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SMOKE-INDUCED SEED GERMINATION IN CALIFORNIA CHAPARRAL

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Abstract. The California chaparral community has a rich flora of species with different mechanisms for cuing germination to postfire conditions. Heat shock triggers germination of certain species but has no stimulatory effect on a great many other postfire species that are chemically stimulated by combustion products. Previous reports have shown that charred wood will induce germination, and here we report that smoke also induces germination in these same species. Smoke is highly effective, often inducing 100% germination in deeply dormant seed populations with 0% control germination. Smoke induces germination both directly and indirectly by aqueous or gaseous transfer from soil to seeds. Neither nitrate nor ammonium ions were effective in stimulating germination of smoke-stimulated species, nor were most of the quantitatively important gases generated by biomass smoke. Nitrogen dioxide, however, was very effective at inducing germination in *Caulanthus heterophyllus* (Brassicaceae), *Emmenanthe penduliflora* (Hydrophyllaceae), *Phacelia grandiflora* (Hydrophyllaceae), and *Silene multinervia* (Caryophyllaceae). Three species, *Dendromecon rigida* (Papaveraceae), *Dicentra chrysantha*, and *Trichostema lanatum* (Lamiaceae), failed to germinate unless smoke treatment was coupled with prior treatment of 1 yr soil storage.

Smoke-stimulated germination was found in 25 chaparral species, representing 11 families, none of which were families known for heat-shock-stimulated germination. Seeds of smoke-stimulated species have many analogous characteristics that separate them from most heat-shock-stimulated seeds, including: (1) outer seed coats that are highly textured, (2) a poorly developed outer cuticle, (3) absence of a dense palisade tissue in the seed coat, and (4) a subdermal membrane that is semipermeable, allowing water passage but blocking entry of large (molecular mass > 500) solutes. Tentative evidence suggests that permeability characteristics of this subdermal layer are altered by smoke. While the mechanism behind smoke-induced germination is not known, it appears that smoke may be involved in overcoming different blocks to germination in different species. For example, in *Emmenanthe penduliflora*, NO_2 in smoke was sufficient to induce germination, and most forms of physical or chemical scarification also induced germination. For *Romneya coulteri*, NO_2 alone failed to induce germination, and scarified seeds required addition of gibberellic acid. In *Dicentra chrysantha*, none of these treatments, nor smoke alone, induced germination, but germination was triggered by a combination of soil burial followed by smoke treatment. Smoke-stimulated species differed substantially in the duration of smoke exposure required to induce germination, and this was inversely correlated with tolerance to smoke exposure. We suggest that such differences in response may affect postfire community structure.

Key words: California chaparral; fire; germination, smoke-induced; gibberellin; hard-seeded plant taxa; imbibition; NO_2; scarification; seed coat; smoke, stimulation of germination.

INTRODUCTION

Wildfires are a natural and widespread feature of temperate ecosystems, and many plant species have seedling recruitment restricted to habitats created by such disturbances (Keeley 1994, Bond and van Wilgen 1996). Life-history approaches to timing of recruitment to postfire conditions include postfire dispersal to the site (e.g., many pines), fire-stimulated flowering leading to second-year recruitment (e.g., most geophytes), or maintenance of seed banks cued by fire. Seed banks accumulate either in serotinous cones and fruits, where seeds are maintained in a quiescent state within the canopy, or in the soil, where deep dormancy delays germination until fire. Many species with soil-stored seeds have evolved barriers to germination that are normally overcome only by fire-related cues.

Fire-triggered germination is the result of either heat shock or chemical products of combustion, and species appear to utilize one or the other of these modes. Heat-shock-stimulated germination is widespread in the Fabaceae, Rhamnaceae, Convolvulaceae, Malvaceae, Cistaceae, and Sterculiaceae, and is found in many ecosystems (Ballard 1973, Christensen and Muller 1975,

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Bewley and Black 1982, Egley 1989, Keeley 1992, Kelly et al. 1992, Thanos et al. 1992, Bell et al. 1993). While an exhaustive study of germination characteristics for these taxa is lacking, those that have been studied are described as ''hard seeded,'' with a prominent waxy cuticle and dense palisade layer of sclerids that enforces dormancy by forming a water-impermeable barrier. Brief heat shock between 80° to 120°C is sufficient to induce imbibition by loosening cells in localized regions such as the hilum, chalazal cap, or strophiolar plug, or possibly denaturing inhibitors (e.g., Bell et al. 1993). This alone is sufficient to overcome dormancy in many species, although in some species heat shock must be coupled with light and/or cold stratification (Keeley 1987). This heat cue is not specific to fire, and soil heating on exposed sites, created by disturbances other than fire, can also induce germination.

For a substantial number of species with fire-triggered germination, heat shock has no effect on germination, rather germination is induced by chemicals from combustion products (Keeley 1991). Charred wood was first shown to stimulate germination in the postfire annual *Emmenanthe penduliflora* (Wicklow 1977, Jones and Schlesinger 1980) and also reported for many other species in western North America (Keeley et al. 1985, Keeley 1987, Keeley and Keeley 1987) and South Africa (Keeley 1992). Smoke also is an important chemical stimulant for germination of many ''fire type'' species, being demonstrated first by de Lange and Boucher (1990) for a South African fynbos shrub, and later for many other fynbos species (Brown 1993), a savannah grass (Baxter and van Staden 1994), a Great Basin annual (Baldwin et al. 1994), and a large number of Australian heath shrubs (Dixon et al. 1995). Smoke-stimulated germination has recently been reported for the California chaparral annual, *Emmenanthe penduliflora* (Keeley and Fotheringham 1997).

It is unclear whether or not the chemicals in charred wood that are responsible for triggering germination are the same as those responsible for smoke-induced germination. Several studies have attempted to determine the components responsible for charred wood (Keeley and Pizzorno 1986) and smoke-stimulated germination (Baldwin et al. 1994, van Staden et al. 1995), but have not identified the active component(s). Based on the observation that neither wood ash nor concentrated Hoagland's solution stimulated germination of several California chaparral species, it was suggested that dormancy is not broken by elevated levels of inorganic nutrients (Keeley 1991). On the other hand, Thanos and Rundel (1995), reported germination of *Emmenanthe penduliflora* in response to 10 mol/m^3 nitrate and concluded that this and other nitrogenous ions were responsible for fire-stimulated germination. This hypothesis is attractive since nitrate-stimulated germination has been demonstrated for many weedy species (Karssen and Hilhorst 1992) and has been identified as a potential gap-detection mechanism (Pons 1989). However, further studies with *Emmenanthe penduliflora* found that the nitrate ion alone failed to induce germination (Keeley and Fotheringham 1998), rather nitrogen oxides were the compounds responsible for smoke-stimulated germination (Keeley and Fotheringham 1997).

Relative to heat-shock-stimulated germination, little is known of the mechanism behind how fire-produced chemicals stimulate germination. Two broad categories of mechanisms are that these chemicals either (1) cause changes in the seed coat or other external layers, which overcome water-impermeability barriers, as is the case with heat-shock-stimulated seeds, or (2) act as internal signals and mediate germination by induction of enzymes or production of growth regulators. Studies of the Great Basin annual *Nicotiana attenuata* (Baldwin et al. 1994) and of *Emmenanthe penduliflora* (Keeley and Fotheringham 1997*a*) support the second hypothesis.

Based on the widespread occurrence of smoke-stimulated germination in other mediterranean-climate ecosystems, convergent-evolution theory would predict it to be widespread in California chaparral. The present study investigates the role of smoke-stimulated germination in a wide variety of chaparral species and addresses the following hypotheses and questions. (1) Is smoke-stimulated germination found in the same species that respond to charred wood and will vapors alone from charred wood stimulate germination? (2) Does smoke-stimulated germination require that seeds be directly exposed to smoke or can chemicals adsorbed onto soil particles stimulate germination? (3) Are the nitrogenous ions effective germination cues in smoke-stimulated species and, because nitrate stimulates germination by overcoming dark inhibition (Hilhorst and Karssen 1989), is smoke-stimulated germination light dependent? (4) Are smoke-stimulated seeds water impermeable and does smoke alter the imbibition characteristics, as is the case with heat-shock-stimulated seeds?

Methods

Species

Seeds of 34 species were collected from recently burned sites throughout southern California (USA) and, for some species, multiple populations were collected. Unless noted otherwise, seeds were stored at room temperature in closed glass bottles. For comparison with a heat-shock-stimulated species, seeds of *Ceanothus crassifolius*, collected from Santa Barbara County (California) chaparral, were purchased from S&S Seeds (Carpinteria, California, USA). Experiments were conducted over a period of 18 mo and no change in response was observed during this period.

