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Smoke derived from burnt vegetation stimulates germination of arable weeds

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Abstract

A commercially available smoke-water solution (Seed Starter®) stimulated the germination of caryopses and intact florets of *Avena fatua* L. The solution was most effective when diluted (5–50%) and presented to intact or dehulled grain that had received a short period of dry after-ripening. It was less effective when applied at full strength or to grains that had been freshly harvested. The same stimulatory effect was observed in partly after-ripened caryopses of nine different wild oat biotypes obtained from three different cropping regions of the world. When freshly harvested caryopses were re-tested with the commercial solution (100%) for just 7 days prior to placement on to distilled water, a much higher germination percentage was possible than seen with continuous smoke-water incubation. The stimulatory ability of smoke water was more closely matched to that of gibberellic acid than to potassium nitrate, which had little or no effect on freshly harvested caryopses. The smoke-water solution (5–100%) was tested on the germination of 18 other cool temperate arable weed species. All monocotyledonous species tested (viz. *Avena sterilis* ssp. *ludoviciana* L., *Alopecurus myosuroides, Sorghum halepense, Phalaris paradoxa*) responded positively, while those of the dicotyledonous species were either strongly stimulated (⩾40% stimulation *Malva neglecta*), moderately stimulated (⩾20% stimulation *Galium aparine, Veronica persica*), slightly stimulated (*Polygonum persicaria, P. pennsylvanicum, Fallopia convolvulus*), unaffected (*P. aviculare, Sinapis arvensis, Heracleum sphondylium, Angelica sylvestris, Mercurialis annua, Veronica hederifolia*) or inhibited (*Lamium purpureum*). The optimal concentrations required to stimulate germination of the monocotyledonous species were similar to those observed for *A. fatua* (5–10%). However, for the dicotyledonous species slightly stronger solutions were required (10–20%). When the unaffected species were retested using a 10-day pre-chilling treatment, smoke water showed a small promotive response in three (*S. arvensis, P. aviculare* and *V. hederifolia*) of the six species. When four different smoke-water solutions (Seed Starter®, Regen 2000®, charred-wood solution and wheat-straw solution) were tested on two representative species (*A. fatua* and *M. neglecta*), three formulations were effective in promoting the germination of both species, while the fourth (charred-wood solution) was only active on *A. fatua.* The active concentrations were different for the four solutions. Three solutions were active in the 2–20% dilution range, while the fourth (Regen 2000®) was only active in the 1–2% dilution range and was inhibitory at higher concentrations. These observations are discussed in the context that smoke may play an important ecological role in the management and control of introduced weeds in native and arable communities.

Keywords: *Avena fatua*, germination, seed dormancy, smoke water, weeds

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Introduction

Compounds produced by the combustion or charring of plant matter stimulate germination in a variety of species (Keeley *et al.*, 1985; Keeley and Pizzorno, 1986; Van de Venter and Esterhuizen, 1988; De Lange and Boucher, 1990; Baxter *et al.*, 1994; Dixon *et al.*, 1995; Enright *et al.*, 1997; Davidson and Adkins, 1997; Adkins *et al.*, 2000). To date, germination enhancement has been shown in more than 170 species from 37 families (Roche *et al.*, 1997; Bell, 1999). Most studies have focused upon species native to fire-prone areas, although germination can also be stimulated in lettuce (*Lactuca sativa* L., Drewes *et al.*, 1995), celery (*Apium graveolens* L., Thomas and Van Staden, 1995), red rice (*Oryza sativa*, Doherty and Cohn, 2000) and one species of wild oat (*Avena sterilis* ssp. *ludoviciana* L., Adkins *et al.*, 2000). The compound(s) in smoke that affect germination have not been identified (Baldwin *et al.*,

1994; Brown and van Staden, 1997; Keeley and Fotheringham, 2000), but probably act internally in the seed (Keeley and Keeley, 1987). However, Egerton-Warburton (1998) found that smoke acted on the seed coat in a way similar to scarification, whereby the passage of water and oxygen into the dormant embryo is made easier. Active compounds within smoke are produced by a variety of wood types, are water-soluble and are derived from the hemicellulose fraction of wood (Keeley and Pizzorno, 1986; Baldwin *et al*., 1994). In addition to previous attempts, van Staden *et al.* (1995) reported efforts to purify the biologically active fraction of smoke. Twelve compounds were identified, not all of which were present in all smoke extracts examined. In further investigations, Keeley and Fotheringham (1998a, b, 2000) concluded that the most likely active component was nitrogen oxide. However, liquid smoke extracts lacking nitrogen oxides also elicit dormancy-breaking activity (Doherty and Cohn, 2000).

