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The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants

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Abstract Exposure of dormant seed to cold smoke derived from burnt native vegetation had a positive influence on germination in one or more seed provenances in 45 out of 94 species of native Western Australian plants that are normally hard to germinate. When tested under controlled conditions some species showed earlier germination in smoke treatments than controls; in others smoke-treated seeds continued to germinate for several weeks after controls had achieved full germination. In the remainder, treated and control seeds germinated to similar time schedules. A group of 23 species which responded positively had previously been recorded as extremely difficult or impossible to germinate using conventional techniques. These included members of the genera *Geleznowia* (Rutaceae), *Hibbertia* (Dilleniaceae), *Stirlingia* (Proteaceae), *Verticordia* (Myrtaceae), *Actinostrobus* (Cupressaceae) and *Pimelea* (Thymelaeaceae). Both large- and small-seeded species were encountered amongst the positively responding taxa, which encompassed representatives of 15 families and 26 genera of dicotyledons, 5 families and 8 genera of monocotyledons and the gymnosperm *Actinostrobus acuminatus*. Sowing seeds on smoke-fumigated filter papers or watering with aqueous eluates of smoke elicited similar degrees of stimulation of germination, as did exposure to gaseous smoke in a readily germinating species *Anigozanthos manglesii* (Haemodoraceae) and the normally intractable species *Lysinema ciliatum* (Epacridaceae). Exposing recently burnt and unburnt natural bushland sites to smoke, smoked water or smoked dry sand elicited a significant germination response in 15 species. Over one third of the species sampled in the burnt site exhibited germination additional to that caused by the fire. Data are discussed in relation to previous germination studies on Australian and other taxa.

Key words Fire · Smoke · Germination · Seed bank

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Introduction

Fire has undoubtedly played a significant role in the evolution of the Australian flora at least since the onset of arid conditions in the mid-Tertiary (Kemp 1981; Walsh 1990), and may be held responsible for moulding the development of a plethora of divergent and convergent structures and life forms within disparate taxonomic groupings (Bell et al. 1984; Pate et al. 1985; Pate 1993). Burning of habitats is also the most important trigger of natural germination events, whether through direct effects of heat in breaking seed-coat-imposed dormancy or fostering release of canopy-stored seed in serotinous species (Fordham 1968; Gill 1981; Bradstock 1991; Lamont et al. 1991; Bell et al. 1993). Nevertheless, germination of many of such supposedly fire-responsive taxa has proved difficult or impossible under glasshouse or laboratory conditions without recourse to excised embryo culture (Meney and Dixon 1988; Meney et al. 1994) or special pretreatments such as application of hormones (Bell et al. 1993).

A relatively small number of investigations has indicated that products of fire rather than direct effects of heat may stimulate germination. Thus, water-soluble products of charred, but not ashed, vegetation have been shown to be promotive to germination of certain native Californian taxa (Keeley et al. 1985; Keeley and Pizzorno 1986; Keeley 1991), and smoke produced from combustion of vegetation has been found to be similarly stimulatory to habitat germination (de Lange

and Boucher 1990) or ex situ germination (Brown 1993) of South African species. Ammonia has been specifically implicated in the latter regard (van de Venter and Esterhuizen 1988).

This study demonstrates a promotive role of cool gaseous smoke and derived adsorbed or eluted combustion products in ex situ (glasshouse) and in situ (habitat) germination of seeds of a range of Western Australian native species. The techniques developed are viewed as a means of opening up new opportunities for horticultural development of species previously found to be recalcitrant in establishment from seed, and for evaluating soil seed bank dynamics in fire prone environments.

Material and methods

Glasshouse germination studies

Seeds of 94 species (Table 1) from 30 families of native Western Australian plants were chosen on the basis of previously having shown low, zero or erratic germination under laboratory testing or in the field situation. An easy-to-germinate species, *Anigozanthos manglesii*, was also included in the treatments to test for toxic or negative effects of smoke on germination.

Seeds were counted and/or weighed to obtain test replicates of equal or near-equal number. Seed number per replicate for most species was 100–300 but, where seed of a species was limited, only 30 seeds per replicate were used. Each assay included two control and three treatment replicates, sown in 14×8.5 cm plastic punnets containing a pasteurised soil mix of composted hardwood fines, hardwood sawdust and quartz sand in the ratio 1:3:2. No fertilizer was added. Seeds were spread evenly over the surface of the soil and covered with a layer of sieved quartz sand of a depth approximately equal to the diameter of the seed.

Smoke treatments

Sown punnets for cool smoke treatment were placed into a sealed, steel-framed plastic tent measuring $2 \times 1.5 \times 1$ m. Smoke was generated in a large metal drum by slow, controlled combustion of a mixture of fresh and dry plant material collected from native *Banksia-Eucalyptus* woodland sites near Perth. The drum was fitted with an inlet through which air was pumped at the rate of 30–50 l/min, and the resulting smoke passed into a 1.5 m water-cooled galvanised pipe and then through a 2-m length of flexible plastic hosing before passage into the fumigation tent. Soil surfaces of the punnets assumed a brown colouration during smoking and emitted a distinctive smoked odour which lasted for 6–8 days.

