Table 31.2). The following fynbos species have the above life-history characteristics: *Pseudopentameris macrantha* (Schrad.) Conert (*Poaceae*), *Staberoha cernua* (L.f.) T.Durand & Schinz (*Restionaceae*), *Eriocephalus africanus* L. (*Asteraceae*), *Erica deflexa* Sinclair (*Ericaceae*), *Cyclopia intermedia* E.Mey. (*Fabaceae*), *Pelargonium crithmifolium* Sm. (*Geraniaceae*) and *Erepsia anceps* (Haw.) Schwantes (*Mesembryanthemaceae*). In contrast, species

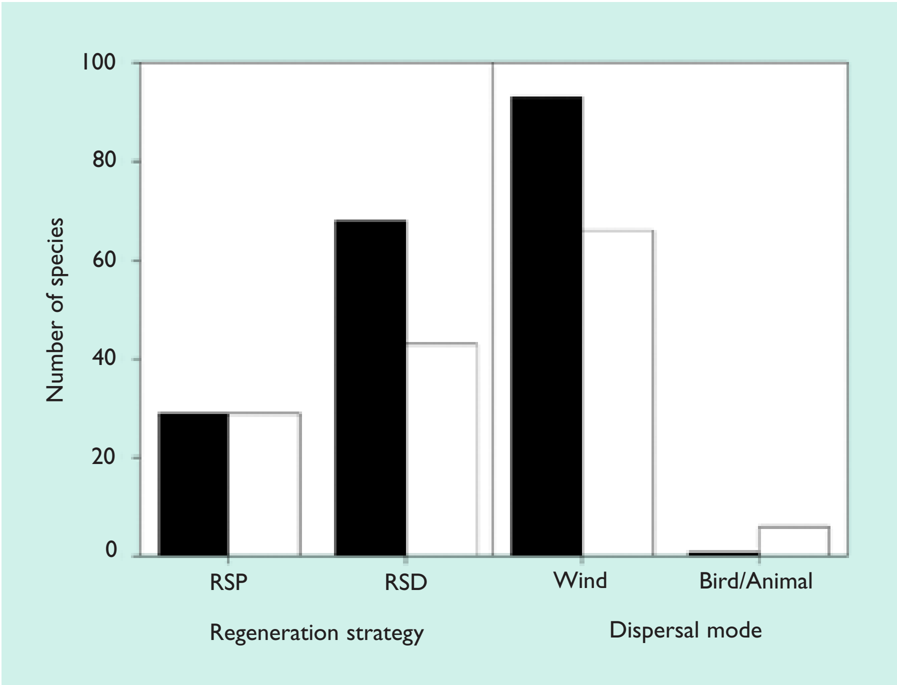


Figure 31.1 Number of fynbos species with different regeneration strategies and different dispersal modes responding to smoke-mediated germination. RSP = re-sprouter; RSD = re-seeder. Solid bars are species that respond to smoke.

that are least likely to response to smoke are geophytes and species with animal/bird dispersed seeds (Figure 31.1 and 31.2; Table 31.2). However, the low levels of significance in the analysis indicate that none of the life-history characteristics included in the analysis (with the possible exception of geophytes) are reliable and absolute predictors of a species' response to smoke. This is contrary to the hypotheses in the chapter's Introduction and suggests that, in fynbos, there is little directional selection on different plant functional groups for a germination response to smoke. This is supported by the work of Dixon and Roche (1995) who found that for the kwongan the promotive effect of smoke is independent of seed size, seed shape and plant life form and fire regeneration strategy.

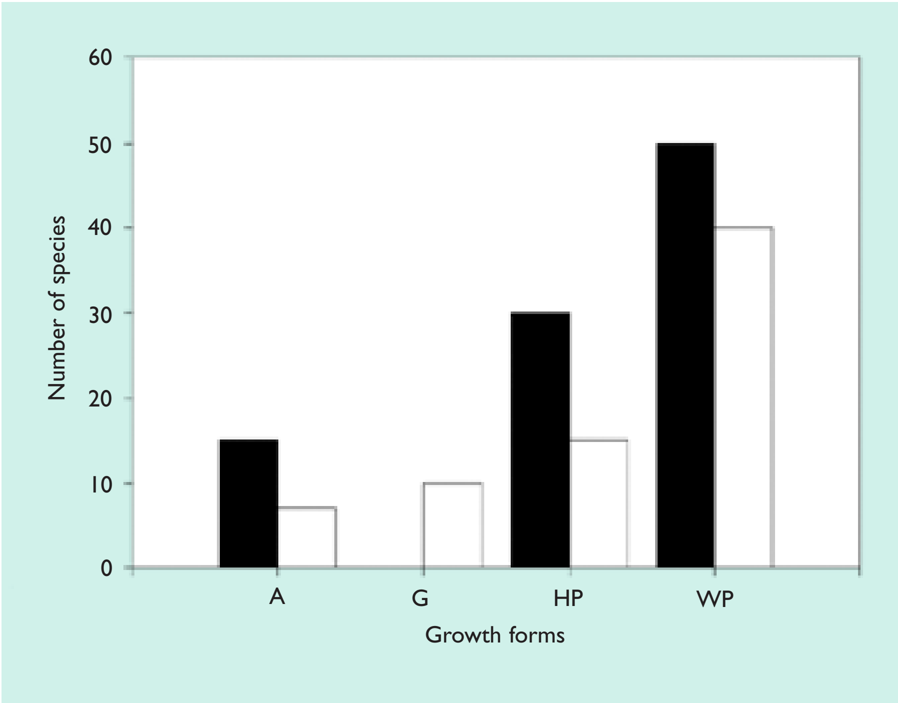


Figure 31.2 Number of fynbos species with different growth forms exhibiting to smoke-mediated germination. A = annuals; G = geophytes; HP = herbaceous perennials; WP = woody perennial. Solid bars are species that respond to smoke.