Smoke is effective on species from a wide range of families, which vary in ecology, reproductive strategy, seed size and morphology (Dixon and Roche, 1995). For this reason, the commercial development of smoke treatments for the stimulation of seed germination is considered a viable option. Several products containing smoke in solution are on the market and include 'Regen 2000®', 'Seed Starter®' and 'Kirstenbosch Instant Smoke Plus®' seed primer. The latter two of these products significantly stimulated seed germination of a wide range of South African native species (Brown and van Staden, 1997).

The use of smoke water has applications in the rehabilitation of disturbed areas, horticultural industries, ecological management, and crop production, particularly organic farming systems. Such applications are primarily for species that are difficult to germinate under normal circumstances. Investigation of smoke for rehabilitation has been carried out predominantly on species from Mediterranean climates (Keeley and Fotheringham, 2000). In Australia these constitute mainly native species, of which the majority are stimulated by smoke (Bell, 1999). However, very little examination of the effect of smoke on germination of weedy species has been carried out (Doherty and Cohn, 2000). One feature of many annual weeds is their ability to persist in the soil seed bank for several years due to dormancy. Should smoke prove to be an effective agent in breaking annual weed seed dormancy, then this will have implications for rehabilitation of sites with native species and may give rise to a treatment that can be used to deplete the arable weed seed banks in agricultural circumstances.

The aims of the present study were: (1) to develop a better understanding of the stimulation conditions of smoke water upon germination under laboratory conditions; and (2) to investigate the effect of smoke water upon the germination of a wide range of arable weeds that are commonly found across northern Europe or in subtropical agricultural locations.

Materials and methods

Seeds were obtained from several different sources, each lot being stored in paper envelopes at room temperature until required for experimentation. Studies were undertaken on seed lots following post-harvest storage for different periods of time (Table 1). From each species, uniform filled seeds were selected for study. To determine the percentage of full seeds present in a sample, 100 seeds from each batch were taken at random, and a sharp scalpel blade was used to cut longitudinally down through each seed. A binocular microscope was used to assess the presence and appearance of the embryo. If a well-formed, disease-free embryo was present, the seed was assumed to be viable. Based on this form of assessment, viability of all seed lots used in this study was above 90%. All experiments reported here were repeated at least once.

Unless otherwise stated, the grasses used in the germination tests were dehulled (to yield caryopses) manually by hand.

Smoke solutions

The main smoke-water solutions used (unless otherwise stated) were diluted from a stock solution of 'Seed Starter®'(manufactured at Kings Park and Botanical Gardens, Perth, WA, Australia). In some experiments a full range of smoke-water concentrations was used (viz. 0, 1, 5, 10, 20, 50 and 100%), while in others only selected concentrations were used. The pH of the solutions ranged from 3.2 (100% solution) to 4.2 (1% solution) with the exception of the distilled water control, which was pH 5.5. In one experiment (Fig. 2), three other smoke-water solutions were used, viz. Regen 2000® (Tecnica Propriety Limited, Bayswater, Victoria, Australia) and two solutions prepared at the Institute of Arable Crops Research (IACR), Long Ashton Research Station, Bristol, United Kingdom. The first IACR solution was prepared from the combustion of wheat (*Triticum aestivum* L.) straw, while the second was prepared from charred willow (*Salix* sp.) wood chips (Thornton *et al*., 1999).

Incubation conditions

For the germination studies three replicates of between 20 and 50 seeds (Table 1) were removed from storage and placed in 9-cm-diameter Petri dishes

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Table 1. The species and/or biotypes used in the present study showing their source, viability, age and how they were stored after harvest and prior to use in the germination studies