After 90 min in the smoke tent, punnets were transferred to the glasshouse and thereafter watered with rainwater as required. Emerging seedlings were scored weekly and observations continued until no further germination events occurred.

Testing of seed quality

Random samples of 30 seeds were selected from each seed lot of each species and sectioned by hand to determine presence or absence of endosperm or embryo, and to check for any abnormalities or symptoms of decay which one would normally associate with inviable seed. Germination values were then expressed on the basis of proportions of apparently healthy germinable seed in each control and treatment of a species. Percentage germination values were arcsine transformed prior to statistical analysis. *t*-tests were performed for final percentage germination values of the control and smoked replicates.

Studies using smoked filter papers or eluates of smoke

Smoked filter papers were produced by hanging dry, 9 cm Whatman Seed Testing papers (no. 182) in the fumigation tent and exposing to smoke for 90 min. "Smoked water" was produced by bubbling cooled smoke (generated as described above) through a 20 l container of distilled water for a period of 90 min.

Seeds of two species (*Anigozanthos manglesii* and *Lysinema ciliatum*) which had responded positively to bulk smoking of seed punnets in the tent were weighed or counted into five lots, surface sterilised in 1% sodium hypochlorite for 3–4 min, and washed in several changes of distilled water before transfer onto plastic containers containing the dry smoked or unsmoked (control) Whatman Seed Testing papers. Each treatment was replicated 3 times. In a parallel study conducted in a similar manner, filter papers were used which had been previously moistened with smoked water (generated as described above) or distilled water (control). All containers were incubated in the dark at 21° C and germination (radicle emergence) events scored after 3 weeks. Percentage germination values were again expressed on the basis of "viable" seed, and arcsine transformed before being subjected to one-way analysis of variance.

Habitat germination studies

Treatments were undertaken in February 1993 at sites located in natural *Banksia* woodland, 50 km north of Perth, Western Australia. Juxtaposed unburnt and burnt areas separated by a narrow track were selected for study. Both areas were considered representative of the vegetation of the locality and neither had been burnt for 8 years prior to a prescribed fire (November 1992) applied to the burnt area immediately prior to this investigation.

Smoke fumigation treatments were applied for 30, 60 and 90 min in unburnt sites, and for 60 min in burnt sites, using the same smoke-generating apparatus and fumigation tent as described above. Each randomly selected smoked or control area was 2×1.5 m in area and comprised uniformly vegetated areas of understorey vegetation in regions at least 1 m distant from the *Banksia* trees. In addition, smoked water (as prepared above), distilled water controls and smoked and unsmoked fine quartz dry sand were applied to each of 16 randomly selected 0.25 m^2 (unsmoked) quadrats in the unburnt site. The smoked sand was prepared by fumigating a 1-cm-thick layer of fine, dry quartz sand for 90 min in the same smoke fumigation tent utilised for the glasshouse germination experiments.

Germinants at the study site were collected and identified by comparison with nearby adult or juvenile plants. Germinants were scored at the end of spring, 8 months after treatment application. Total numbers of germinants were recorded for the 0.25 m^2 smoked sand, smoked water and control quadrat treatments. For the direct smoke fumigation treatments , sixteen 0.25 m^2 quadrats were randomly assigned within each 2×1.5 m treatment and control area, and subsequently assessed for the presence of seedlings. Results were analysed using one-way analysis of variance for treatments at the unburnt site. *t*-tests were performed between control and smoke treatments at the burnt site.

Results

Glasshouse germination studies

Of the 94 species (113 provenances) tested, 45 (49 provenances) responded positively to smoke fumigation (Fig. 1a, b). Among these positive species, 24

Table 1 Species studied in relation to effects of cold smoke on seed germination. Seed size and age of seed provenances examined are indicated. *Numbers in parentheses* following a specific epithet refer to number of seed provenances of a species tested and/or provenance identification (see also Fig. 1a, b): No germination was recorded in either control or treated replicates of species marked by *asterisks* (*n/a* not applicable)

