Convergent seed germination in South African fynbos and Californian chaparral

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Abstract

California chaparral and South African fynbos are fire-prone communities dominated by species exhibiting remarkable similarities in germination response. In both regions there are a substantial number of species with germination stimulated chemically by charred wood and smoke. This type of germination behaviour has arisen independently in distantly related families and is interpreted as convergent evolution. Heat-shock is also an important germination trigger that is widespread, although in both regions it is most common in the same families. Phylogeney may play an important role in the presence of this postfire germination cue in both regions, but a much more rigorous analysis is required to show that this trait represents a single unique event in each lineage. In both regions, germination response is not randomly distributed across growth forms and there are marked regional similiarities in the type of germination behaviour associated with certain growth forms. Geophytes largely lack refractory seeds, which require fire-type cues for germination, but the presence of fire-stimulated flowering of bulbs and corms may time recruitment to subsequent postfire years. Annuals that cue germination to postfire conditions are predominantly triggered by chemicals from smoke and/or charred wood.

Introduction

Mediterranean-climate ecosystems are commonly cited examples of convergent evolution in vegetation structure and function (di Castri & Mooney 1973; Mooney 1977; Cowling & Campbell 1980; Shmida & Whittaker 1984; Arroyo et al. 1994; Keeley 1992). These landscapes are dominated by sclerophyll evergreen vegetation that dry sufficiently during the long summer droughts to produce a predictable and extended wildfire season (Mooney & Conrad 1977). There is evidence that species in these communities have evolved to exploit fires for population expansion and some have adapted to these disturbances to the extent that they are 'fire-dependent' for completion of their life cycle (Gill 1981; Kruger 1983; Keeley 1986; van Wilgen et al. 1992; Trabaud & Prodon 1993). Many species regenerate primarily in the first year or two after fire, either because fire stimulates flowering, or seed release from serotinous cones or breaking of seed dormancy by heat or from chemicals in charred wood or smoke.

Despite widespread postfire recruitment in mediterranean-climate floras, communities include species representing other recruitment patterns as well. For example, in Californian chaparral disturbance-dependent recruitment from dormant soil seed banks characterizes a substantial portion of the flora, but a significant number of species recruit solely in the absence of fire (Keeley 1991). While postfire disturbance-dependent species produce deeply dormant seeds with germination triggered by heat or chemicals, spe-

cies with 'disturbance-free' recruitment produce non-refractory seeds that lack deep dormancy and consequently such species have relatively short-lived transient seed banks. Additionally, refractory and non-refractory germination behaviours are not randomly distributed across growth forms, rather some such as geophytes (cryptophytes), lack fire-stimulated germination behaviour.

Remarkable similarities in species responses to fire exist between Californian chaparral and South African fynbos (Kruger 1983; Keeley 1992), including numerous species with persistent seed banks triggered to germinate by either heat or smoke (de Lange & Boucher 1990; Brown 1993a; Keeley 1994) and many geophytes with fire-induced flowering (Le Maitre & Brown 1992; Stone 1951; Rundel 1997). On the other hand there are marked differences, such as the abundance of aboveground seed storage in serotinous fruits and widespread myrmechochory in fynbos (Bond et al. 1984, 1990; Le Maitre & Midgley 1992). Markedly different soils between these regions, and different phylogenetic pathways, have been suggested as reasons for these and other instances of non-convergence (Cody & Mooney 1978; Keeley 1992).

Evolutionary convergence, of course, is only one explanation for shared patterns of adaptation. Derived traits that are passed down through lineages likewise may account for similar adaptations of species in different communities. Such phylogenetic effects may produce repeated patterns that arise from homologous traits, whereas convergence explains the repeated and independent derivation of traits across lineages and focuses on analogous traits. Failure to consider history in studies of convergence has been recognized as a significant short-coming in earlier studies (Peet 1978; Barbour and Minnich 1990).

The purpose of this investigation was to compare the germination characteristics of representatives of the predominant growth forms in Californian chaparral and South African fynbos. Convergent evolution theory predicts that similar climates have selected for a similar range in germination behaviours and a similar growth-form distribution for each type of germination behaviour. While recognizing the value of rigorous approaches to recognizing phylogenetic effects (e.g., Donoghue 1989; Eggleton & Vane-Wright 1994; Losos 1996), we considered these methods to be beyond the scope of this project, but have considered such effects in the discussion.

Much of the data for California has been published (Keeley 1987, 1991; Keeley and Fotheringham 1997a, b) and will be summarized here. The bulk of experimental data presented will be for South African fynbos and will present the response to heat and to chemicals from charred wood and smoke and to light and dark, across different growth forms and compare the patterns that emerge with those found in California.

Materials and methods

Seeds were collected from natural populations in California and South Africa and voucher specimens deposited in LOC. Choice of species was determined largely by availability. Seeds were stored in bottles at room temperature for 6 mo to 1 yr prior to germination experiments. Germination was conducted in 55×15 mm sterilized polystyrene petri dishes on one filter paper (55 mm Whatman No. 1) with 2 ml distilled water. Treatments were placed on separate trays and enclosed in 4 mil polyethylene ziplock bags to reduce desiccation and inadvertent transfer of vapors from charred wood or smoke. For each species 3 replicates of 30 seeds were tested. All seeds were given a one-month cold (4–5 °C) stratification prior to incubation under 12 h photoperiod (100 μmol m^{-2} s^{-1}) of 18 °C light/12 °C dark. Heat shock treatments were given to air-dry seeds in a forced convection oven at 80 °C for 30 min and 115 °C for 5 min, treatments demonstrated to effectively break dormancy in 'hard-seeded' species (Keeley 1994).