Germination experiments

Germination was conducted in 60 × 15 mm sterilized polystyrene petri dishes with one piece of 55-mm

Whatman Number 1 filter paper with 30 seeds; there were three replicates per treatment. Petri dishes were placed on trays and, following treatment, germination was initiated by addition of 1.5 ml H_2O (Barnstead NANOpure II [Sybron Corporation, Dubuque, Iowa, USA] purified water used in all applications) or a test solution and given 1 mo cold stratification under dim light at 4°C, followed by incubation in Percival seed incubators under 12:12 light : dark photoperiod (photosynthetically active radiation, PAR = 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$) at 20°C:12°C. Treatments were separated on different trays and enclosed in ziplock bags to reduce evaporation and transfer of gases between treatments. Dark treatments were incubated in the same incubator but trays were covered with another tray and wrapped in multiple layers of black plastic and we assessed germination of seeds in a darkroom with dim green light. Germination was determined as the emergence of the epicotyl, and, for the smaller seeds, was done under a 7× dissecting scope, once a week for 1 mo. The percentage germination was arcsine-transformed prior to either one-way or multi-way ANOVA. Pairwise comparisons were made with the Bonferroni test.

Heat-shock treatments were applied to dry seeds in 60-mm outside-diameter glass petri dishes in a forced convection oven at 105°C or 115°C. Ovens were set above these temperatures and a metal tray with dishes was rapidly placed inside and air temperature within the oven was monitored with a thermocouple. Air temperature returned to the designated level within 1 min, after which the oven was maintained at that temperature (±1°C) for 5 min. This temperature range has been shown to be effective in breaking dormancy for a great many plant species (Keeley 1994).

Charred wood was prepared from the chaparral shrub *Adenostoma fasciculatum* by heating on a hot plate until ignited and then grinding in a Wiley mill to pass a 2-mm mesh sieve, then leached overnight in distilled water with stirring. Unless otherwise specified, a 5% (5 g/100 mL) solution was applied to seeds on filter paper. Fresh uncharred *Adenostoma* wood was tested in a similar manner.

Smoke treatments were performed by heating small branches and leaves of *Adenostoma* in a 150-mm (inside diameter) metal pan on a hot plate. A glass funnel with 150-mm (inside diameter) mouth was placed upside down on the pan and smoke escaped through a thick 50-cm long, 10-mm inside diameter, rubber hose, which fed into a smoke-tight 70-L glass chamber. Smoke was pulled into the tank by a vacuum line attached at the opposite end, and after 1 min filling, all ports were sealed and dry seeds (in petri dishes with filter paper) were incubated for various lengths of time. Temperature and relative humidity within the chamber were monitored during several trials with a 21× Campbell Micrologger [Campbell, Logan, Utah, USA] with copper-constantan thermocouples and CSI 207 relative-humidity probe. The temperature within the chambers normally would rise 1–2°C above ambient, which varied from 20–22°C. The relative humidity ranged from <60% for dry foliage to ~90% for fresh foliage.

The effect of indirect exposure of seeds to smoke was designed to test the potential for (1) the aqueous transfer of smoke products from soil to seed and (2) gaseous transfer from soil to seeds. First, aqueous transfer was tested by sowing untreated seeds directly into smoke-treated soil, which had been prepared 1–2 h earlier by exposing 10 g sand to smoke (one replicate on unsterilized water-washed sand and others on sterilized acid-washed Fisher S-25 sand), and addition of 2.75 mL H_2O (this experiment also was repeated using smoked filter paper in place of sand). Another test of aqueous transfer was the application of smoke-treated water to untreated seeds and filter paper; water samples were prepared by exposing 30 mL H_2O in an open 100-mm (outside diameter) petri dish to smoke. Second, gaseous transfer of smoke products was tested by exposing untreated seeds to vapors emitted by smoked sand or filter paper. Seeds had no physical contact with the smoke-treated sand (or paper) but were enclosed in a small chamber (180 cm^3 airspace) so they shared the same atmosphere. Specifically, 5 g of smoked soil (plus 5 mL H_2O) were placed in a 100-mm (outside diameter) petri dish bottom, along with a 60-mm (outside diameter) open petri dish of seeds and filter paper (plus 2 mL H_2O). This chamber was enclosed with an inverted 100-mm petri dish bottom on top and wrapped with parafilm (this experiment was repeated with smoke-treated filter paper or charred wood in place of sand).

Nitrate and ammonium ion (KNO_3 and NH_4NO_3, each at 1, 10, and 100 mol/m^3) and gibberellic acid (1, 5, and 10 $mmol/m^3$) solutions were prepared from freshly purified water or in buffered solutions of 25 mol/m^3 citrate-phosphate (pH range: 2.5–5), MES (2-[N-Morpholino]ethanesulfonic acid) buffer (pH 6; Sigma M-5287 [Sigma Chemical Company, Saint Louis, Missouri, USA]), or HEPES (N-[2-Hydroxyethyl] piperizine-N′-[ethanesulfonic acid]) buffer (pH 7 and 8; Sigma H-7523) and 2.0 mL added to a petri dish with filter paper. Hydrogen peroxide, nitric acid, sulfuric acid, and acetic acid were tested by soaking seeds in different molarity solutions for 6, 12, 18, or 24 h, followed by two distilled water rinses and then sowing on filter paper in petri dishes.

A potential confounding effect in these experiments involving aqueous solutions was the hydrophobicity of some species, which resulted in seeds floating on the solution surface. This effect was readily overcome by soaking seeds in lipase solution. Lipase concentrations of from 400–4000 *U*/mL (Sigma L-8525) (where *U* = moles of substrate converted per minute per milligram protein) in 50 mol/m^3 HEPES pH 7.7 buffer were effective in rapidly overcoming the hydrophobic character of the seed coat. All chemical treatments and

TABLE 1. Chaparral species demonstrating statistically significant smoke-induced germination (nomenclature according to Hickman [1993]). Seeds of all annual species were collected in southern California from first-year burns, and others were collected on 2–3 yr old burns. Seeds were 6–18 mo old at the time of experiments.

Family	Species	Growth form
Asteraceae	*Chaenactis artemisiifolia*	Annual
Boraginaceae	*Cryptantha clevelandi*	Annual
	C. micrantha	Annual
Brassicaceae	*Caulanthus heterophyllus*	Annual
Caryophyllaceae	*Silene multinervia*	Annual
Hydrophyllaceae	*Emmenanthe penduliflora*	Annual
	Eucrypta chrysanthemifolia	Annual
	Phacelia grandiflora	Annual
	P. minor	Annual
Lamiaceae	*Salvia apiana*	Shrub
	S. columbariae	Annual
	S. leucophylla	Shrub
	S. mellifera	Shrub
Loasaceae	*Mentzelia micrantha*	Annual
Onagraceae	*Camissonia californica*	Annual
Papaveraceae	*Romneya coulteri*	Suffrutescent†
Polemoniaceae	*Allophyllum glutinosum*	Annual
Scrophulariaceae	*Antirrhinum coulterianum*	Annual
	A. kelloggii	Annual
	A. nuttallianum	Annual
	Mimulus clevelandii	Suffrutescent†
	Penstemon centranthifolius	Suffrutescent†

† Suffrutescent = herbaceous with woody caudex.

water-uptake experiments were tested both with and without prior lipase treatment.

Gases in smoke were tested individually by exposing dry seeds (and filter paper) to commercially prepared gases in a glass chamber over a time course of from 0.5 to 1440 min. Concentrations were: carbon dioxide (7.7×10^3 or 1.5×10^6 mg/m^3), carbon monoxide (9.7×10^3 mg/m^3), nitrous oxide (100 mg/m^3), nitrogen dioxide (790 or 7.7×10^3 mg/m^3), ethylene (98 mg/m^3), and methane (55 mg/m^3), with the balance gas as N_2. Since the precise concentration and combination varies with fuel type, moisture, and combustion conditions, predicting their levels requires a chemically complex model (Ohlemiller et al. 1987, Lobert and Warnatz 1993); however, the levels used here were within the published ranges for biomass smoke.

To evaluate the effect of storage conditions on subsequent germination, a selection of species were placed in nylon bags and buried in soil outdoors in the autumn. After one year they were excavated, air-dried, given smoke treatments, and compared with seeds that had been stored over the same period in jars in the lab.

Seed coat characteristics

Physical scarification was performed by cutting with a scalpel, or puncturing with a pointed probe, through the coat until the underlying endosperm was exposed. Seeds were immediately wetted and incubation begun.