Taxon	Seed size (mg)	Seed age (years)
Anthericaceae		
Agrostocrinum scabrum (R. Br.) Baillon*	5	<1
Chamaescilla corymbosa (R. Br.) F. Muell.	0.3	<1
Johnsonia lupulina R. Br.*	3	2
Sowerbaea multicaulis E. Pritzel in Diels.*	4	<1
Thysanotus multiflorus R. Br.	4	<1
Apiaceae		
Xanthosia huegelii (Benth.) Steudel*	0.7	2
Asteraceae		
Brachyloma preissii Sonder in Lehm., Pl. Preiss	10	<1
Chloanthaceae		
Lachnostachys eriobotrya (F. Muell.) Druce (1)	2	<1
(2)*	2	<1
Colchicaceae		
Burchardia umbellata R. Br.	1	1
Cupressaceae		
Actinostrobus acuminatus Parl.	3	<1
Cyperaceae		
Gahnia decomposita (R. Br.) Benth.*	0.4	4
Lepidosperma angustatum R. Br.*	n/a	<1
Lepidosperma gladiatum Labill.*	3	8
Dasypogonaceae		
Lomandra preissii (Endl.) Ewart*	40	<1
Dilleniaceae		
Hibbertia amplexicaulis Steudel	2	1
Hibbertia lasiopus Benth.	20	<1
Hibbertia mylnei Benth.*	2	<1
Hibbertia quadricolor Domin	20	<1
Droseraceae		
Drosera erythrorhiza Lindley*	0.2	2
Drosera macrantha Endl.*	0.05	1
Epacridaceae		
Andersonia involucrata Sonder*	0.3	2–3
Andersonia lehmanniana Sonder	0.2	1
Astroloma pallidum R. Br.*	6	<1
Conostephium pendulum Benth. in Endl.*	50	<1
Croninia kingiana (F. Muell.) J. Powell	10	2–3
Iridaceae		
Patersonia occidentalis R. Br. (1)	3	1
(2, 3)	3	<1
Lamiaceae		
Hemiandra pungens R. Br.	4	?
Malvaceae		
Alyogyne hakeifolia (Giord.) Alef.	4	9
Alyogyne huegelii (Endl.) Fryx.	7	4
Myrtaceae		
Actinodium cunninghamii Schauer*	n/a	10
Calytrix aurea Lindley*	5	7
Hypocalymma angustifolium Endl.	0.4	<1
Scholtzia laxiflora Benth.*	2	?
Verticordia densiflora Lindley	2	<1
Pittosporaceae		
Billardiera bicolor (Putterl.) E. M. Bennett	5	2
Poaceae		
Amphipogon turbinatus R. Br.	n/a	<1
Neurachne alopecuroidea R. Br.	3	<1
Proteaceae		
Conospermum huegelii R. Br. in Endl.*	5	7
Conospermum incurvum Lindley (1)	4	12
(2)	4	<1
Leucopogon capitellatus D. C.*	7	2–3
Leucopogon crassiflorus F. Muell.*	20	2–3
Leucopogon hirsutus Sonder in Lehm.*	5	2
Leucopogon obtectus Benth.*	50	2–3
Leucopogon parviflorus (Andrews) Lindley	10	2–3
Leucopogon propinquus R. Br.*	40	2–3
Leucopogon verticillatus R. Br. (1)*	8	2–3
(2, 3)*	8	<1
Lysinema ciliatum R. Br.	1	<1
Sphenotoma capitatum (R. Br.) Lindley	0.2	?
Styphelia aff *pulchella* (Stschegl.) Druce*	40	?
Styphelia tenuiflora Lindley (1)*	50	<1
(2)*	50	2–3
Euphorbiaceae		
Adriana quadripartita (Labill.) Gaudich.*	50	4
Adriana tomentosa Gaudich.*	70	9
Goodeniaceae		
Goodenia caerulea R. Br.*	0.8	<1
Lechenaultia biloba Lindley (1)*	1	15
(2,3)	1	1
Lechenaultia floribunda Benth. in Endl.	0.4	6
Lechenaultia formosa R. Br.	0.6	?
Lechenaultia macrantha Krause in Engl.	2	9
Scaevola calliptera Benth.	20	<1
Velleia rosea S. Moore*	3	?
Gyrostemonaceae		
Codonocarpus cotinifolius (Desf.) F. Muell.	2	8
Gyrostemon ramulosus Desf.	0.9	?
Haemodoraceae		
Anigozanthos bicolor Endl. in Lehm.	0.8	9
Anigozanthos humilis Lindley	0.5	10
Anigozanthos manglesii D. Don (1)	0.7	5
(2)	0.7	1
Conostylis neocymosa S. D. Hopper	0.6	<1
Conostylis setosa Lindley	0.5	1
Macropidia fuliginosa (Hook.) Druce (2)*	10	1
Rutaceae		
Geleznowia verrucosa Turcz. (1)	8	<1
(2)*	8	3
(3)	8	1
Phebalium anceps DC.*	2	4
Santalaceae		
Anthobolus foveolatus F. Muell.*	n/a	?
Choretrum glomeratum R. Br.*	30	3
Exocarpos sparteus R. Br. (1)*	20	<1
(2)	20	<1
Stackhousiaceae		
Stackhousia huegelii Endl.*	3	1
Stackhousia pubescens A. Rich	3	?
Triptercoccus brunonis Endl.*	1	<1
Sterculiaceae		
Rulingia platycalyx Benth.	0.8	?
Thomasia angustifolia Steudel in Lehm.	1	?
Thymelaeaceae		
Pimelea leucantha Diels.*	3	<1
Pimelea spectabilis Lindley (1)*	5	?
(2)	5	1
Pimelea sylvestris R. Br. (1)	2	<1
(2)	2	1
(3)*	2	<1