Smoke treatments were applied to dry seeds in a large sealed chamber with smoke, generated by combustion of the chaparral shrub *Adenostoma fasciculatum* foliage on a hot plate. This species was readily available and previous studies have demonstrated that charred wood or smoke derived from a wide range of native and non-native species in both California and South Africa is equally effective in triggering germination (Keeley & Pizzorno 1987; Baxter et al. 1995; Keeley unpublished data); indeed, commercially available 'liquid-smoke' used for food-flavouring is equally effective (Baldwin et al. 1994; Jäger et al. 1996). Smoke was funneled into a hose attached to the lid of the chamber and smoke was drawn in by a vacuum at the opposite end of the lid. After 1 min filling, seeds on filter paper in open dishes at ambient temperature were incubated in smoke for a further 5 min. Charred wood treatments received 0.5 g of charred *Adenostoma* wood ground (to pass a 2 mm sieve) and an additional 1 ml water.

For the South African species, all experiments were repeated on a complete set ($n = 3$ replicates) maintained in the dark; in the same incubators but enclosed in multiple layers of black plastic. Germination of dark treated seeds was recorded under a green light (< 0.05 μmol m^{-2} s^{-1}). Air-dry seed weights of room-stored seeds were determined on all but 6 species, which were omitted due to insufficient seed.

Germination experiments were analyzed with 1-way ANOVA (fixed effects) on arc-sine transformed data for each species separately. Growth-form distribution was examined by testing the null hypothesis of random association using χ^2 calculated from contingency tables.

Results

Californian chaparral

The range of germination responses for Californian species is illustrated in Figure 1 and for all species there was a highly significant treatment effect ($P < 0.001$). The two species with non-refractory seeds (*Zygadenus fremontii* and *Calochortus splendens*) were inhibited by the 115 °C treatment, which was apparently lethal as evident from the fact that these seeds rotted. The other four species with deeply dormant seeds were stimulated by either heat-shock or chemicals from smoke or charred wood, but not both heat and smoke/charred wood. The two species responding to charred wood also responded similarly to smoke, although commonly smoke was more effective.

Based on these and published data (Keeley 1991) the responses by growth-form for chaparral are summarized in Table 1. In this community the type of germination behaviour is not randomly associated with growth-form, indicated by the highly significant χ^2. None of the geophytes tested had fire-stimulated germination, although some may have been stimulated by cold stratification. All growth- forms also had a sizable number of species with non-refractory seeds, however, the majority of shrubs (phanerophytes) and annuals (therophytes) had dormant seed banks that were triggered by either heat-shock or chemicals from charred wood and smoke. Although the selection of species does not represent a rigorously controlled random selection, it is believed that these patterns provide a relatively accurate picture of germination responses for chaparral communities.

Table 1. Growth form distribution of seed germination mode in Californian chaparral and coastal sage scrub ($\chi^2 = 71.2$, $P < 0.001$). Based on Figure 1 and Keeley (1991). Raunkiar growth form equivalents in parentheses.

	Non-refractory	Heat-shock	Smoke or charred wood
Shrubs/trees (phanerophytes)	18	32	12
Subshrubs/suffrutescents (chamaephytes)	7	2	2
Herbaceous perennials (hemicryptophytes)	10	1	5
Geophytes (cryptophytes)	18	0	0
Annuals (therophytes)	17	6	26

South African fynbos

The range of responses from South African fynbos was remarkably similar in that many species lacked fire-stimulated germination (Figure 2) and postfire recruiting species had germination stimulated by either heat-shock (Figure 3) or chemicals from charred wood or smoke (Figure 4). In this study over 100 species were tested, but only the 57 species which had at least 20% germination are listed by germination response in Appendix I. Other species will not be discussed here since it is unknown whether poor germination was due to deep dormancy or low viability. The majority (75%) of the 57 fynbos species reported were light neutral. Of the remaining 25% (e.g., Figures 5 and 6) there was no significant association of light response with either growth-form or presence of fire-stimulated germination ($P > 0.05$, $n = 57$ with 2-way ANOVA).

The distribution of germination response by growth-form is summarized in Table 2 and shows a highly significant departure from a random distribution of growth-form and germination behaviour. Comparison of California and South Africa (Tables 1 and 2) reveals marked similarity in that geophytes almost entirely lacked fire-stimulated germination, whereas the majority of annuals in both regions were chemically stimulated by smoke/charred wood. In both regions the shrub flora included a substantial number of species with non-refractory germination as well as species with heat-shock and/or chemically induced germination.