Uptake of dyes was determined by soaking either untreated or smoked seeds in eosin (1.6 mol/m^3, molecular mass = 624). Every day for a week, seeds were removed and blotted, and hand-cut thin sections were examined under 25× magnification. Seeds also were treated with lucifer yellow carbo-hydrazide (1.6 mol/m^3, molecular mass = 522), an apoplastic fluorescent tracer (Owens et al. 1991) (where ''apoplastic'' refers to that portion of the plant outside cellular protoplasts) and examined under a fluorescent scope at 25×. Using this lucifer yellow method, sites of dye impermeability within seeds are distinct and readily distinguished by their strong fluorescent emission. Since phenols and other cellular components may fluoresce, seeds soaked in water were compared for presence of autofluorescence.

Imbibition curves were determined by weighing dry seeds and re-weighing tissue-blotted seeds that had been emersed in water for periods of from 1 h to 1 wk.

Light micrographs of 1.5-μm transverse sections were sliced from seeds that had been fixed in paraformaldehyde-glutaraldehyde (pH 7.3), postfixed in 1% osmium tetroxide, stained in uraryl acetate, dehydrated in an alcohol series, and embedded in Spurr's resin.

RESULTS

Smoke and heat shock

Smoke induced a highly significant ($P < 0.001$) increase in germination for 22 (Table 1) of the 34 species

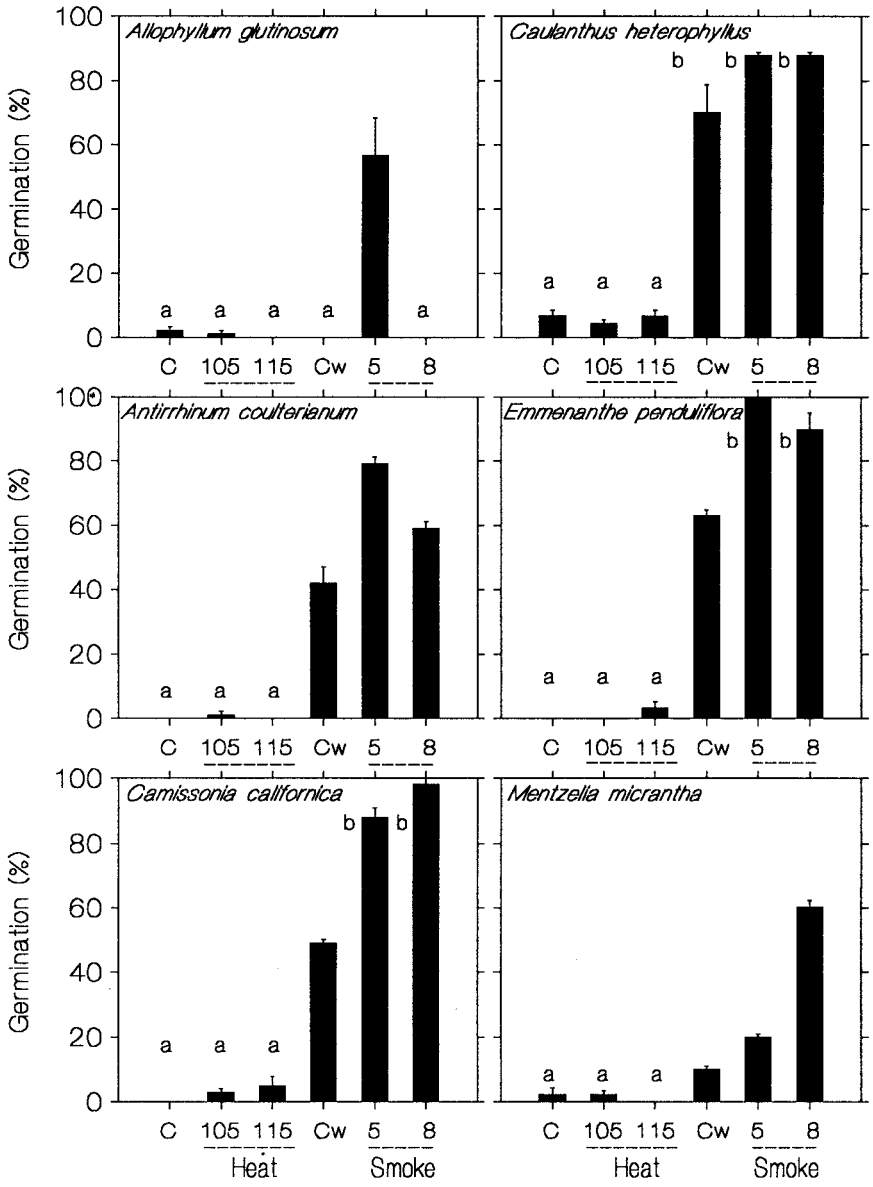

FIG. 1. Germination response for controls (C), and for treatments involving 5-min heat shock at 105°C and 115°C, 5% aqueous leachate of charred wood (Cw), and 5- and 8-min exposure of seeds plus filter paper to smoke, for 12 smoke-stimulated species from California chaparral. Data are means and 1 SE. Treatments (within a panel) with the same lowercase letter above the histogram bars are not significantly different ($P > 0.05$, $n = 3$ replicate dishes); bars without a letter are significantly different from all other treatments.

tested. The effect of heat shock, charred wood, and smoke on seeds resulted in several patterns that hold for all 22 smoke-stimulated species: (1) heat shock had no stimulatory effect, (2) charred wood also induced germination, and (3) smoke-stimulated germination was inhibited when coupled with either 105°C or 115°C treatment. In addition, some species stimulated by 5-min smoke exposure were inhibited by 8-min exposure; this was a lethal effect, as evidenced by the fact that, unlike controls, ungerminated seeds rotted.

Eight species (*Chaenactis glabriuscula, Cryptantha micromeres, C. muricata, Guillenia lasiophylla, Nicotiana attenuata, N. quadrivalis, Papaver californicum,* and *Silene antirrhina*) were not dormant and had >75% control germination, but all showed a significant drop in germination for one or the other of the heat-shock or smoke treatments.

Dendromecon rigida (Papaveraceae), *Dicentra chrysantha* (Papaveraceae), *Phacelia brachyloba* (Hydrophyllaceae), and *Trichostema lanatum* (Lamiaceae) did not germinate under any of the test conditions, including the combination of heat shock plus smoke (not

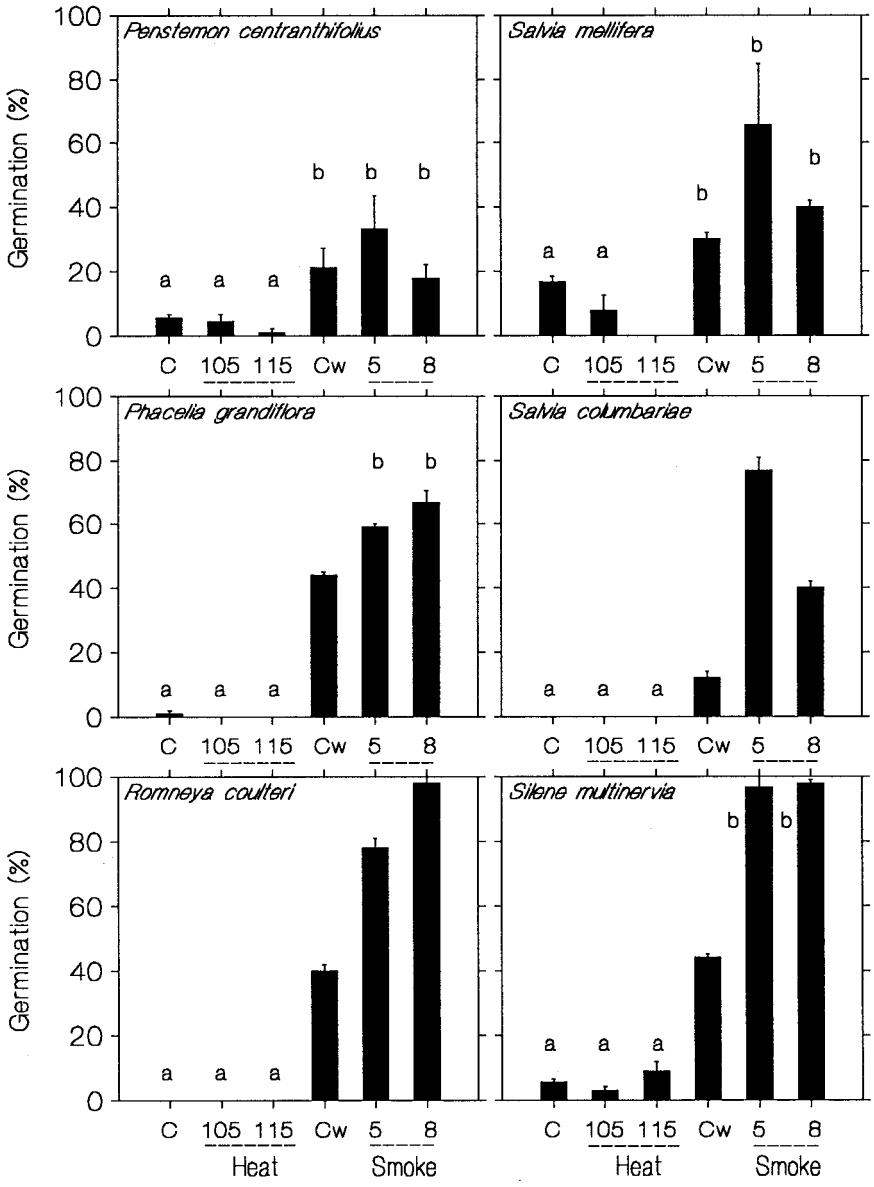

FIG. 1. Continued.

shown). Lack of germination in response to these factors is of particular interest because these four species are very closely linked to fire, and seldom if ever establish except in the first post-fire year. Further experiments (see *Soil storage effects,* below) were conducted with these species.