Table 1 (continued)

Taxon	Seed size (mg)	Seed age (years)	Taxon	Seed size (mg)	Seed age (years)
Proteaceae			Tremandraceae		
Conospermum stoechadis Endl.*	4	4	*Tetratheca hirsuta* Lindley	7	<1
Conospermum triplinervium R. Br.	4	<1	Violaceae		
Grevillea wilsonii Cunn.	50	<1	*Hybanthus floribundus* (Lindley) F. Muell.	n/a	?
Persoonia longifolia R. Br.*	30	?			
Petrophile drummondii Meissner	30	<1			
Stirlingia latifolia (R. Br.) Steudel (1)	6	<1			
(2)*	6	<1			
Synaphea acutiloba Meissner in Lehm.*	10	?			
Synaphea petiolaris R. Br.*	10	<1			
Rhamnaceae					
Siegfriedia darwinioides C. Gardner	1	?			
Spyridium globulosum (Labill.) Benth.	2	?			
Rutaceae					
Boronia fastigiata Bartling*	2	1			
Eriostemon spicatus A. Rich (1)	1	9			
(2)	1	1			

(30 provenances) exhibited germination only in the smoke- treated replicates (Fig. 1b). Smoked replicates of *Lachnostachys eriobotrya* and *Amphipogon turbinatus* also produced germinants, although both of these species had been previously rated as containing virtually no viable seed. A further 7 species (*Alyogyne hakeifolia, A. huegelii, Brachyloma preissii, Croninia kingiana, Hemiandra pungens, Hybanthus floribundus, Thomasia angustifolia*) had appreciably greater germination after fumigation but the smoke effects proved not to be statistically significant. Positive responses to smoke were observed across a wide variety of life forms including monocotyledons and dicotyledons, herbaceous perennials, woody shrubs, fire ephemerals, seeder (fire-sensitive) and resprouter (fire-tolerant) species. Of the positively responding species, 77% had seeds in the mass range 0–4 mg and 11.5% in each of the 5–19 mg and 20–50 mg ranges. This compares with respective values of 60%, 22% and 18% within the same ranges of mass for the whole study sample of 94 species (Table 1). Further, within the Epacridaceae, only small-seeded (< 1 mg), as opposed to large-seeded or woody-fruited taxa, responded positively (Table 1).

Of the 50 species (54 provenances) not responding to smoke, 7 had no evidence of healthy endosperm, 12 had seed older than 3 years and 9 had "viability" of less than 10%. Among seven species from this smoke-unresponsive category, seeds from a second provenance of the species responded positively to smoke (viz. in the species *Conospermum incurvum, Geleznowia verrucosa, Lachnostachys eriobotrya, Lechenaultia biloba, Pimelea spectabilis, P. sylvestris* and *Stirlingia latifolia*: see Table 1). In each of these cases the unresponsive conspecific provenance comprised old seed of doubtful quality or low "viability".

When the number of germination events was plotted against time (Fig. 2), four distinct response patterns were observed amongst the positively responding species:

A. Control and smoked replicates attained final germinant numbers more or less simultaneously within 3 weeks of the first recorded germination event. This response type was shown by *Conostylis neocymosa* (Fig. 2a), *C. setosa, Anigozanthos manglesii, A. humilis,* and *Neurachne alopecuroidea.*

B. First germination events occurred noticeably earlier in smoked treatments than in controls. Species in this category were *Grevillea wilsonii* (Fig. 2b), *Actinostrobus acuminatus, Andersonia lehmanniana, Hypocalymma angustifolium, Petrophile drummondii* and *Stackhousia pubescens.*

C. Control germination was limited to 1 week, whereas smoked treatments continued to germinate over several successive weeks. Species showing this response were *Siegfriedia darwinioidies* (Fig. 2c), *Andersonia lehmanniana, Anigozanthos bicolor* and *Rulingia platycalyx.*

D. Differences between control and treatments became apparent only after several weeks. Two species typifying this class of response were *Spyridium globulosum* (Fig. 2d) and *Tetratheca hirsuta.*

Responses to smoked filter paper and smoked water

Seeds of *Anigozanthos manglesii* responded positively ($P < 0.05$) to both smoked paper or smoked water treatments, both of these treatments showing significantly greater germinant numbers than either their respective controls (distilled water) or the treatment involving combined smoked water plus smoked paper (Fig. 3a).