Species	Biotype	Source[a]	Viability[b] (%)	Age[c] (months)	Prior storage[d] (°C)
Alopecurus myosuroides		HS	92	12	RT
Angelica sylvestris		HS	92	12	RT
Avena fatua	Pearce	ICAR	100	0–3	RT
	Rewe	ICAR	100	12	RT
	CS40	US	100	48	–20
	M73	US	90	48	–20
	AN84	US	100	48	–20
	AN51	US	90	48	–20
	AN265	US	95	48	–20
	Tarooma	UQ	90	48	–20
	Northam	UQ	100	48	–20
Avena sterilis ssp *ludoviciana*		ICAR	96	12	RT
Bromus dyandrus		ICAR	100	3	RT
Fallopia convolvulus		HS	100	12	RT
Galium aparine		HS	100	12	RT
Heracleum sphondylium		HS	94	12	RT
Lamium purpureum		HS	93	12	RT
Malva neglecta		HS	100	12	RT
Mercurialis annua		HS	90	12	RT
Phalaris paradoxa		ICAR	100	1	+5
Polygonum arviculare		HS	100	24	RT
Polygonum persicaria		HS	95	12	RT
Polygonum pennsylvanicum		HS	100	12	RT
Sinapis arvensis		HS	98	12	RT
Sorghum halepense		HS	96	24	RT
Veronica persica		ICAR	96	3	RT
Veronica hederifolia		HS	92	12	RT

[a] IACR, Institute of Arable Crops Research, Long Ashton, UK; US, University of Saskatchewan, Saskatoon, Canada; UQ, University of Queensland, Brisbane, Australia; HS, Herbiseed, Ascott, UK.
[b] Viability was assessed by a cut seed test applied to 100 seeds of each species or is the result of a germination test carried out by Herbiseed.
[c] The age of the seed lot at the time of the germination studies.
[d] Storage temperature after harvest: RT, room temperature (*c.* 15°C).

lined with four layers of 9 cm Whatman No. 2 filter paper moistened with 8 ml of distilled water (control) or smoke-water solution. All dishes were incubated in a darkened incubator at a constant temperature of 15 ± 1°C in an atmosphere saturated with water vapour. Germination (protrusion of coleorhiza through testa and pericarp for the monocotyledonous species and emergence of root through the testa for dicotyledonous species) was recorded periodically and the germinated seedlings removed. Any dead caryopses or seeds were also removed at the same time. Germination was assayed for 35 d, at which time germination had ceased for at least 10 d.

Statistical analysis

Analyses of variance (ANOVA) were performed on the data to evaluate the differences in final germination percentages with various treatments. The data did not undergo arc-sine transformation as it was not deemed necessary.

Results

Germination studies on Avena fatua

Smoke water was able to overcome dormancy in *Avena fatua*, stimulating germination from 0% (control) to 92% (best treatment). Optimal germination was observed over a range of smoke-water concentrations (from 2 to 20%) and in caryopses that had received an 8–12-wk period of after-ripening (Fig. 1). At higher concentrations (50 and 100% smoke water) germination was reduced and root damage (data not shown) was observed, indicating toxic side-effects. When the husk was retained, the effect of smoke water was less than when applied to the caryopses alone.

The stimulatory effect of smoke water was observed for a range of *A. fatua* biotypes (Table 2) from a region of western Canada (CS40, AN51, AN84 and AN265), the northern United States of America (M73), from England (Pearce, Rewe) and Australia

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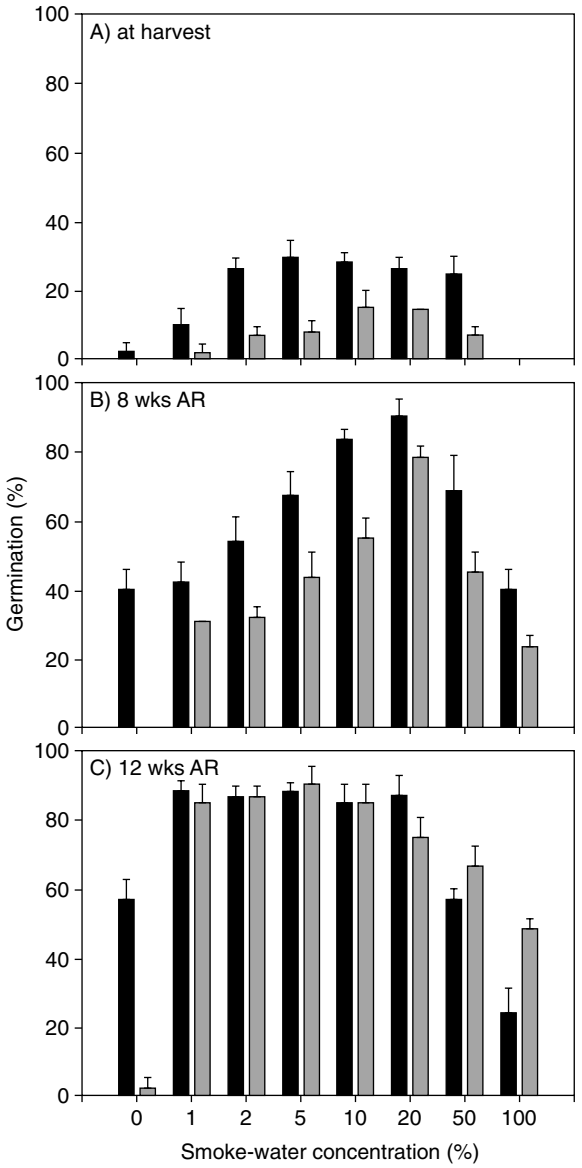