Smoke-stimulated species (Fig. 1) were tested several times over a period of 18 mo and no statistically significant difference ($P > 0.05$) was observed in response to smoke. Although an exhaustive study of the effect of wood type was not included, we did test smoke from pine ''sawdust'' on *Emmenanthe* and *Romneya* and found that it was equally as effective as smoke from *Adenostoma* wood. All species (Table 1) were investigated for the interaction between smoke stimulation and length of cold stratification for 0, 1, or 4 wk at 4°C. None of the species required cold treatment for substantial smoke-induced germination; however, three species—*Emmenanthe, Romneya,* and *Salvia columbariae*—had significantly ($P < 0.01$) higher germination after 1-wk cold treatment, and sometimes there were further increases after 4 wk cold.

Nitrogenous ions and light

All but one of the 22 smoke-stimulated species failed to respond to continuous incubation in 1, 10, or 100 mol KNO_3/m^3 (e.g., Fig. 2). *Silene multinervia* was stimulated slightly by nitrate, and this response was light dependent (Fig. 3), but nitrate failed to produce the level of germination induced by smoke (Fig. 2). In

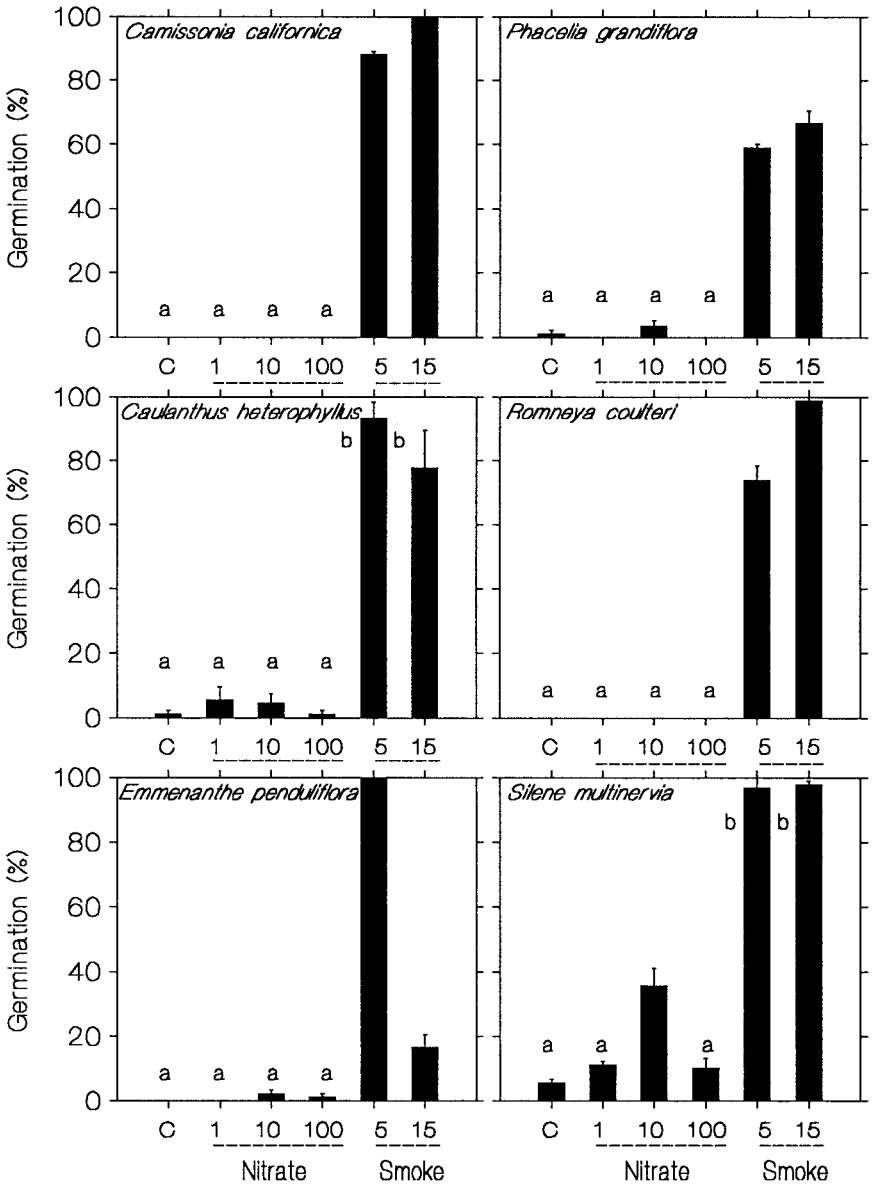

FIG. 2. Germination response for controls (C), and for treatments involving unbuffered 1, 10, and 100 mol KNO_3/m^3 and 5- and 15-min exposure of seeds plus filter paper to smoke, for six smoke-stimulated species (all smoke-stimulated species were tested; see *Results: Smoke and heat shock*). Data and treatment codes are as in Fig. 1.

no species was germination induced by either 10 mol NH_4NO_3/m^3 or by fresh uncharred *Adenostoma* wood (examples in Fig. 3).

Smoke-stimulated germination generally was not light dependent, although in two cases, *Romneya* (Fig. 3) and *Allophyllum*, smoke-induced germination was significantly ($P < 0.01$, not shown) less in the dark. In many species, smoke-stimulated germination was significantly ($P < 0.01$) greater than 5% (mass/volume) charred-wood extract (e.g., Fig. 1), but not greater than a 10% extract (e.g., Fig. 3).

Two of the species responding most markedly to smoke (*Emmenanthe* and *Romneya*) were selected for more detailed studies of their response to nitrogenous ions. Solutions of 10 mol/m^3 potassium nitrate and sodium nitrite were prepared at pH 3, 4, 5, 6, and 7. In contrast to previous experiments with KNO_3 in water (Figs. 2 and 3), *Emmenanthe* exhibited substantial germination in KNO_3 at all pHs ≤ 5, but failed to germinate at pH 7 (Table 2). Although complete germination was induced at pH 3, this solution was lethal to the seedlings soon after emergence from the seed coat. Continuous incubation of *Emmenanthe* in $NaNO_2$ was largely lethal (i.e., seeds rotted) at all