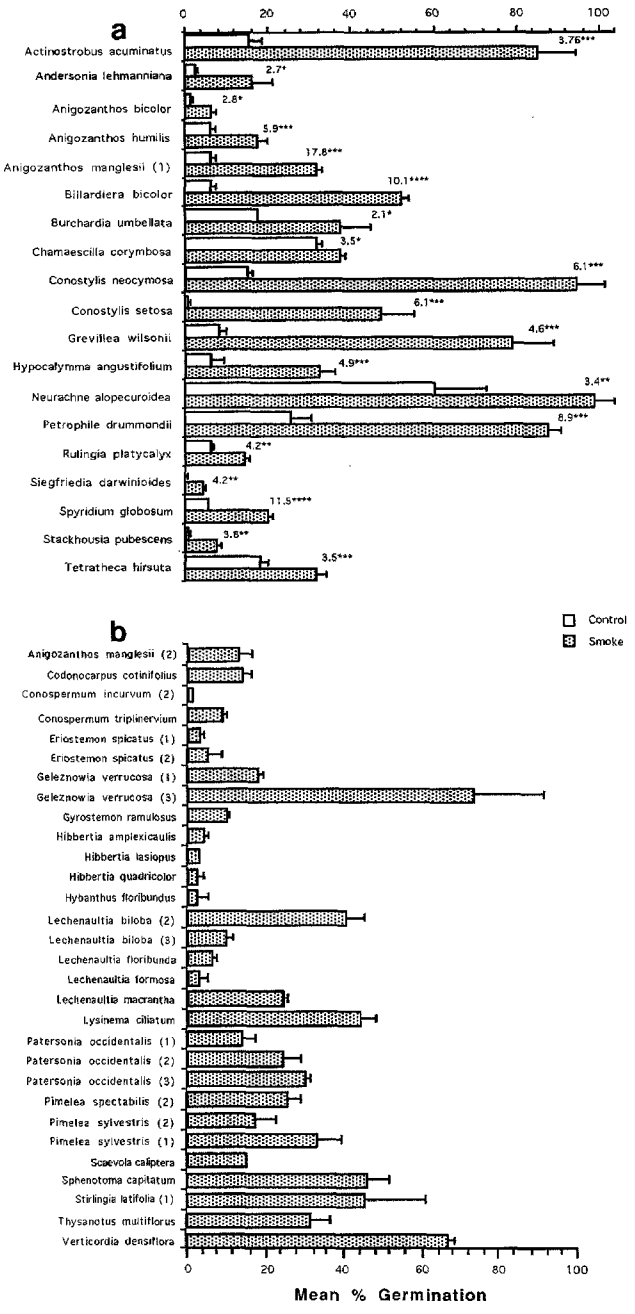

Fig. 1a, b Glasshouse germination studies. **a** Species for which there was a significant difference in germination between control and smoked replicates (*open* and *closed boxes*, respectively). Figures represent mean germination percentages (± standard error) of the viable (i.e. with endosperm) seeds within test replicates. Germination percentages were subjected to arcsine transformation and results were analysed using *t*-tests. *t*-values are shown and levels of significance indicated thus: $*P < 0.05$; $**P < 0.025$; $***P < 0.01$; $****P < 0.001$. *Numbers in parentheses* following a specific epithet refer to provenances responding positively (see also Table 1). **b** Species in which there was a positive response (3–72% germination) in smoked replicates (*closed boxes*) but zero germination in controls. Figures represent mean germination percentages (± standard error) of the viable (i.e. with endosperm) seeds within test replicates. *Numbers in parentheses* following a specific epithet refer to provenances responding in the stated manner (see also Table 1)

In the case of *Lysinema ciliatum*, germination responses of treatments were significantly different from one another. The best response was from smoked paper (Fig. 3b), but all forms of smoke treatment elicited much greater germination than the control.

Habitat germination studies

Germinants of 30 species were identified in the treatment quadrats of burnt and unburnt regions of the study site, and 15 of these were present in sufficient number for statistical analysis of the data. In each case germination was positively influenced by the application of smoke or smoked product in the unburnt habitat (summarised in Table 2), where greatest overall germination occurred upon exposure to smoke for 60 min and was significantly inhibited when increased to 90 min (Fig. 4a).

Both smoked water and smoked sand elicited germination, smoked water being the more effective of the two (Fig. 4a). Application of smoke was also found to have an additive effect on seed germination in the burnt habitat (Fig. 4b).

There was a marked variation in germination response between species from the same family or genus following in situ application of smoke (Table 2). Of particular interest were the responses of members of the Epacridaceae in the unburnt habitat (Table 2) where *Conostephium preissii* and *Leucopogon leptanthus* seedlings appeared in greatest numbers in quadrats smoked for 60 or more minutes, whereas *L. conostephioides* and *L. striatus* showed inhibition of germination when smoked for longer than 30 min. *L. striatus* was the only species to be significantly enhanced by smoked sand and smoked water but not smoke fumigant. All Epacridaceae tested failed to show an additive effect of smoking upon seed germination in burnt habitat (Table 2).