An interesting situation was found in *Erica sessiliflora*, the only species with canopy stored (serotinous) seeds in the *Ericaceae*. Apparently, the seeds are dormant when dispersed and require light for germination. They also respond to smoke, and this treatment is an effective substitute for the light requirement (Figure 31.3). These results suggest that in *E. sessiliflora* a combination of environmental cues may be required for germination. These may act additively or sequentially, resulting in a better chance of seedling survival and establishment. This apparent interaction suggests that further work is needed to understand both the active components of smoke and its mode of action as well as the ecological role of smoke in stimulating germination in the field and its consequences for regeneration success.

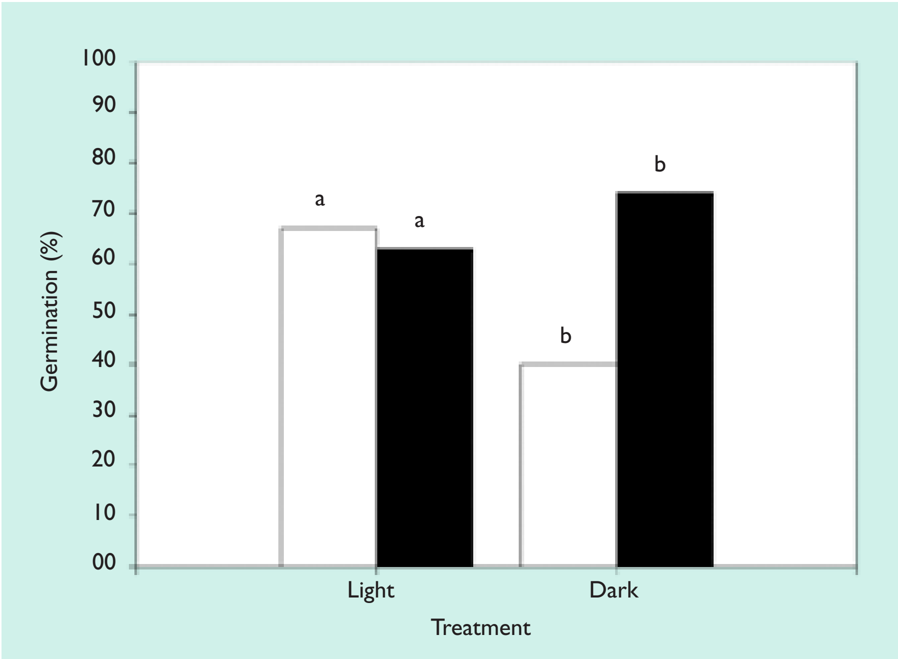


Figure 31.3 Germination of *Erica sessiliflora* in response to a 1:50 dilution of smoke extract. Seeds were germinated in the light and dark both with and without aqueous smoke extract. Open bars are minus and solid bars are plus smoke treatment. Different letters indicate significant differences ($P < 0.05$) after 92 d of incubation.

## Conclusions

A positive germination response to smoke may be advantageous since smoke may indicate the absence of established vegetation and hence a suitable site for seedling regeneration. Our results indicate that a smoke response is found in a wide range of families which is in agreement with Keeley and Bond (1997) who reported that responses to smoke have arisen independently in distantly related families which they interpreted as convergent evolution.

This current study found that there are few robust, predictable patterns in the smoke response of fynbos species: those identified in this study, with the exception of geophytes, were only marginally significant. Similarly, Dixon and Roche (1995) found that there were few predictable patterns of response (in relation to life-history variables) to smoke for kwongan vegetation. Furthermore, even within families and genera patterns of smoke response

Table 31.2 **Log-likelihood ratio test for each two parameter reduced logistic model compared to the full three parameter model. Values for the log-likelihood test are presented for each reduced model, compared to the full model, in addition to the associated *P*-value for $\chi^2$ with d.f. = 1. For definition of growth forms 1, 2 and 3 see Materials and Methods. Odds-ratios are provided for terms that make a significant contribution to the model. These indicate the change in likelihood of a species not responding to smoke when changing from the variable coded 0 to the variable coded 1. Thus, for example, species with animal dispersed seeds are 8.96 times as likely to not respond to smoke as species with wind dispersed seeds.**

| Term removed from full model | Log-likelihood | $2[\log L_{full} - \log L_{reduced}]$ | *P*-value | Odds ratio |
|---|---|---|---|---|
| **None** | -102.768 | n/a | n/a | n/a |
| **Regeneration strategy** | -102.901 | 0.266 | ns | n/a |
| **Dispersal mode** | -104.923 | 4.310 | 0.038 | 8.96 |
| **Growth form(1)** | -103.374 | 1.212 | ns | n/a |
| **Growth form(2)** | -108.961 | 12.386 | <0.001 | 102 |
| **Growth form(3)** | -104.819 | 4.102 | 0.043 | 0.59 |

ns = not significant.

were not consistent. This suggests there may be little selection pressure for species to respond to smoke, i.e., there is little advantage to responding to smoke. Thus in evolutionary terms the smoke response may be a neutral trait. Clearly, further field-work is required to elucidate whether (1) smoke induced germination is important for stimulating regeneration in the field and (2) its consequence(s), if any for vegetation composition.

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