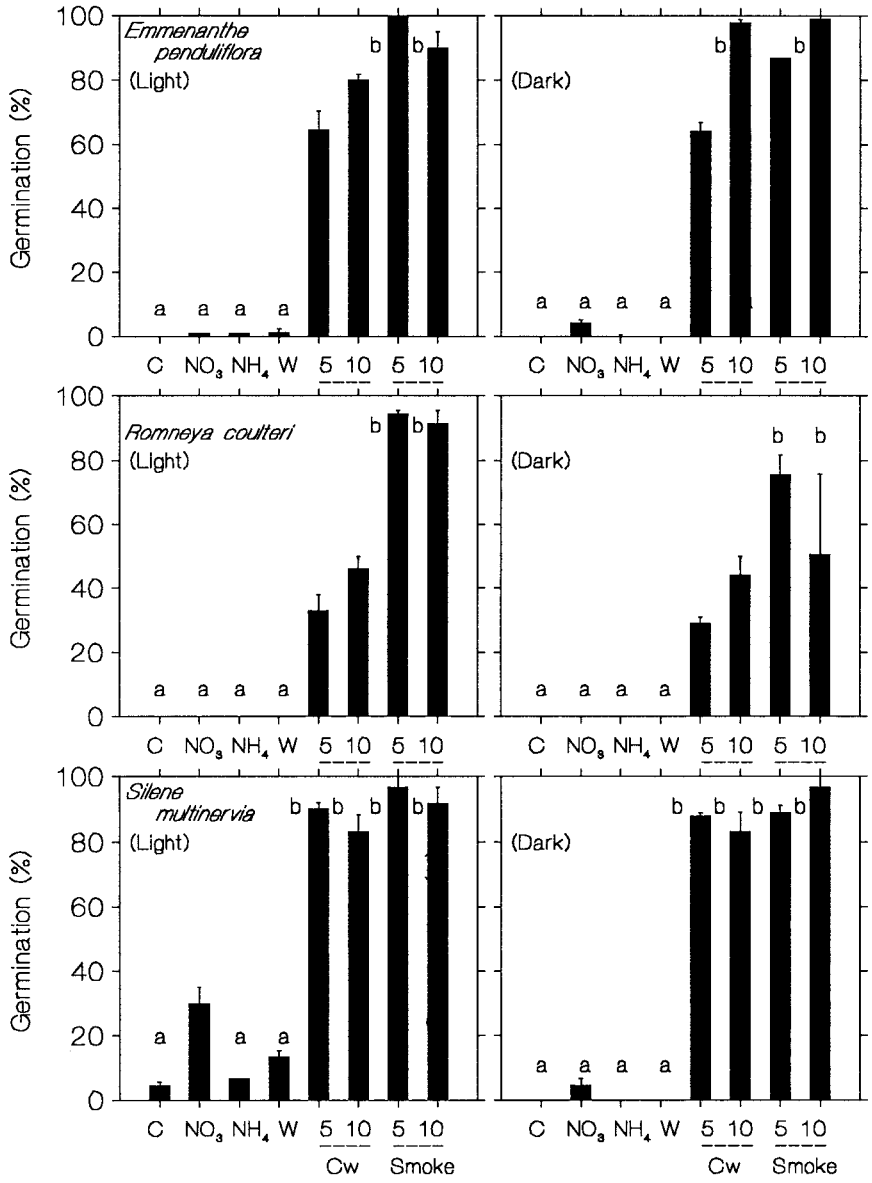

FIG. 3. Germination response to light (left side) and dark (right side) for controls (C), and for treatments involving unbuffered 10 mol KNO_3 /m^3, 10 mol NH_4NO_3/m^3, 10% aqueous leachate of fresh uncharred *Adenostoma* wood (W), 5% and 10% aqueous leachate of charred wood (Cw), and 5- and 15-min exposure of seeds plus filter paper to smoke. These three species represent the range of responses observed for smoke-stimulated species tested. Data and treatment codes are as in Fig. 1.

pHs, but with a 12-h pulse prior to incubation, germination was greatly stimulated (Table 2). *Romneya* failed to respond to KNO_3 at any pH, but nitrite stimulated germination at low pH.

Smoke tolerance and mode of transfer

It was apparent from the initial smoke experiments (Figs. 1–3) that species differed in duration of smoke exposure required to induce germination or in tolerance to the longer smoke exposures; e.g., 15-min exposure was lethal to *Emmenanthe* germination but optimum for *Romneya* germination (Fig. 2). In these initial experiments both seeds and filter paper (used as incubation medium) were exposed to smoke. In subsequent trials reported in this section, we tested the effect of direct exposure of seeds alone (followed by incubation on untreated filter paper) (Fig. 4A), vs. indirect exposure produced by sowing untreated seeds on smoked sand (or filter paper) (Fig. 4B), or by exposing seeds only to vapors emitted from smoked sand or filter paper (Fig. 4C). These experiments demonstrated significant ($P < 0.001$) effects due to time and treatment and sig-

TABLE 2. Germination response of smoke-induced species to nitrogenous compounds (10 mol/m^3) across the pH range 3–7, with continuous application in the incubation medium, except where indicated otherwise (n = 1 dish of 30 seeds).

	Germination (%)				
	pH 3	pH 4	pH 5	pH 6	pH 7
Emmenanthe					
Control	0	0	0	0	0
KNO_3	100	90	90	0	0
$NaNO_2$	0	0	0	20	10
$NaNO_2$ (12-h pulse)	0	30	100	90	0
Romneya					
Control	0	0	0	0	0
KNO_3	0	0	0	0	0
$NaNO_2$	0	0	0	75	0

nificant interactions between species and time and treatment. *Romneya* required very long direct exposure to smoke, and then barely exceeded 50% germination, but, in contrast, *Emmenanthe* germinated completely with only a few minutes of direct smoke exposure (Fig. 4A). Both *Emmenanthe* and *Romneya* were induced to germinate by exposure to smoke-treated substrates (Fig. 4B). Other species (not shown) with significant ($P < 0.001$; mean ± 1 SE) germination on smoke-treated sand were *Phacelia grandiflora* (92 ± 4%) *Caulanthus* (45 ± 4%), *Silene multinervia* (72 ± 6%), and *Camissonia* (62 ± 5%).

Comparison of germination in response to direct (Fig. 4A) and indirect (Fig. 4B) smoke exposure indicates that substrates are more effective than seeds at absorbing germination-inducing chemicals (evident with *Romneya*) and substrates are also more effective at absorbing lethal chemicals (evident with *Emmenanthe*).

The mode of transfer of smoke chemicals from soil particles to seeds is by aqueous leachates and gases. Aqueous transfer is demonstrated by germination induction with smoke-treated water (Fig. 5). Lethal chemicals are also water soluble as these solutions inhibited the germination of some species such as *Emmenanthe* (Fig. 5)—water exposed to 10-min smoke completely inhibited germination (in both populations tested), but 1/10 and 1/20 dilutions of 10-min smoke-treated water gave high germination (Fig. 5); in addition, highly significant germination was still recorded with 1/50 dilution (not shown). In contrast, other species such as *Romneya* tolerated full-strength solutions prepared from 10-min exposure, but declined with dilution (Fig. 5).

Gaseous transfer of smoke chemicals is apparent from the high germination induced in both *Emmenanthe* and *Romneya* seeds when untreated moist seeds were exposed indirectly to vapors emitted from moistened smoked sand (or filter paper) (Fig. 4C). Complete germination was also observed when dry seeds were exposed to gases emitted from dry media that had previously been exposed to smoke (data not shown). Based

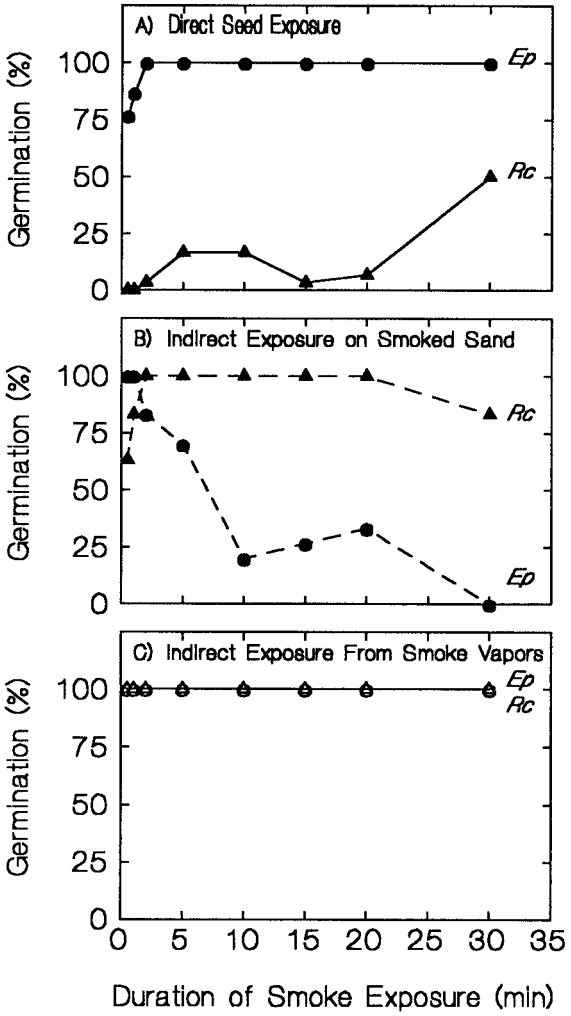

FIG. 4. Germination response for *Emmenanthe penduliflora* (*Ep*) and *Romneya coulteri* (*Rc*) seeds: (A) exposed directly to smoke—filter paper not smoke-treated as in Figs. 1–3, (B) exposed indirectly by sowing untreated seeds on smoked sand, and (C) exposed indirectly to vapors emitted by smoke-treated sand. Both experiments (B) and (C) were repeated using smoke-treated filter paper, and the results were nearly identical.

on this observation, we hypothesized that charred wood induced germination by emitting vapors that also occur in smoke. Exposure of *Emmenanthe*, *Romneya*, and *Caulanthus* seeds to charred-wood vapors induced 79%, 44%, and 38% germination, respectively ($P < 0.001$ over controls).