Certain of the species which responded to in situ smoking of unburnt habitat are fire or disturbance opportunists in terms of their normal germination requirements. Such species included *Stipa compressa*, *Lobelia rhombifolia* and *Mitrasacme paradoxa*, all three of which showed maximum response in the smoked water treatments. *Eriostemon spicatus* was the only species which germinated in control untreated and unburnt plots. This species germinates freely after any form of disturbance.

Discussion

This study shows that application of cool smoke enhances germination of 45 of the 94 native Australian taxa tested under glasshouse conditions. At least 23 taxa which respond to smoke have previously been totally unamenable to conventional propagation from

Table 2 Analysis of the responses of a range of species to applications of smoke or derived products in recently burnt and unburnt habitat within native *Banksia* woodland in SW Australia. Hypotheses: (1) smoke elicits a germination response from species in an unburnt habitat (Anova: unburnt site: control vs smoke 30 s vs smoke 60 s vs smoke 90 s), (2) there is an optimum stated duration for the treatment. (Anova as above), (3) an aqueous solution of smoke will elicit a germination response (Anova: unburnt site: water vs smoked water), (4) smoked sand will elicit a germination response (Anova: unburnt site: sand vs smoked sand), (5) aqueous solution of smoke is more effective in eliciting a germination response than smoked sand (Anova: unburnt site: smoked water vs smoked sand), and (6) there is an additive effect of burning and smoking on germination response (*t*-Test: burnt control vs burnt + 60 s smoke)

Taxon	Hypotheses 1	2	3	4	5	6
Actinotus leucocephalus Benth.	Yes	90 s	Yes*	No	No	No
Conostephium preissii Sonder in Lehm.	Yes	90 s	No	No	No	No
Conostylis sp.	Yes	60 s/90 s NS	No	No	No	No
Eriostemon spicatus A. Rich	Yes	60 s/90 s NS	No	No	No	Yes*
Hibbertia sp.	Yes	60 s/90 s NS	No	No	No	No
Laxmannia sp.	Yes	60 s/90 s NS	Yes**	No	Yes**	Yes*
Leucopogon conostephioides DC.	Yes	30 s	No	No	No	No
Leucopogon leptanthus Benth.	Yes	60 s	No	No	No	No
Leucopogon striatus R. Br.	Yes	30 s	Yes***	Yes*	No	No
Lobelia rhombifolia Vriese	Yes	60 s	Yes***	No	Yes***	No
Mitrasacme paradoxa R. Br.	Yes	30 s/60 s/90 sNS	Yes***	No	No	Yes*
Stipa compressa R. Br.	Yes	60 s	Yes***	No	Yes***	No
Stylidium brunonianum Benth in Endl.	Yes	30 s/60 s NS	No	No	No	Yes***
Stylidium sp.	Yes	60 s	No	No	No	Yes**
Unidentified legume	Yes	60 s	No	No	No	No
Germinants of all species recorded	Yes	60 s	Yes***	Yes**	Yes***	Yes**

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS not significantly different