One notable difference between regions is the general lack of serotinous species in chaparral relative to
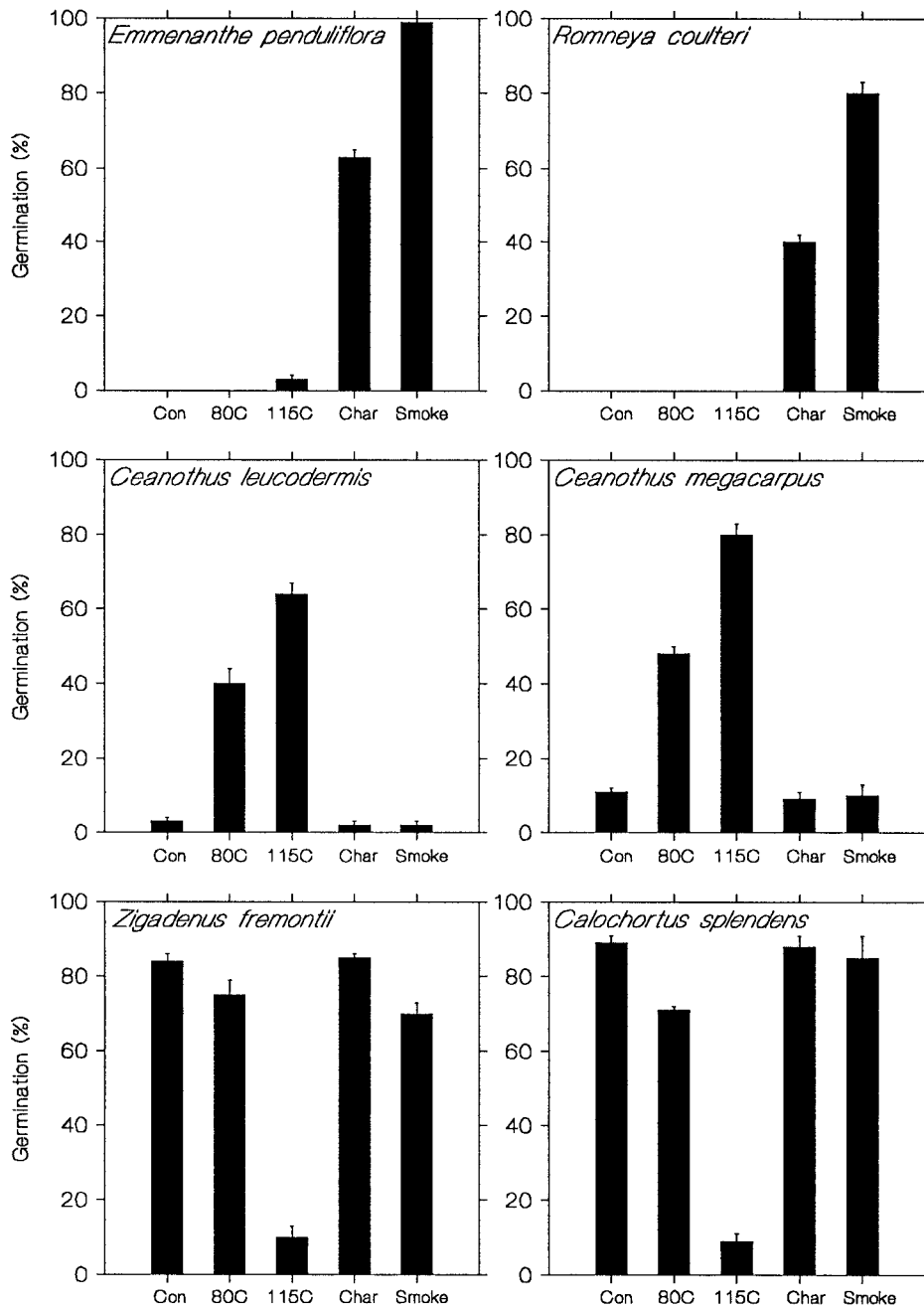
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Figure 1. Germination response to control (Con), or pre-incubation heat-shock treatments of 80 °C for 30 min or 115 °C for 5 min, or pre-incubation smoke treatment or incubation with powdered charred wood (Char) ($n = 3$, error bars = S.E.) for Californian chaparral species. *Emmenanthe* = annual, *Romneya* = suffrutescent, *Ceanothus* spp. = shrubs, *Zygadenus* and *Calochortus* = geophytes.

fynbos (Keeley 1992). If the South African woody flora is separated into serotinous and non-serotinous species, there is further evidence of non-random distribution of germination response; all serotinous species tested (*Widdringtonia nodiflora, Syncarpha eximium, Aulax umbellatum,* and *Leucadendron salicifolium*), distributed in three families, had non-refractory seeds.
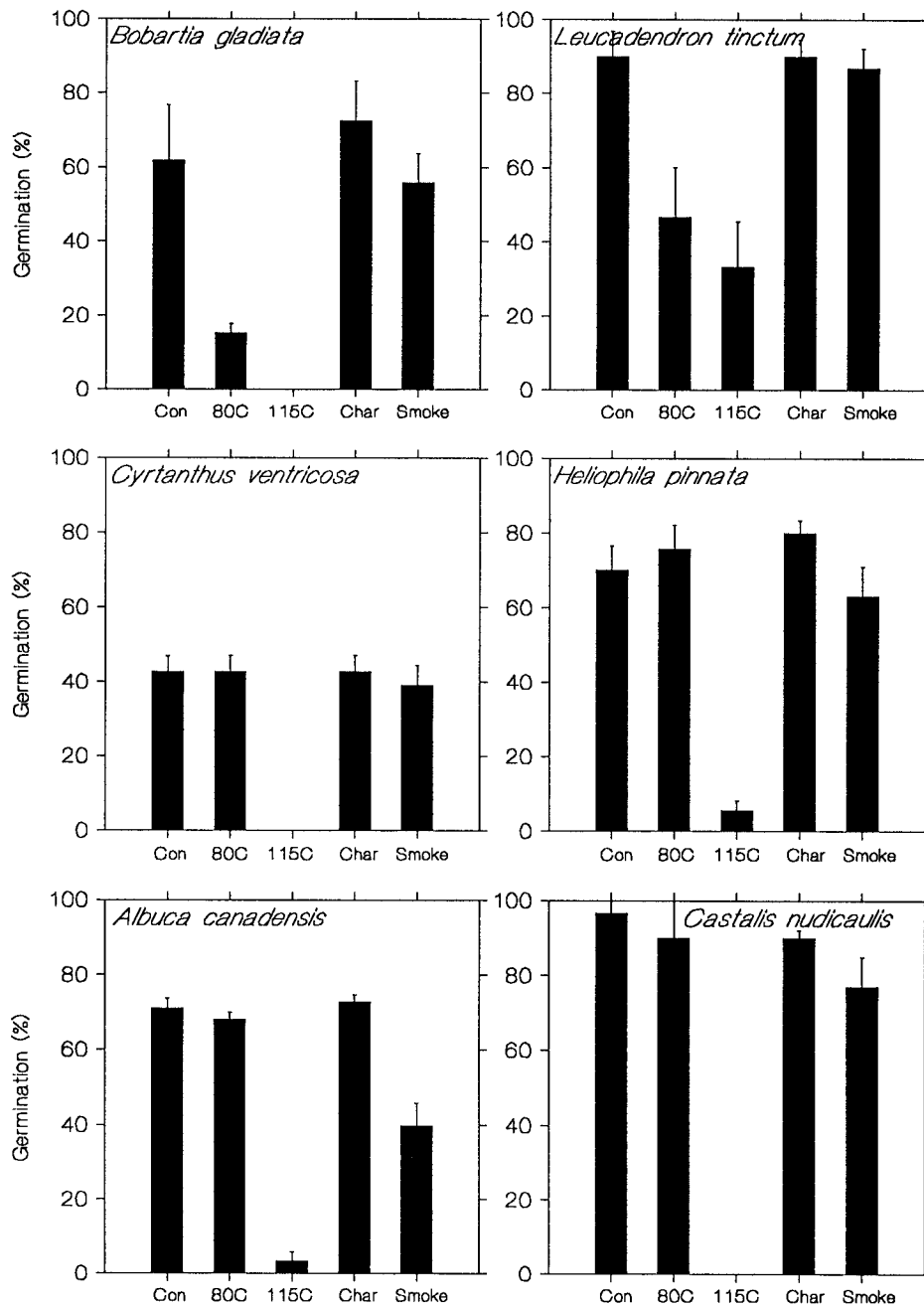
Figure 2. Germination response of South African fynbos species with non-refractory seeds (details in Figure 1 legend, growth forms designated in Appendix I).