Soil storage effects

Seeds of four species that completely failed to germinate in the initial smoke experiments were buried outdoors for 1 yr, dried, and then smoke-treated. Following this long-term soil storage, three of these species—*Dendromecon*, *Dicentra*, and *Trichostema*—were stimulated to germinate by smoke treatment (Fig. 6), but soil-stored seeds of the fourth species, *Phacelia*

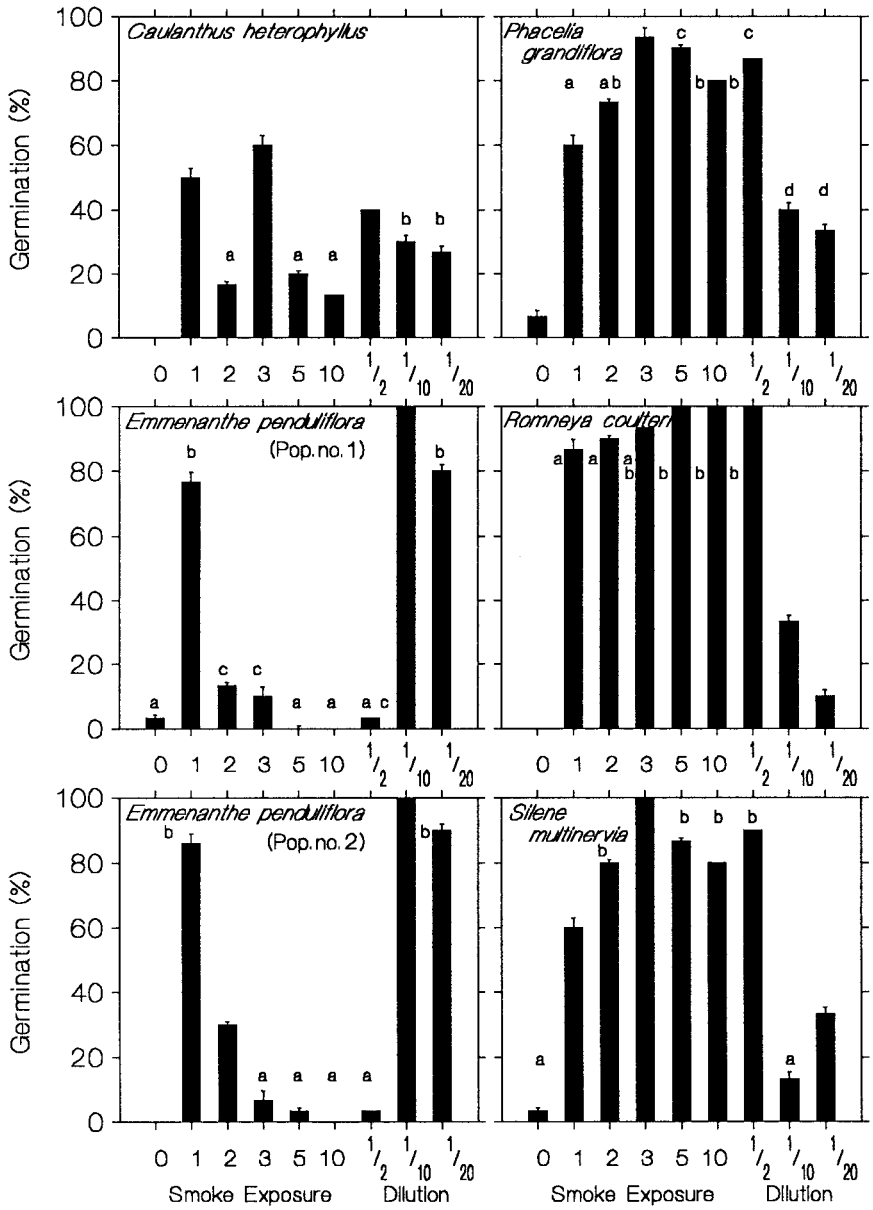

FIG. 5. Germination response of two *Emmenanthe penduliflora* populations and four other smoke-stimulated species to application of smoke-treated water samples exposed to 0 (control), 1, 2, 3, 5, or 10 min of smoke or different dilutions of the 10-min smoke-treated sample. Data are means and 1 SE. Treatments (within a panel) with the same lowercase letter above the bars are not significantly different ($P > 0.05$, $n = 3$ replicate dishes); bars without a letter are significantly different from all other treatments.

brachyloba, still failed to germinate (not shown). Several other species exhibiting smoke-stimulated germination in the original experiments (from room-stored seed) were also buried for 1 yr and then re-tested. In some species, e.g., *Emmenanthe*, there was no change in germination response. Buried *Romneya* seeds were found to be smoke-stimulated at shorter durations of smoke exposure, and others, e.g., *Phacelia minor*, exhibited significantly ($P < 0.001$) higher smoke-induced germination following long-term soil burial (data not shown).

Seed coat scarification

The effect of physical scarification of the seed coat exhibited three patterns in smoke-induced species. (1) In the majority of species tested, scarification was sufficient to induce high germination (Table 3). (2) In *Romneya*, scarification alone was largely ineffective,

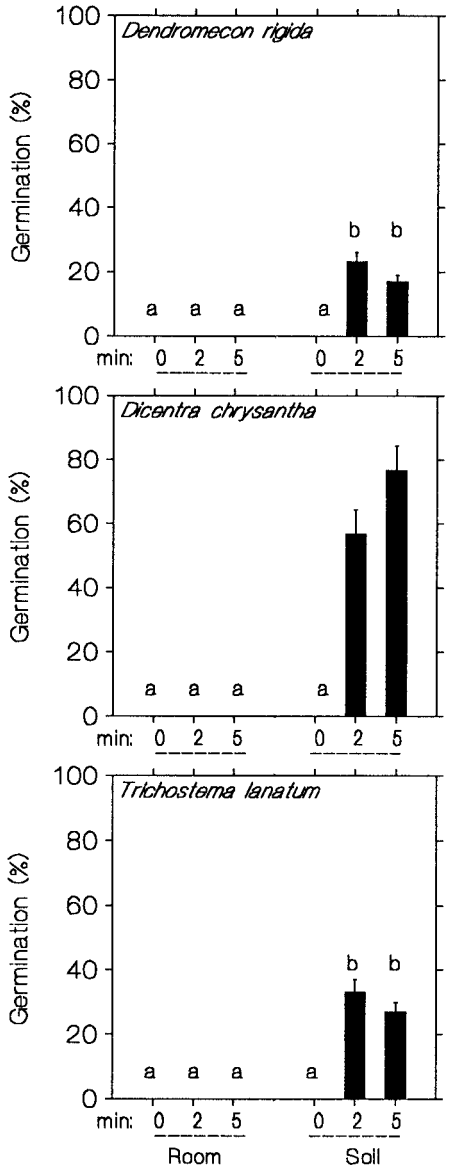

FIG. 6. Smoke-stimulated germination in three species (*Dendromecon rigida, Dicentra chrysantha,* and *Trichostema lanatum*) which failed to germinate in the original experiments (Figs. 1–3). Here germination is compared between seeds stored dry in bottles at room temperature and seeds stored outdoors in soil for 1 yr, then air-dried and smoke-treated for 0 (controls), 2, or 5 min. Experiments were done 1 yr after those reported in Fig. 1. Data and treatment codes are as in Fig. 5.

but, scarification plus gibberellic acid (GA) induced complete germination—though scarification plus potassium nitrate, ethylene, or carbon dioxide failed to stimulate germination. (3) In *Dicentra, Dendromecon,* and *Phacelia brachyloba* neither scarification, nor scarification + GA, induced germination in either room-stored or soil-stored seed.

Exposure to acids, which may have caused chemical scarification of the seed coat, also induced germination in some smoke-stimulated species, but not others (Fig. 7). *Emmenanthe* germinated well with pulses of 10 mol/m^3 of acid, and *Silene multinervia* germinated best with 100 mol/m^3 of acid (Fig. 7). On the other hand, *Romneya* failed to respond to any acid treatment (Fig. 7), including continuous application of 50 or 100 mmol/m^3 of acids (not shown). Although not illustrated, similar results were obtained with acetic acid (*Emmenanthe* = 77% germination with 10 mol/m^3, *Romneya* = 0% with 1, 10, and 100 mol/m^3 and *Silene* = 66% with 100 mol/m^3). Other species induced to germinate by acid treatment were *Phacelia grandiflora* (23% with a 6-h pulse of 10 mol/m^3 of nitric acid) and *Caulanthus* (100% with an 18-h pulse of 100 mol/m^3 of nitric acid). In these latter two species sulfuric acid was about half as effective, and acetic acid was ineffective.