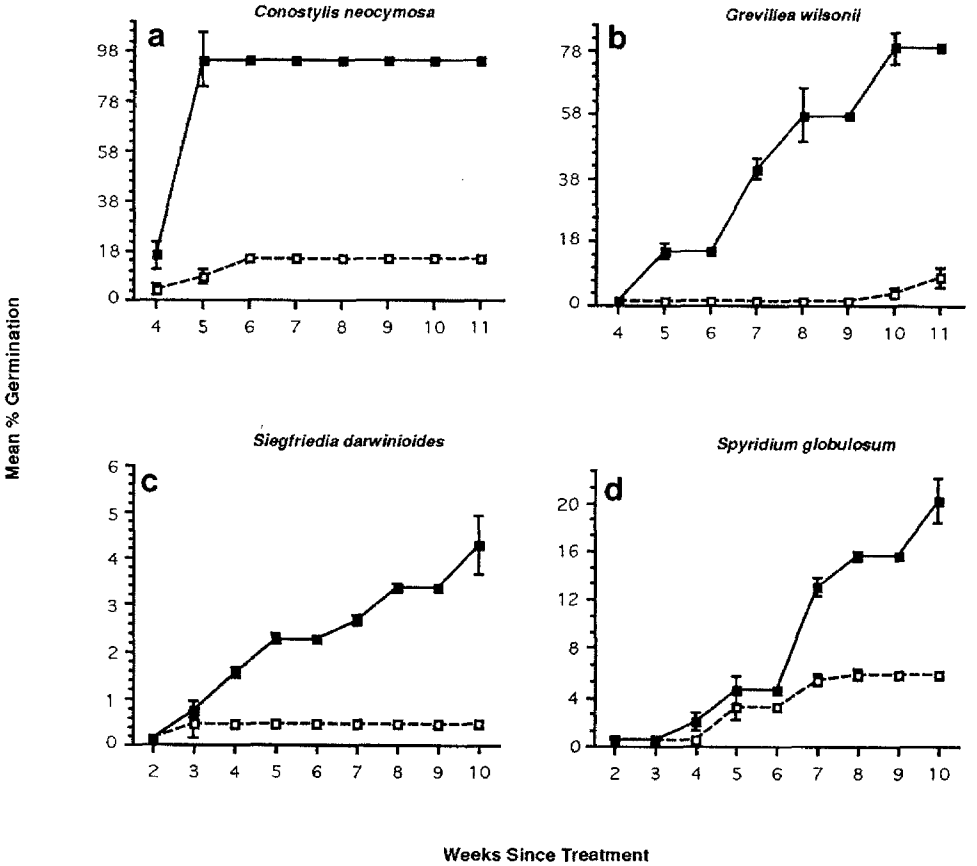

Fig. 2a–d Time courses of germination events in glasshouse germination studies. **a** *Conostylis neocymosa*; **b** *Grevillea wilsonii*; **c** *Siegfriedia darwinioides*; **d** *Spyridium globulosum*. Figures represent mean cumulative germination percentages (± standard error) of the viable (i.e. with endosperm) seeds within test replicates for control (*open boxes*) and smoked (*closed boxes*) replicates. Note different scales on axes

seed, including members of the genera *Conospermum*, *Eriostemon*, *Codoncarpus*, *Gyrostemon*, *Lechenaultia*, *Patersonia*, *Scaevola* and *Sphenotoma*. Germination responses to smoking are also achieved in what might be regarded as "difficult-to-germinate" taxa such *Geleznowia verrucosa*, *Hibbertia* spp., *Pimelea* spp., *Stirlingia latifolia*, *Verticordia densiflora*, and *Actinostrobus acuminatus*. The positive results obtained

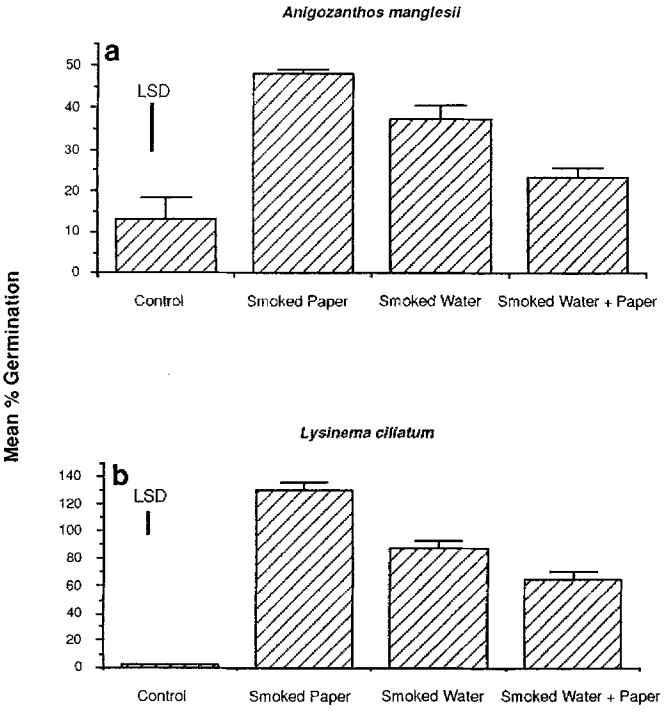

Fig. 3a, b Germination responses under laboratory conditions to smoked filter paper, smoked water, and a combination of both. **a** *Anigozanthos manglesii*; **b** *Lysinema ciliatum*. Figures represent mean germination percentages (± standard error) of the viable (i.e. with endosperm) seeds within test replicates. Germination percentages were subjected to arcsine transformation, and results analysed using one way analysis of variance. Fisher's least significant differences (*LSD*) are indicated. Note different scales on axes