In the fynbos, seed mass was significantly associated with growth-form ($P < 0.05$) but not with germination response ($P > 0.05$); annuals had the lightest seeds ($X = 0.2$ mg, S.D. = 0.3, $n = 16$), geophytes intermediate ($X = 1.9$ mg, S.D. = 3.3, $n = 12$), and shrubs and trees the heaviest ($X = 3.5$ mg, S.D. = 0.8, $n = 12$).

Table 2. Growth form distribution of seed germination mode in South African fynbos ($\chi^2 = 41.8$, $P < 0.001$). Based on Appendix I.

	Non-refractory	Heat-shock	Smoke or charred wood
Shrubs/trees (phanerophytes)	8	1	4
Subshrubs/suffrutescents (chamaephytes)	1	5	2
Herbaceous perennials (hemicryptophytes)	4	1	4
Geophytes (cryptophytes)	11	0	1
Annuals (therophytes)	1	1	14

Discussion

Convergent evolution is a theory which predicts that given similar environments, natural selection will drive the evolution of structural and functional similarities between organisms. In the case of chaparral and fynbos, it is not only the mediterranean-climate that links these two regions but the highly predictable fire regime. In both regions, fires occur at intervals on the order of decades (Keeley 1982; Brown et al. 1991) providing establishment opportunities for plants with diverse fire-stimulated reproductive behaviour. We conclude that similar germination responses, which includes both heat shock and chemicals from charred wood/smoke, plus the non-random interaction of germination response and growth form, supports the theory of convergent evolution. However we also recognize the additional role of phylogenetic effects, which in these systems remains to be determined.

Smoke & charred wood-stimulated germination

Charred wood induced germination, in the absence of any heating, was first documented in chaparral seeds (Wicklow 1977; Jones & Schlesinger 1980; Keeley et al. 1985) and later extended to fynbos species (Keeley 1992; Brown 1993b). Later, smoke-induced germination was documented for fynbos (de Lange & Boucher 1990, 1993; Brown 1993a; Brown et al. 1993) and has now been demonstrated for chaparral (Figure 1, Keeley & Fotheringham 1997a). It is evident that species responding to charred wood also respond to smoke (Figures 1 and 4, also Brown 1993b), suggesting per-

haps similar chemicals may be involved. This is supported also by the observation that water extracts of both charred wood and smoke are equally effective in triggering germination (de Lange & Boucher 1993; Brown 1993a; Baldwin et al. 1994; van Staden et al. 1995), as well as vapors from charred wood or smoke adsorbed on to soil particles (Keeley & Fotheringham 1997b). Therefore the term smoke-stimulated will be used to include both that and charred wood-stimulated germination.

The precise mechanism(s) behind smoke-induced germination is unknown, but differs from heat-stimulated germination in important aspects. The latter species are 'hard-seeded' and germination is triggered by the induction of imbibition. Detailed studies of smoke-stimulated seeds from six plant families in California chaparral, revealed that dormant seeds lacked a water-impermeable testa and therefore germination was not induced by the induction of imbibition (Keeley & Fotheringham 1997b). Such studies have yet to be done on fynbos species.

Despite extensive studies (Baldwin et al. 1994; van Staden et al. 1995), the active component of smoke/charred wood has remained elusive. Recently Keeley & Fotheringham (1997a) have demonstrated that nitrogen oxides, at concentrations present in smoke, can induce complete germination of deeply dormant seeds of the chaparral annual *Emmenanthe penduliflora,* in a manner similar to smoke (Figure 1). This could explain why species from fire-free habitats respond to smoke (van Staden et al. 1995; Pierce et al. 1995), since nitrogen oxides are generated by biogenic processes in many soils (Anderson et al. 1988). Possibly the cue selected to trigger postfire germination has been selected to time germination to other, perhaps seasonal changes, in the fire-free habitats studied by Pierce et al. (1995).