Figure 1. The effect of smoke-water concentrations on the germination of caryopses (black bars) or intact florets (grey bars) of *Avena fatua* L., biotype Pearce. Seeds were tested at harvest (A) and after 8 (B) or 12 (C) weeks of after-ripening (AR) at room temperature (20–25°C). The data represent the mean ± standard deviation of three replicates of 20 caryopses, assessed 35 days after the start of imbibition at 15 ± 1°C in the dark.

(Tarooma, Northam). For all caryopses tested, concentrations of smoke water in the range of 5–20% remained strongly stimulatory, with optimum stimulation at 10% smoke water for most biotypes.

Increased germination of freshly harvested caryopses could be obtained if the incubation period in the smoke-water solution was reduced from continuous to 7 days, with the remaining time on distilled water. Using such a system, germination could be raised from 30 (best continuous treatment) to 55%. A similar effect was seen in partly after-ripened caryopses with a smoke-water incubation time of 9 days, increasing germination from 48 (best continuous treatment) to 77% (Table 3).

Smoke water overcame dormancy in a good proportion of the freshly harvested caryopses, and its effect was similar to that of gibberellic acid, which is a potent stimulator of *A. fatua* germination (Table 4), and less like that of potassium nitrate, which was only effective in promoting germination in partly after-ripened caryopses of *A. fatua*.

Germination studies on a range of species

All of the additional monocotyledonous species tested either germinated well in water (were non-dormant, e.g. *Bromus dyandrus*) or were strongly stimulated by smoke water, e.g. *Avena sterilis* (Table 5). The dicotyledonous species, on the other hand, were either strongly stimulated (*Malva neglecta*), moderately stimulated (*Veronica persica*, *Galium aparine*), slightly stimulated (*Polygonum persicaria, P. pennsylvanicum, Fallopia convolvulus*), unaffected (*P. aviculare, Sinapis arvensis, Heracleum sphondylium, Angelica sylvestris, Mercurialis annua, Veronica hederifolia*) or inhibited (*Lamium purpureum*). The best concentrations required to stimulate the monocotyledonous species were similar to those seen for *Avena fatua* (5–10%). However, for the dicotyledonous species, slightly stronger solutions were required (10–20%). When comparing responses of species within the same genus, differing responses were found; three *Polygonum* and one *Veronica* species were slightly stimulated, while one species each from these two genera were unaffected.

If the non-responding species were re-tested following a 10-d chilling treatment (Table 6), the smoke-water treatment applied showed only a small promotive response in three (*P. aviculare, S. arvensis* and *V. hederifolia*) of the six species tested.

Germination studies using a range of smoke solutions

When smoke-water solutions prepared from different organic sources (Seed Starter®, Regen 2000®, a charred-wood solution and a wheat-straw smoke solution) were tested on two representative species (*A. fatua* and *M. neglecta*), three solutions were active in promoting the germination of both species, while the fourth (charred-wood solution) was only active on *A. fatua* (Fig. 2). Three solutions were active at 2–20% dilutions, while the fourth (Regen 2000®) was only active at 1–2% and toxic at higher concentrations.

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Table 2. The effect of smoke-water concentration on the germination percentages of caryopses (dehulled) of nine biotypes of *Avena fatua* L. The first five are from North America, Pearce and Rewe are from England and Tarooma and Northam are from Australia. Each value represents the mean ± standard deviation of three replicates of 20 caryopses assessed 35 days after the start of imbibition at 15 ± 1°C in the dark. The intact florets had been partly after-ripened for between 2 and 20 weeks under laboratory conditions before being stored dry at –20°C for up to 4 years before use. Significance is shown in rows as a result of a two-way ANOVA on final germination percentages between biotypes and smoke-water concentration