These acid treatments were not effective when buffered at higher pH; solutions adjusted to pH 3, 4, 5, 6, 7, and 8 showed *Emmenanthe, Phacelia grandiflora, Caulanthus,* and *Silene multinervia* were stimulated only at pH $\leq$ 6 (data not shown). However, buffered controls failed to induce germination in any species at any pH. Neither *Romneya* nor *Dicentra* germinated in response to nitric or sulfuric acids solutions buffered at pH3-8. Hydrogen peroxide pulses were also highly effective for some species such as *Emmenanthe* and *Silene multinervia,* but not for others such as *Romneya* (Fig. 8). Induction of germination by hydrogen peroxide could be due to either chemical scarification of the seed coat or to an enhancement of the oxygen levels. To evaluate the latter, species were incubated for either 24 h or 1 wk in water supersaturated with 100% oxygen. *Emmenanthe, Phacelia grandiflora, Romneya,* and *Silene multinervia* failed to respond to this treatment. *Caulanthus* and *Camissonia californica* produced 50% and 93% germination, respectively, with 24-h oxygen (controls were 5% and 7%, respectively).

One potential confounding effect in these experiments is that seeds of some species are profoundly hydrophobic and floated on top of these solutions, whereas other, less hydrophobic species, were submerged in these solutions. Of five smoke-stimulated species tested, we ranked them from most to least hydrophobic as follows: *Dicentra* > *Romneya* $\gg$ *Emmenanthe* > *Phacelia grandiflora* > *Silene multinervia* > *Caulanthus.* This effect was readily overcome by soaking seeds in lipase (4000 Units/mL) solution, and generally 10 min was sufficient to result in seeds sinking in solutions. Nonetheless, lipase treatments of 10 min, 1 h, or 2 h failed to have a positive or negative effect on subsequent response to nitric acid, sulfuric acid, hydrogen peroxide treatments, or controls.

Gases

The gases CO_2, CO, N_2O, C_2H_4, and CH_4. had relatively little significant effect on germination, but nitrogen oxides, in particular NO_2, were highly effective

TABLE 3. Effect of physical seed-coat scarification and gibberrillic acid (GA_3) on germination of a heat-shock-stimulated *Ceanothus* (for comparison) and smoke-stimulated species. Data are means ± 1 SE; $n = 3$ replicate dishes.

Species	Germination (%)						
	Control		GA(1, 5, and 10 mmol/m^3)		Seed-coat scarification		Scarification + GA (10 mmol/m^3)
Ceanothus crassifolius	0 ± 0		0 ± 0	**	90 ± 3		92 ± 2
Emmenanthe penduliflora							
Pop. no. 1	0 ± 0		0 ± 0	**	100 ± 1		100 ± 1
Pop. no. 2	0 ± 0		0 ± 0	**	70 ± 5		65 ± 2
Phacelia grandiflora	1 ± 0		0 ± 0	**	99 ± 1		95 ± 2
Romneya coulteri							
Pop. no. 1	0 ± 0		0 ± 0	**	19 ± 1	**	100 ± 0
Pop. no. 2	0 ± 0		0 ± 0	*	4 ± 2	**	63 ± 0
Caulanthus heterophyllus	1 ± 1		1 ± 1	**	53 ± 3		45 ± 4
Silene multinervia	8 ± 3	**	29 ± 4	**	98 ± 1		95 ± 2
Camissonia californica	0 ± 0		0 ± 0	**	75 ± 2		82 ± 4
Dicentra chrysantha							
Room	0 ± 0		0 ± 0		0 ± 0		0 ± 0
Soil	0 ± 0		0 ± 0		0 ± 0		0 ± 0

* $P < 0.05$, ** $P < 0.01$, significant difference beteen treatments.

in breaking dormancy (Fig. 9), and there were significant ($P < 0.001$) effects due to duration and species. All seeds of both *Emmenanthe* populations and *Silene multinervia* germinated in response to NO_2, but the former species responded to much shorter durations of exposure. *Phacelia grandiflora* and *Caulanthus* had statistically significant ($P < 0.001$) increases in germination with NO_2 exposure. *Romneya* failed to respond to any NO_2 exposure (Fig. 9), and repeated trials with both NO_2 and NO, and both dry and pre-moistened seeds and soil-stored seeds failed to elicit a response in this species. *Dicentra* (both room-stored and soil-stored seed) also failed to respond to NO_2 treatment (data not shown). Sulfur dioxide did enhance *Emmenanthe* germination to 57% but was ineffective for other species. Sowing untreated seeds in NO_2-treated sand induced germination in *Emmenanthe* (87%), *Phacelia grandiflora* (33%), and *Silene multinervia* (43%) but not in *Romneya* (0%).

Imbibition

With the exception of *Silene multinervia*, the moisture content of dormant seeds was similar among smoke-stimulated species and not unlike the single heat-shock species, *Ceanothus crassifolius*, included for comparison (Table 4). For all species, imbibition curves were initially steep (Phase I), but within 24 h the net uptake of water plateaued (Phase II) and remained at this level for a week or more, until germination (Phase III). Comparison of Phase II water-uptake levels for chaparral plants (Table 4) showed a striking difference in the pattern observed for a typical heat-shock-stimulated species (*Ceanothus crassifolius*) and those of selected smoke-stimulated species studied here. The hard-seeded *Ceanothus crassifolius* had a water-impermeable seed coat that blocked water uptake until heat treatment broke this barrier (Table 4). Dormant seeds of smoke-stimulated species, on the other hand, readily imbibed water and smoke treatment produced no change in imbibition. Water uptake varied markedly across species, but was exceptionally high in *Caulanthus*, due to the swelling of the gelatinous outer sheath.

Seed coat characteristics

Eosine-dye uptake patterns were markedly different between the heat-stimulated *Ceanothus* and the smoke-stimulated species. Dye did not penetrate beyond the outer cuticle of dormant *Ceanothus* seeds, whereas in dormant smoke-stimulated species it was readily adsorbed by the testa, but was blocked from penetrating the endosperm by a subdermal barrier—a pattern observed for *Emmenanthe*, *Phacelia grandiflora*, *Romneya*, and *Dicentra*. Following smoke treatment dye readily permeated the endosperm and embryo in these species.

Two smoke-stimulated species that differed from this pattern were *Camissonia* and *Eucrypta*. In the former species dye penetration was blocked by an outer cuticle, and in the latter species dye permeated through the endosperm of dormant seeds but was blocked from entry into the embryo. In both species smoke treatment resulted in complete dye penetration throughout the seed. The presumed-apoplastic, lucifer-yellow fluorescent dye demonstrated similar patterns. However, penetration following smoke treatment was not highly con-