It appears that the smoke-response is phylogenetically widespread in fynbos (Figure 4, Appendix I; also, Brown 1993a; Brown et al. 1993), chaparral (Keeley & Fotheringham 1997b) and Western Australian communities (Dixon et al. 1995). In California it is most extensively represented in the Hydrophyllaceae, Papaveraceae and Scrophulariaceae. In fynbos only the last of these three families is represented in smoke-stimulated species (Appendix I), rather the same germination behaviour is present in Southern Hemisphere endemic families such as Restionaceae, Proteaceae and Penaeaceae (Brown 1993a; Brown et al. 1995; Appendix I).
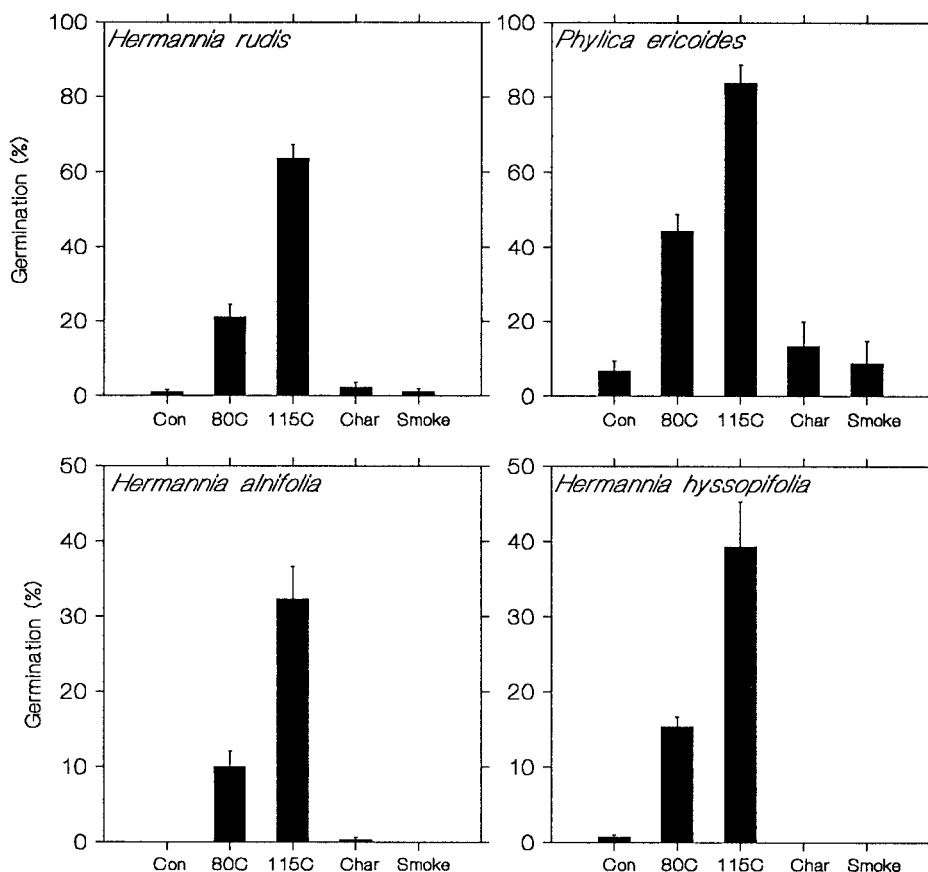
Figure 3. Germination response of fynbos species with heat-shock stimulated seeds (details in Figure 1 legend, growth forms designated in Appendix I).

We hypothesize that smoke/charred wood-induced germination has evolved independently in different lineages on both continents and consider this germination response to be an example of evolutionary convergence. At this point we lack sufficient phylogenetic information to precisely evaluate the degree of homology between species and acknowledge that this idea requires more rigorous testing (e.g., Pagel 1994; Losos 1996).

Heat shock-stimulated germination

Heat shock-stimulated germination is common in both Californian chaparral and South African fynbos, but in contrast to smoke-stimulated germination, there is a much stronger phylogenetic component. A large number of heat-stimulated species, in both California and South Africa are in the Fabaceae (Jeffrey et al. 1988; Keeley 1994), and this family has many species with heat-stimulated germination in Western Australia (Bell et al. 1993), and other parts of the world (Quinlivan 1971). Other families include the Rhamnaceae, which has such species in both chaparral (*Ceanothus*, Figure 1) and fynbos (*Phylica*, Figure 3; also Kilian & Cowling 1972) and the Sterculiaceae with *Fremontodendron* in California (Keeley 1991; Young & Young 1992) and *Hermannia* in South Africa (Figure 3). Heat shock-stimulated germination is known as well from more narrowly distributed lineages in both regions (Musil & de Witt 1991; Keeley 1994).

Heat-stimulated germination in similar lineages suggests a stronger role for phylogeny, but in order to rule out convergence. a more thorough phylogenetic analysis would be required to determine if this germination behaviour represents a single unique event in each lineage. In support of a strong role for phylogeny is the observation that heat-stimulated germination is tied to structural changes in localized regions of the palis-
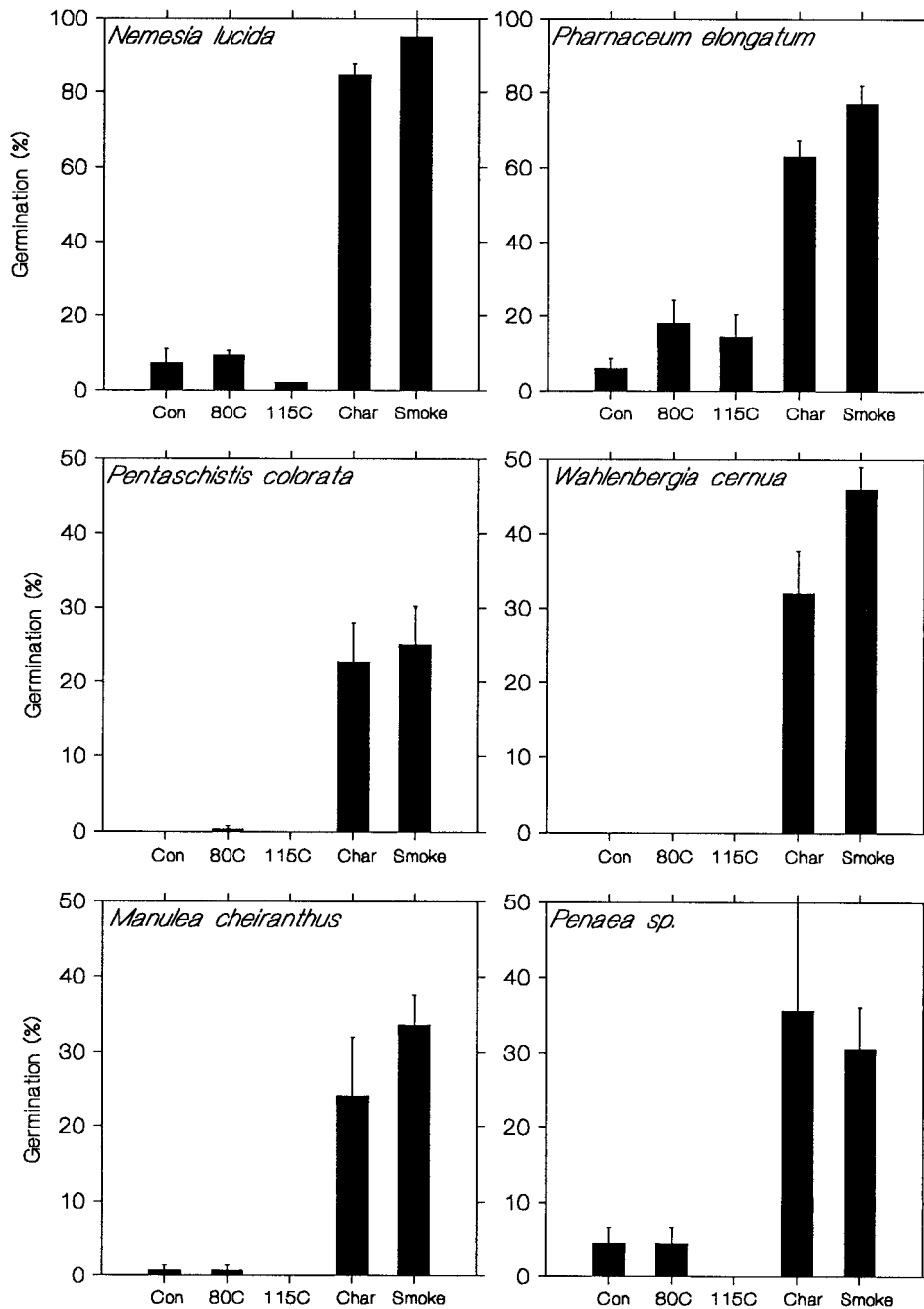
Figure 4. Germination response of South African fynbos species with charred wood and smoke stimulated seeds (details in Figure 1 legend, growth forms designated in Appendix I).