		Smoke water concentration (%)*			
Line	Age (weeks)	0	5	10	20
CS40	10	95 ± 0a	88 ± 3a	97 ± 6a	98 ± 3a
M73	20	55 ± 10a	88 ± 3b	97 ± 3b	97 ± 3b
AN84	10	30 ± 5a	98 ± 3b	100 ± 0b	97 ± 6b
AN51	10	13 ± 3a	92 ± 8b	93 ± 12b	90 ± 8b
AN265	10	17 ± 3a	75 ± 5b	87 ± 6b	93 ± 6b
Pearce	10	37 ± 3a	87 ± 3b	93 ± 3b	85 ± 5b
Rewe	10	0 ± 0a	50 ± 10b	60 ± 20b	70 ± 10b
Tarooma	10	0 ± 0a	34 ± 2b	39 ± 1b	38 ± 2b
Northam	10	20 ± 4a	39 ± 2b	100 ± 0c	37 ± 2b

* Values followed by the same letter are not significantly different ($P < 0.05$).

Table 3. The effect of the imbibition period in smoke water (100%), prior to imbibition on water, on the final germination percentages. *Avena fatua* L. biotype (Pearce) was used, and the values represent the mean ± standard deviation of three replications of 20 caryopses assessed 35 d after the start of imbibition at 15 ± 1°C in the dark. The florets used for the isolation of the caryopses were stored at ambient temperatures (approximately 20°C) for 6 weeks prior to treatment and are referred to as partly after-ripened (PAR). Significance is shown in columns, a result of a one-way ANOVA performed on the final germination percentage for each caryopsis age, with length of imbibition time in smoke water as the treatment

	Final germination (%)*	
Days in smoke solution	Freshly harvested	PAR
0	0 ± 0a	33 ± 6a
1	36 ± 8b	38 ± 6a
3	47 ± 12b	47 ± 12ab
5	50 ± 10b	53 ± 6b
7	55 ± 9b	67 ± 3c
9	35 ± 5b	77 ± 8c
11	7 ± 3a	53 ± 3b
Continuous (100%)	0 ± 0a	48 ± 12b
Best continuous treatment*	30 ± 5b	87 ± 2c

The best continuous treatments were 5% smoke water with freshly harvested caryopses and 20% smoke water for partly after-ripened caryopses (PAR).
* Values followed by the same letter are not significantly different ($P < 0.05$).

Discussion

Smoke-water treatments and germination of a single species

Smoke water has the ability to overcome dormancy in a number of species that are classified as weeds of arable land of northern Europe. For *Avena fatua*, a major weed of temperate cereal production areas around the world, smoke water can promote germination or inhibit it, depending on the concentration. The effective concentration range of smoke water may depend on the solution preparation procedures. Standard saturated solutions (Seed Starter®, charred-wood and wheat-straw smoke solutions) were active at 5–20% dilutions, whereas Regen 2000®, which is manufactured using a concentration step, was active in the range of 1–2%.

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Table 4. The effect of three germination promoters on the stimulation of germination of *Avena fatua* L. The biotype used was Pearce and values represent the mean ± standard deviation of three replicates of 20 caryopses assessed 35 d after the start of imbibition at 15 ± 1°C in the dark. Some florets were stored at ambient temperatures (approximately 20°C) for 9 weeks prior to smoke treatment and are partly after-ripened (PAR). The smoke-water concentrations and durations used had previously been determined to be optimal for these substances in promoting germination and were applied for 7 d for freshly harvested and 9 d for PAR material. Significance is shown in columns, a result of a one-way ANOVA on the final germination percentages for each age, with the chemical concentration as treatments

	Germination (%)*	
	Freshly harvested	PAR
Control	8 ± 14a	40 ± 5a
Smoke water (100%)	55 ± 9b	76 ± 8b
Potassium nitrate (50 mM)	12 ± 3a	93 ± 12b
Gibberellic acid, GA_3 (1 µM)	93 ± 3c	95 ± 9b

* Values followed by the same letter are not significantly different ($P < 0.05$).

Table 5. The effect of smoke water on propagules of 18 arable weeds. Each value represents the mean ± standard deviation of percentage germination for three replicates of 50 seeds (dicotyledonous species) or 20 (monocotyledon species) caryopses. The assessment was made 35 d after the start of imbibition at 15 ± 1°C in the dark. Statistical analysis involved a two-way ANOVA on final germination percentages for each species with the smoke-water concentrations as treatments. Significance is shown across the rows