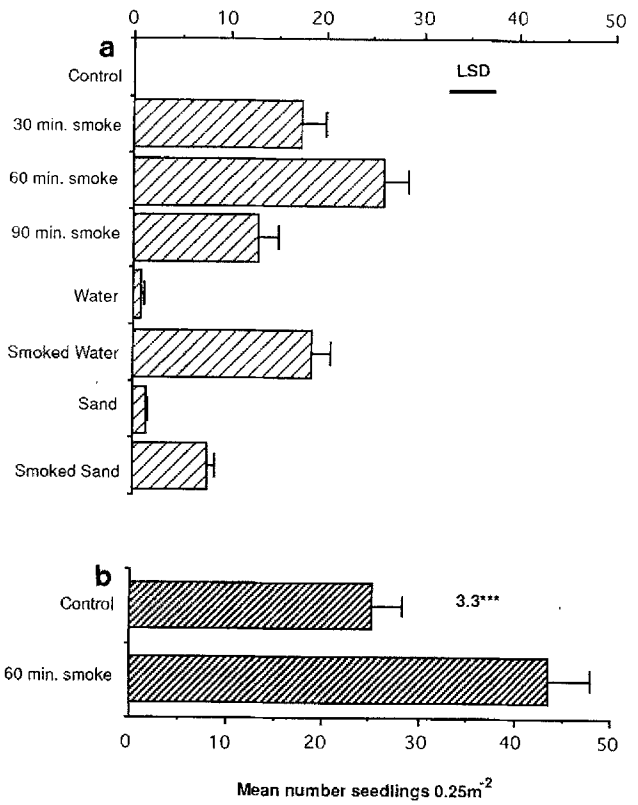

Fig. 4a, b Mean number of seedlings per 0.25 m^2 quadrat in unburnt and burnt native *Banksia* woodland at Yeal Reserve, Western Australia (see also "Germinants of all species recorded", Table 2). (**a**) Standard error of means and Fisher's least significant difference are indicated for each treatment in the unburnt site; (**b**) standard error of means, *t*-value and level of significance is indicated for the burnt site (***$P < 0.01$)

generally agree with those previously published for South African species (de Lange and Boucher 1990; Brown 1993) in which 13 species (of 19 tested) from five families were found to show significantly improved germination after exposure to smoke. Interestingly, both the South African study and the present investigation record smoke-stimulated germination of a species storing seed in its canopy, namely *Protea compacta* (South African member of the Proteaceae) and *Actinostrobus acuminatus* (West Australian member of the Cupressaceae). This runs contrary to the conclusion of Bell et al. (1993) that such species do not normally exhibit dormancy upon release of seed from infructescences.

Some eight of the study species with markedly positive responses to smoke (*Thysanotus multiflorus*, *Burchardia umbellata*, *Lechenaultia biloba*, *Anigozanthos manglesii*, *Conostylis setosa*, *Grevillea wilsonii*, *Geleznowia verrucosa*, *Pimelea spectabilis*) have been reported previously as responding positively to heating/boiling treatments, nicking of seed coats, exposure to charcoal eluates or treatment with heat plus charcoal eluates (Bell et al. 1987, 1993; Paynter and Dixon 1991). However, in this study, five of the above species exhibited several-fold greater germination percentages following smoking than in any previously published treatment. *Conostylis setosa*, the first Australian non-legume, previously shown to germinate in response to heat (Bell et al. 1987), also responded in the present study to the application of smoke. Results of the above kind collectively suggest that seed banks of certain species may have to react sequentially and possibly additively to a number of stimuli before specific members become committed to germinate. The role of smoke diffusing to layers of the soil out of range of stimulation by heat may have special significance in this connection, especially in the case of deeply buried seeds.

The enhanced germination of seed of Californian chaparral species in response to charred wood (see Keeley et al. 1985; Keeley and Pizzorno 1986) closely parallels our present studies on effects of smoke and smoke products. Indeed, adsorption of germination-enhancing principles from smoke onto charcoal during or immediately after fire, and the subsequent elution in rain water of active compounds, may well explain the germination enhancements suggested for chaparral vegetation by the above authors.

There is evidence from the present study that the extent of influence of smoke on germination differs markedly within taxa and between seeds of disparate

age or provenance (e.g. as shown from *Anigozanthos manglesii*, *Geleznowia verrucosa*, *Lechenaultia biloba*, *Patersonia occidentalis* and *Pimelea sylvestris*). Differences of this type are to be expected in view of likely variations in seed quality, seed dormancy patterns and seed longevity. Furthermore, in our laboratory studies of *Anigozanthos manglesii* and *Lysinema ciliatum* some evidence was obtained of inhibition with high doses of smoked products, a result matching closely the responses observed by Brown (1993) for certain South African species.

Turning to the effects of in situ smoke in natural habitat, marked positive germination responses are encountered in unburnt habitat and, in certain cases, further emergence of seedlings is promoted by smoking burnt areas of a habitat. Indeed, 38% of species recruiting at the test site exhibit an additive effect of smoke and fire upon their germination. This suggests that the controlled, relatively cool burn at the site was of sufficient intensity to stimulate germination of only a small fraction of the seed bank. In such circumstances seeds at moderate depth, unaffected initially by the heat of the fire, would be those most likely to respond subsequently to artificially applied smoke.

In the absence of information on the nature of the organic components of smoke, no conclusions can be drawn as to which specific substance(s) elicits or enhances germination. The finding of van der Venter and Esterhuizen (1988) that ammonia gas stimulates seed germination of the South African species *Erica hebecalyx* (Ericaceae) lends support to the possibility that it might be one of the agents active in breaking of dormancy. Preliminary analyses of eluates of the smoke used in the present study indeed show ammonium as a major inorganic component (unpublished data). Adsorption of ammonium onto soil grains, followed by leaching through the substrate after rain, are possible modes of delivery of the active principle. In any event, the fact that heterogeneous mixes of randomly selected vegetation were used as substrates for smoke production in our own and the above-mentioned South African studies suggests that the promotive agent(s) may be of widespread occurrence and act relatively indiscriminately on germination across wide ranges of taxa and growth and life forms.

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