ade layer of the seed coat (Ballard 1973; Egley 1989). Dormant seeds are generally 'hard-seeded' meaning they fail to imbibe water unless the seed coat barrier is broken by heat or other types of scarification. These and other anatomical characteristics of seeds are evol-

utionarily conservative traits, commonly characteristic of entire families (Martin 1946; Corner 1976), and familial similarities in germination response are correlated with similarities in anatomy (Atwater 1980). These patterns suggest that heat-stimulated germina-
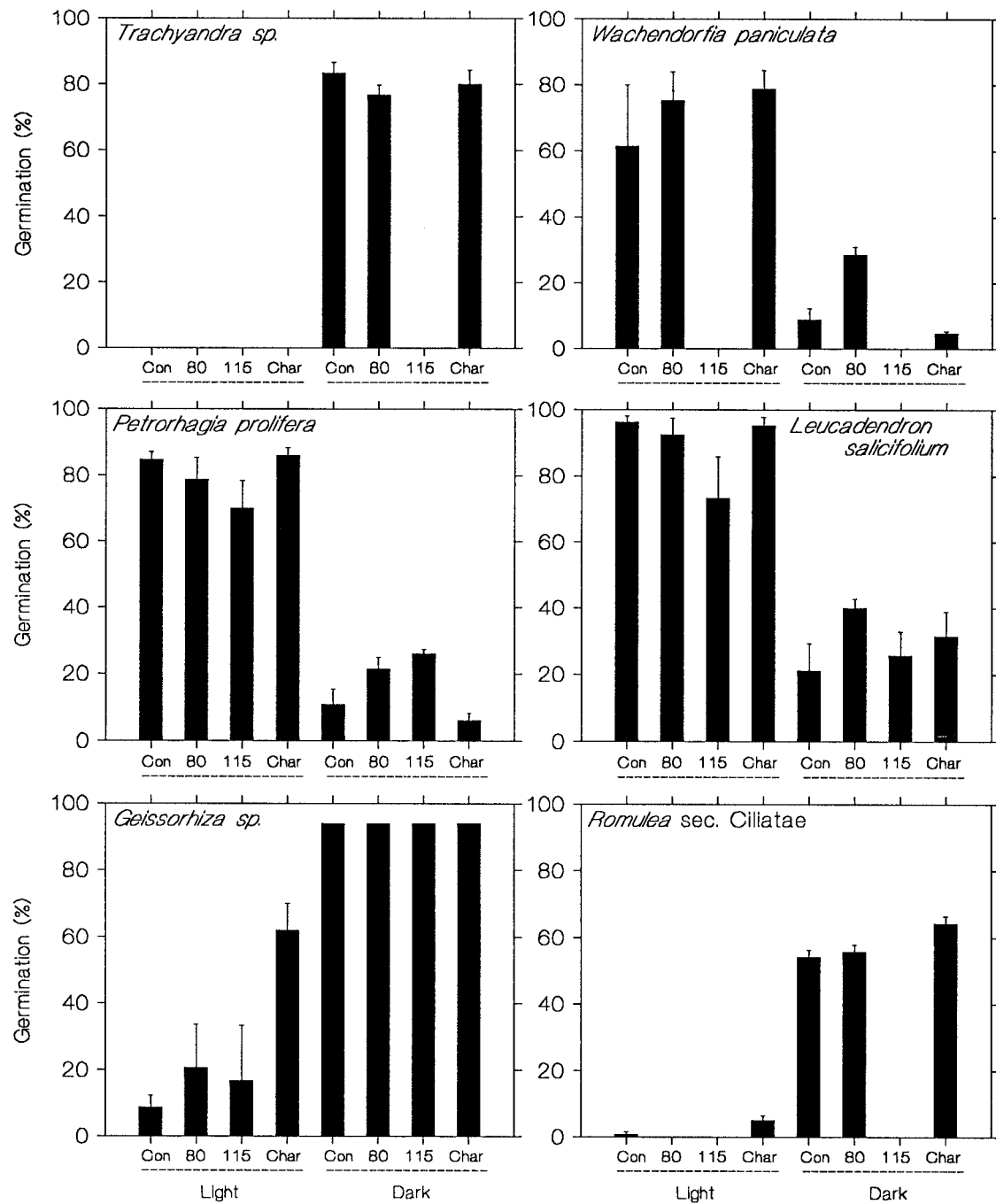
Figure 5. Germination response to light and dark for fynbos species with non-refractory seeds (details in Figure 1 legend, growth forms designated in Appendix I).