	Smoke water concentration (%)*					
Species	0	2	5	10	20	50
Monocots						
Alopecurus myosuroides	45 ± 9a	48 ± 12a	47 ± 6a	77 ± 8b	88 ± 12b	78 ± 8b
Avena sterilis ssp. *ludoviciana*	12 ± 6a	52 ± 10b	83 ± 6c	93 ± 3d	80 ± 17cd	38 ± 13b
Bromus dyandrus	85 ± 0b	78 ± 0ab	82 ± 12ab	82 ± 2ab	77 ± 3a	78 ± 6a
Phalaris paradoxa	50 ± 5b	88 ± 3c	98 ± 3d	100 ± 0d	90 ± 17cd	27 ± 3a
Sorghum halepense	12 ± 3a	28 ± 3b	40 ± 5c	38 ± 3bc	33 ± 6bc	100 ± 0d
Dicots						
Angelica sylvestris	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Fallopia convolvulus	15 ± 1b	12 ± 0a	15 ± 1bc	19 ± 3c	24 ± 2c	15 ± 1b
Galium aparine	5 ± 1a	7 ± 1a	11 ± 2b	22 ± 5c	27 ± 3c	15 ± 2bc
Heracleum sphondylium	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Lamium purpureum	45 ± 8b	48 ± 7b	34 ± 5ab	27 ± 6a	48 ± 7b	29 ± 1a
Malva neglecta	28 ± 4b	37 ± 6bc	56 ± 4d	73± 12e	45 ± 2c	21 ± 1a
Mercurialis annua	0 ± 0a	2 ± 4a	0 ± 0a	0 ± 0a	1 ± 2a	0 ± 0a
Polygonum arviculare	3 ± 1bc	3 ± 1b	3 ± 4abc	5 ± 1bc	5 ± 1c	0 ± 0a
P. pennsylvanicum	9 ± 1b	10 ± 0c	14 ± 5bc	21 ± 1d	9 ± 3abc	4 ± 4a
P. persicaria	21 ± 2b	28 ± 4c	28 ± 4c	39 ± 2d	22 ± 0b	9 ± 1a
Sinapis arvensis	11 ± 2bc	10 ± 0b	11 ± 1c	11 ± 2bc	9 ± 1bc	5 ± 1a
Veronica persica	79 ± 3b	85 ± 6b	91 ± 8b	100 ± 0c	100 ± 0c	11 ± 1a
V. hederifolia	0 ± 0a	0 ± 0a	1 ± 2a	1 ± 2a	0 ± 0a	0 ± 0a

* Values followed by the same letter are not significantly different ($P < 0.05$).

In *A. fatua* several dormancy mechanisms may be exhibited by freshly harvested grains (Adkins *et al.*, 1988), with at least one by the glumes, at least one in the testa and pericarp and, with some biotypes, a physiological dormancy in the embryo. To some degree, smoke was able to overcome all of these mechanisms of dormancy, as seen by the significant stimulation of germination with differences in smoke concentrations and amount of after-ripening (see Fig. 1, Tables 2–4), and in this capacity its action is similar to gibberellic acid and dissimilar to nitrate, which is only able to overcome dormancy in partly after-ripened grains. However, smoke water does have a greater capacity to overcome dormancy in partly after-ripened versus freshly harvested material, indicating that its primary mode of action is on the longer-lived dormancy mechanism(s). Germination stimulation was observed in a number of *A. fatua*

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Table 6. The effect of 10-d prechilling (5 ± 1°C) treatments on the germination of six arable weeds previously tested to be unresponsive to smoke-water stimulation of germination. One of the prechilling treatments was carried out in a smoke-water solution (5%), while the other was carried out in distilled water (chilling alone). Each value represents the mean ± standard deviation of three replicates of 50 seeds and assessment was 35 days after the start of imbibition. The incubation temperature after chilling was 15 ± 1°C in the dark. Statistical analysis involved a two-way ANOVA on the final germination percentages for each species with incubation conditions as treatments. Significance is recorded across the rows

	Germination (%)*		
	Control (unchilled)	Chilling alone	Chilling with smoke water
Heracleum sphondylium	0 ± 0a	0 ± 0a	0 ± 0a
Mercurialis annua	0 ± 0a	2 ± 2a	3 ± 1a
Angelica sylvestris	0 ± 0a	0 ± 0a	0 ± 0a
Sinapis arvensis	11 ± 1a	15 ± 2ab	18 ± 2b
Polygonum aviculare	3 ± 1a	11 ± 5b	23 ± 8c
Veronica hederifolia	0 ± 0a	2 ± 2a	15 ± 5b

* Values followed by the same letter are not significantly different ($P < 0.05$).

biotypes obtained from three different locations from around the world (viz. England, Australia and North America), indicating that stimulation is a common response in this species. Smoke water can overcome the dormancy of a closely related species, *A. sterilis* ssp. *ludoviciana* (Adkins *et al*., 2000). The inhibitory effects of smoke water are presumably due to the fact that the concentrated solutions are acidic and contain numerous organic substances that may act as growth and development retardants (Baldwin *et al*., 1994). These toxic effects can be partially avoided by first imbibing caryopses on concentrated smoke solutions for a short period of time (approximately 9 days for a 50% solution) and then by transfer to distilled water.