tion in both regions represents homologous evolution in some families. However, while seed coat characteristics giving rise to heat-stimulated germination may be homologous, selective forces maintaining this struc-

tural characteristic may have varied through time, as suggested by the variety of other environmental factors that can induce germination of hard-seeds (Quinlivan 1971).
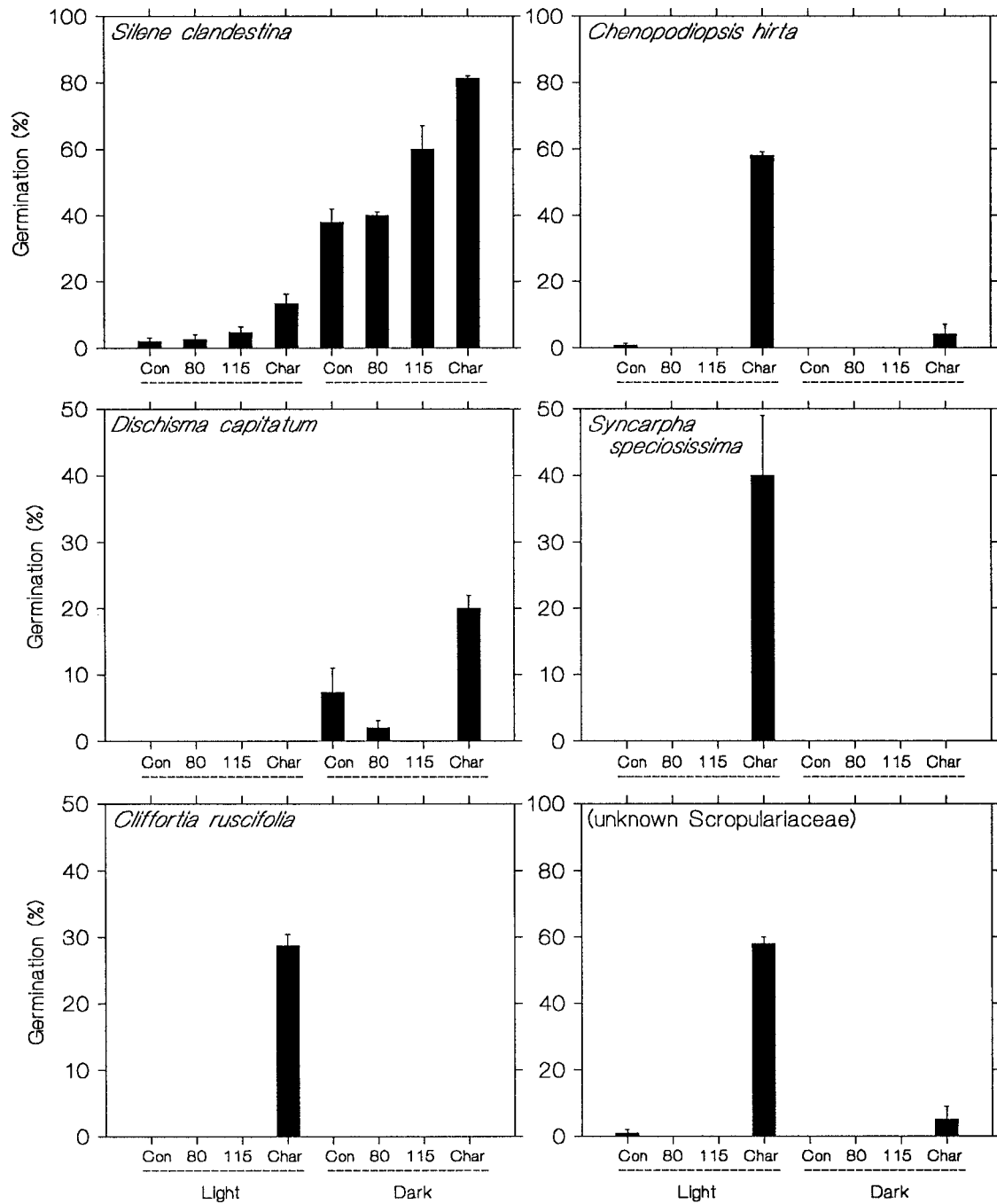
Figure 6. Germination response to light and dark for fynbos species with charred wood/smoke stimulated germination (details in Figure 1 legend, growth forms designated in Appendix I).

Germination and growth form

The non-random distribution of germination response is most evident in the widespread occurrence of non-refractory seeds in geophytes (Tables 1 and 2). The lack of fire-related cues in these is interpreted as a consequence of a life cycle that, in the mediterranean-climate, is somewhat buffered from the impacts of

wildfires. Due to annual aboveground die-back (during the fire season) and deeply buried bulbs and corms, wildfires may have minimal impact on the survivorship of these populations. This growth form is widely distributed in all mediterranean-climate regions (Dafni et al. 1981; Rundel 1996), and generally such geophytes flower prolifically after fire and recruit seedlings in subsequent postfire years (Keeley & Keeley 1984; Bullock 1976; Le Maitre & Brown 1992; Keeley unpublished data). Thus, while seedling recruitment may be tied to fire, it does not require fire-related seed germination cues, although induction of flowering may be cued to smoke (Keeley 1993).

Geophytes with fire-stimulated flowering are not the only species with non-refractory germination. Serotinous species with fire-stimulated seed release from closed cones also have non-refractory seed germination in fynbos (Bond 1985) and in Northern Hemisphere species as well (Keeley & Zedler 1997). It is generally assumed that seeds of these species are in a quiescent state due to lack of adequate moisture. However, the lack of environmentally-imposed dormancy can not be entirely ruled out, as suggested by the observation that one of these serotinous species, *Leucadendron salicifolium*, responded positively to light (Figure 5).