Smoke treatment and germination of a range of species

A wide range of other arable weed species from northern Europe was tested along with arable weed species from subtropical regions. The germination response to smoke was variable, with some species strongly stimulated, others less or not affected and one species (*Lamium pupureum*) perhaps inhibited at all concentrations tested. Of the species tested, the monocotyledons (i.e. *Poaceae*) were by far the most readily stimulated group, while the dicotyledonous species tested were much harder to stimulate. This may indicate that smoke water is able to stimulate those species with a weak coat (e.g. a hull) and/or embryo dormancy, but less effective on species with a thicker seed coat.

For a number of the stimulated species, such as *Galium aparine* and *Veronica persica*, there is no known history of these plants evolving in a fire prone (hence smoke prone) environment. Thus, smoke may be acting on the seed in an unspecialized way, such as acting as a scarifying agent to weaken fruit and seed-coat layers (Egerton-Warburton, 1998), resulting in better and more efficient water and oxygen uptake.

Different types of smoke water were active on at least two annual weed species (*A. fatua* and *M. neglecta*). Both species were stimulated by smoke water generated from burnt Australian vegetation and burnt wheat straw, as well as one being stimulated by a solution washed over the charred remains following the pyrolysis of willow wood chips. One of the smoke solutions (Regen 2000®) had undergone a concentrating step in its manufacture; hence, it was active at one-tenth the concentration of the others.

Active compounds and mode of action

The identity of the compounds of smoke responsible for dormancy release remains unknown, although Keeley and Fotheringham (2000) have suggested that nitrogen oxides are the active components. Identification of the active principals(s) is difficult, due to the large number of volatile compounds produced during plant material combustion (Maga, 1988). De Lange and Boucher (1993) reported that the active component(s) were water soluble, heat stable and relatively volatile. Baldwin *et al*. (1994) revealed that similar compounds were present in smoke extracts from a range of combusted materials. Chromatographic analysis (Jäger *et al*., 1996) identified 12 compounds present in smoke extracts of *Themeda triandra,* of which seven were also present in extracts of smoke from *Passerina vulgaris*. These seven

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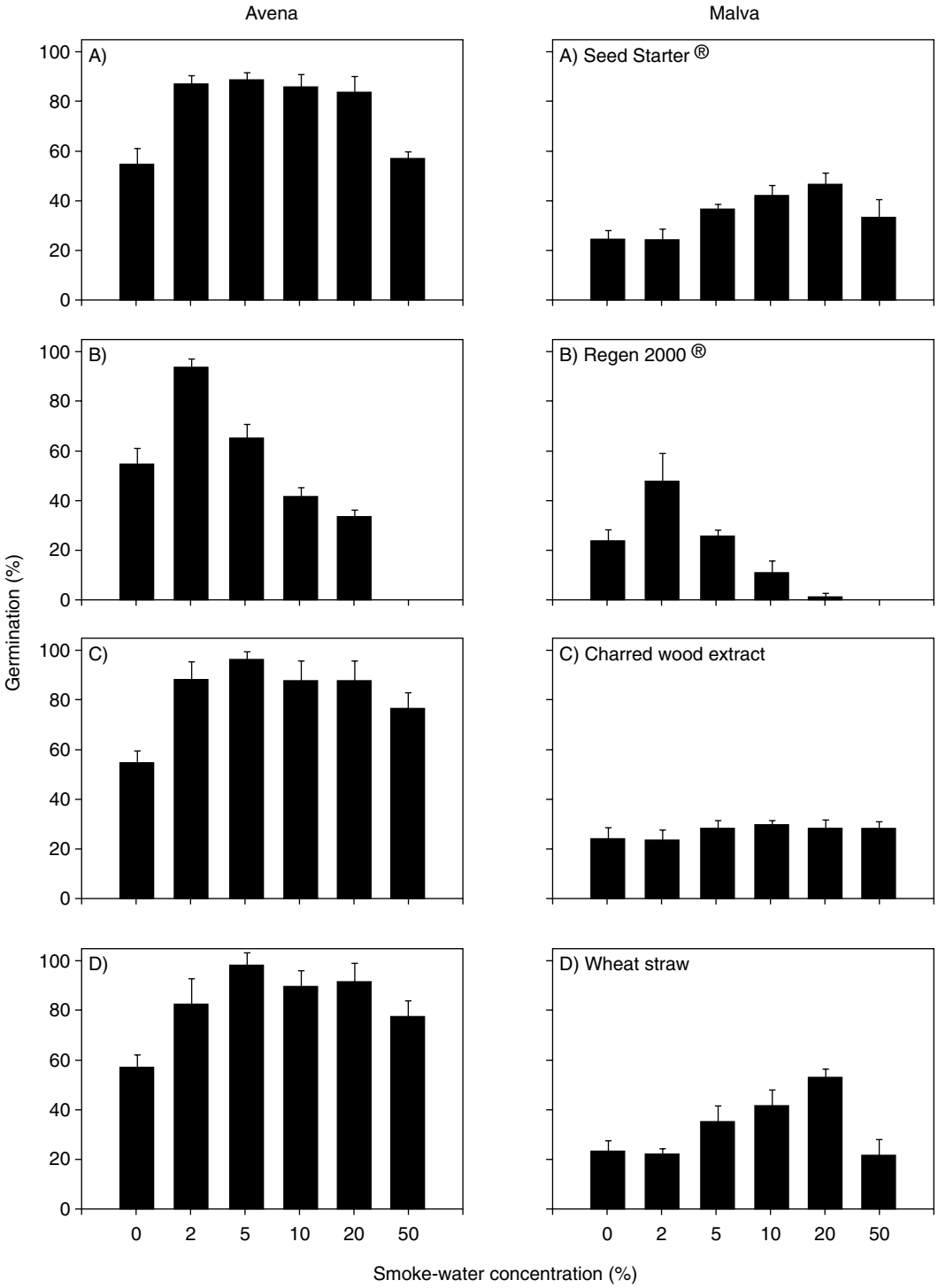

Figure 2. The effects of several different smoke-water solutions on the germination of *Avena fatua* (biotype Pearce) caryopses or *Malva neglecta* seed. The smoke-water solutions came from four different sources: (A) Seed Starter®; (B) Regen 2000®; (C) charred-wood extract; or (D) wheat straw. The data points represent the mean ± standard deviation of three replicates of 20 caryopses (*A. fatua*) or 50 seeds (*M. neglecta*). The assessment was after 35 days' imbibition at 15 ± 1°C in the dark.

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compounds were assayed for their effects on germination, and none was found to release dormancy. Thus, it is likely that either the compound(s) involved have not yet been fully identified and/or that more than one compound is involved in dormancy release. Egerton-Warburton (1998), based on transmission and scanning electron microscopic analysis, reported a surfactant-like effect exerted by smoke water, in which two seed-coat layers were destabilized/reorganized by components of smoke. Previously, Sakuma *et al*. (1980) had shown that the pyrolysis of cellulose produced a large range of compounds, such as aromatic hydrocarbons and ketones, which could modify or dissolve plant waxes. Organic acids are also produced during combustion and have been shown to modify the structure of plant tissues (Espelie *et al*., 1980). Kelley and Fotheringham (1998a, b) have implicated acidification in smoke-mediated release of dormancy, proposing an acid-driven hydrolysis mechanism. In the present series of experiments, it is unknown how the smoke water is acting on seeds to promote germination. It is thought that a surfactant or scarification-like effect is occurring, as the weaker-coated seeds (e.g. *Avena sterilis, Phalaris paradoxa)* are stimulated more than thick-coated seeds (*Polygonum pennsylvanicum, Galium aparine*), and that as seed after-ripens it becomes more responsive. Further investigation into these possibilities is proceeding.

Ecological implications

The positive germination response to smoke solutions would seem to be a fairly common phenomenon. Not all species that respond to smoke have been selected from a smoke-prone environment. Consequently smoke and/or smoke solutions may be found to stimulate the germination of many different kinds of seed bank. Such a use for smoke has already been employed for the revegetation of disturbed lands after mining activities in Australia. It is conceivable that such treatments could also be used as a strategy to deplete a persistent seed bank of a difficult-to-control weed or weeds in arable circumstances, particularly in an organic farming system. This would be done by germination stimulation as a result of smoke application, followed by management/eradication of these weeds before planting a crop.

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