In both regions a significant number of woody species are characterized by transient seed banks that apparently germinate without fire, but sometimes in response to seasonal events (e.g., Pierce & Moll 1994; Le Maitre & Midgely 1992; Keeley 1994). *Anthospermum spathulatum*, *Montinia caryophyllacea* and *Rhus tomentosa* are fynbos examples in our data set (Appendix I). Recruitment patterns in these species contrast sharply with the postfire recruitment that is so prominent in these mediterranean climate regions. Some such species respond to changes in light (e.g., *Petrorhagia prolifera*, Figure 5), perhaps induced by soil disturbance and in others, germination appears to be triggered by alternating temperatures (Brits 1987), but most have no special germination requirements (Keeley 1994).

Both regions are characterized by the majority of species having germination insensitive to light (Keeley 1991; and the present study). Another similarity is the distribution of seed mass; annuals in both regions have the lightest seeds and woody plants the heaviest seeds (Keeley 1991; and the present study). This pattern however, is characteristic of other ecosystems (e.g., Mazer 1989) and is perhaps allometrically tied to

growth form. In our systems seed mass is not obviously related to germination response.

Finally there is a group of species with refractory seeds where the cue(s) has still to be elucidated. Among these are many myrmecochorous species, including *Dendromecon rigida* in California (Keeley 1991) and species of *Hypodiscus, Willldenowia, Cannamois* in the Restionaceae in fynbos (Keeley & Bond unpublished data). Brits et al. (1993) have suggested that heat shock-stimulated germination in some myrmecochorous species in the Proteaceae is induced by desiccation, coupled with alternating temperatures which synchronize post-burn germination with seasonal events (Brits 1987). Recently it has been demonstrated for one strictly postfire-following chaparral species, *Dicentra chrysantha* (Fumariaceae), a combination of long-term outdoor soil storage, followed by brief smoke-treatment, is necessary to induce germination (Keeley & Fotheringham 1997b). It would appear that there are further germination cues yet to be investigated.

Acknowledgements

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Appendix

Appendix I. Species of South African fynbos used in experiments and summary of germination response. Listed are species in which > 20% germination was obtained. Statistically significant (P<0.05) enhancement with either heat-shock or smoke/charred wood is indicated. Nomenclature according to Bond and Goldblatt (1984) except where the B&G synonym appears in brackets. Raunkiar equivalents for growth form names are indicated in Tables 1 and 2.

South African	Growth form	Significant Stimulation	
		Heat-shock	Smoke or charred wood
Gymnospermae			
Cupressaceae			
Widdringtonia nodiflora	Tree	No	No
Angiospermae			
Monocotyledonae			
Amaryllidaceae			
Cyrtanthus ventricosa	Geophyte	No	No
Asphodelaceae			
Trachyandra sp.	Geophyte	No	No
Cyperaceae			
Isolepis incomptula	Annual	Yes	No
Haemodoraceae			
Wachendorfia paniculata	Geophyte	No	No
Hyacinthaceae			
Albuca canadensis	Geophyte	No	No
Albuca sp.	Geophyte	No	No
Iridaceae			
Bobartia gladiata	Geophyte	No	No
Geissorhiza sp.	Geophyte	No	No
Moraea sp.	Geophyte	No	No
Romulea section Ciliata	Geophyte	No	No
Poaceae			
Pentaschistis colorata	Herb. perennial	No	Yes
Dicotyledonae			
Aizoaceae			
Pharnaceum elongatum	Annual	No	Yes
Anacardiaceae			
Rhus tomentosa	Shrub	No	No
Asteraceae			
Castalis nudicaulis	Geophyte	No	No
Eriocephalus africanus	Shrub	No	Yes
Helichrysum tinctum	Herb. perennial	No	Yes
Helipterum exinum	Suffrutescent	No	No
Othonna bulbosa	Geophyte	No	No
O. parviflora	Shrub	No	Yes
Syncarpha [*Helipterum*] *speciosissima*	Herb. perennial	No	Yes
Ursinia paleacea	Suffrutescent	No	Yes

South African	Growth form	Significant Stimulation	
		Heat-shock	Smoke or charred wood
Brassicaceae			
Heliophila macowiana	Annual	No	No
H. pinnata	Annual	Yes	Yes
H. sp.	Annual	No	Yes
Campanulaceae			
Cyphia incisa	Herb. perennial	No	No
Lobelia coronopifolia	Suffrutescent	No	Yes
Wahlenbergia cernua	Annual	No	Yes
Caryophyllaceae			
Dinanthus sp.	Herb. perennial	No	No
Petrorhagia [*Dianthus*] *prolifera*	Herb. perennial	No	No
Silene clandestina	*Annual	No	Yes
Crassulaceae			
Crassula capensis	Geophyte	No	Yes
Crassula sp.	Herb. perennial	Yes	No
Geraniaceae			
Pelargonium sp.	Herb. perennial	No	No
Montinuaceae			
Montinia caryophyllaceae	Shrub	No	No
Penaeaceae			
Penaea sp.	Shrub	No	Yes
Proteaceae			
Aulax umbellatum	Shrub	No	No
Leucadendron salicifolium	Shrub	No	No
L tinctum	Shrub	No	No
Rhamnaceae			
Phylica ericoides	Shrub	Yes	No
Roseaceae			
Cliffortia ruscifolia	Shrub	No	Yes
Rubiaceae			
Anthospermum spathulatum	Shrub	No	No
Scrophulariaceae			
Chenopodiopsis chenopodioides	Annual	No	Yes
C. hirta	Annual	No	Yes
Dischisma capitatum	Annual	No	Yes
Hebenstreitia paarlensis	Herb. perennial	No	Yes
Manulea cheiranthus	Annual	No	Yes
Nemesia versicolor	Annual	No	Yes
N. lucida	Annual	No	Yes
Selago sp.	Annual	No	Yes
Zaluzianskya sp.	Annual	No	Yes
unknown sp.	Annual	No	Yes
Sterculiaceae			
Hermannia alnifolia	Suffrutescent	Yes	No
H. hyssopifolia	Suffrutescent	Yes	No
H. rudis	Suffrutescent	Yes	No
H. sabra	Suffrutescent	Yes	No
H. sp.	Suffrutescent	Yes	No

*Non-native.