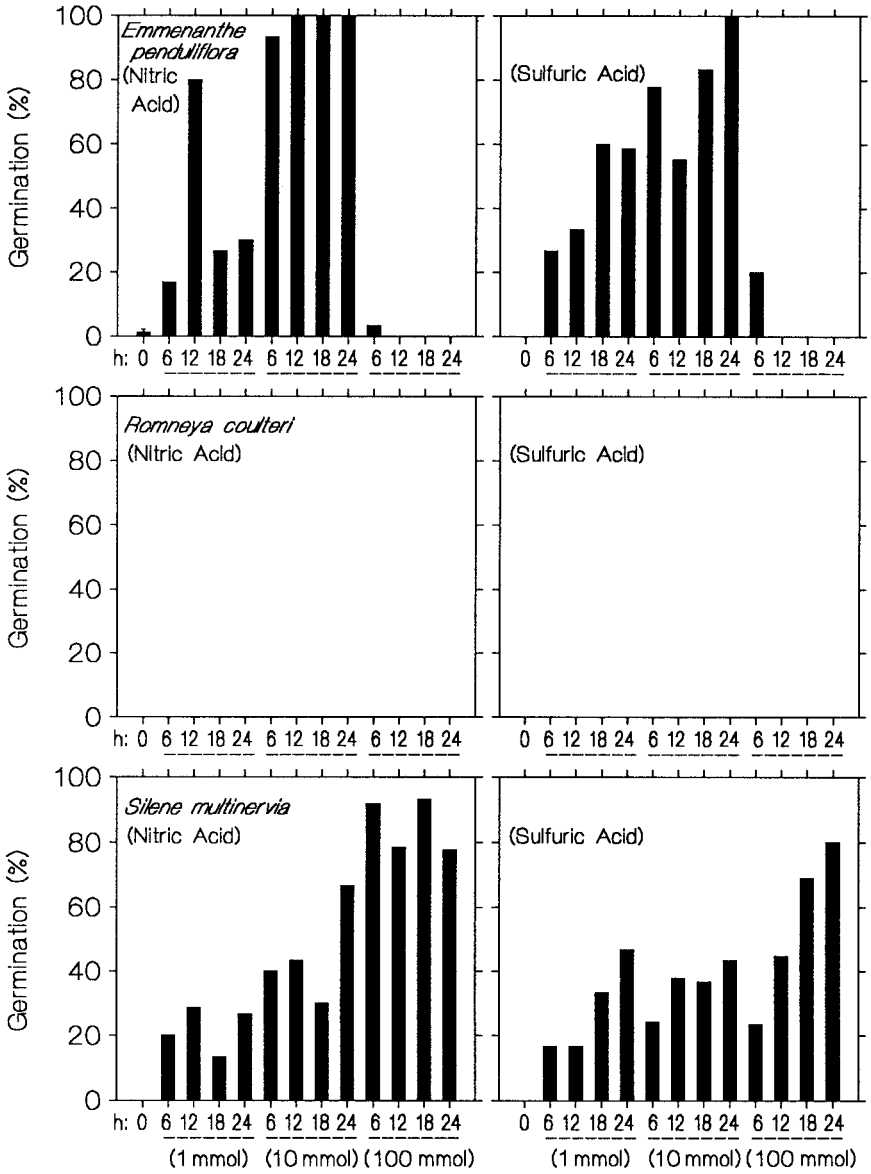

FIG. 7. Germination response to nitric acid (left side) and sulfuric acid (right side) at different molarities and duration of treatment (in hours) for three species, illustrating the range of responses observed for six smoke-stimulated species tested (n = 1 dish of 30 seeds).

sistent and locating it was compromised by natural background fluorescence from phenolics and other cellular components; autofluorescence was often very high in the seed coat (*Dicentra, Romneya*), endosperm (*Phacelia brachyloba*), or embryo (*Eucrypta*).

Structurally, there were several characteristics shared by many of the smoke-stimulated species. For all but *Camissonia, Caulanthus,* and *Salvia* spp. there was a weakly developed outer cuticle and the exterior of the testa was highly sculptured, in contrast to the generally smooth architecture typical of the *Ceanothus* seeds and many other heat-stimulated seeds. None of the species examined had a palisade layer in the seed coat. Based on the types of cells and non-cellular material making up the testas, it would appear that the structures forming the testa were of different origin in different species.

DISCUSSION

Deeply dormant soil seed banks are widespread in California chaparral, and smoke generated during wildfires triggers abundant germination in many distantly related species. Previous reports of charred-wood-stimulated germination (Keeley 1991) appear to represent the same phenomenon, since charred-wood-stimulated species respond as strongly or more strongly to smoke

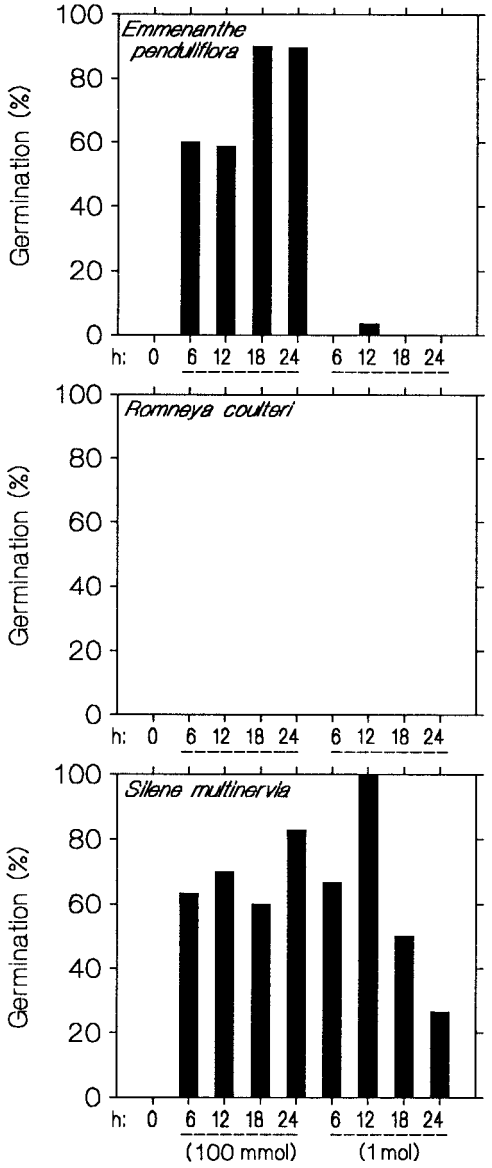

FIG. 8. Germination response to hydrogen peroxide at different molarities and duration of treatment (in hours) for three species, illustrating the range of responses observed for six smoke-stimulated species tested (n = 1 dish of 30 seeds).

(Figs. 1 and 3), and vapors from charred wood can induce significant germination. Smoke can effectively break dormancy by directly penetrating the seed, or indirectly by adsorption onto soil particles and later releasing chemicals in vapors or aqueous leachate (Figs. 4 and 5).

Experiments on a small subset of the flora support the conclusions that smoke-induced species (1) differ in the concentration of smoke-generated chemicals required to stimulate germination, (2) differ in tolerance to duration of smoke exposure, (3) are similar in their response to both direct and indirect exposure to aqueous and gaseous derivatives of smoke, (4) are not ''hard-seeded'' and, unlike heat-stimulated germination, smoke does not obviously alter seed-coat characteristics that would result in changes in imbibition, (5) are similar in possessing a sub-dermal cuticle that blocks solute uptake in dormant seeds and having permeability altered by smoke, and (6) differ in the numbers and types of barriers to germination, suggesting the mechanism of smoke-induced germination may be different within the smoke-induced flora.

Some species such as *Emmenanthe* require only brief exposure to smoke or smoke extracts to induce germination, whereas others such as *Romneya* require longer exposure and an opposite pattern is evident with smoke tolerance (Figs. 4 and 5). These differences suggest that fire behavior may play a role in structuring postfire communities—fires in very dry fuels, driven by high winds, potentially will generate very different smoke exposure than slow smoldering fires in moister fuels (Weise et al. 1991, Lobert and Warnatz 1993, Borchert and Odion 1995, Hardy et al. 1996). The level and moisture content of soil organic matter may play an even greater role, as this is potentially an important source of fuel in the soil environment (DeBano and Conrad 1978). In addition, soil organic matter may greatly affect the postfire chemistry, particularly with regards to organic acids and cation/anion balance (Blank et al. 1996).

The mechanism of smoke-induced germination is distinctly different from that of heat-shock-stimulated germination, typical of chaparral species in the Fabaceae and Rhamnaceae. Heat-shock germination is initiated by heat breaking the water-impermeable testa and inducing imbibition. In smoke-stimulated species, dormant seeds freely imbibe water (Table 4), although most all appear to have a subdermal cuticle that blocks uptake of certain solutes. Smoke increases the solute permeability of this semi-permeable membrane, but it is unknown whether or not this is involved in the induction of germination.

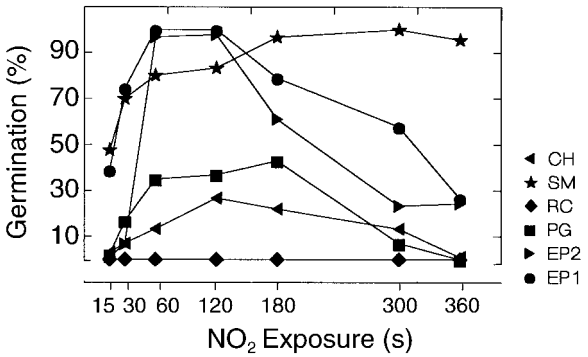

FIG. 9. Germination response to nitrogen dioxide (7.7×10^3 mg/m^3) at different durations of exposure applied to dry seeds for the two populations of *Emmenanthe penduliflora* (EP1 and EP2), *Phacelia grandiflora* (PG), *Romneya coulteri* (RC), *Silene multinervia* (SM), and *Caulanthus heterophyllus* (CH).

TABLE 4. Characteristics of dormant seeds and either heat-treated (*Ceanothus crassifolius* included for comparison) or smoke-treated seeds. Replicates of 100 seeds each are $n = 15$ for seed mass, otherwise $n = 5$. Data are means ± 1 SE.

	Seed mass (mg)†	Moisture (%)‡	Water uptake (%)§		
			Dormant		Treated
Ceanothus crassifolius	9.221 ± 0.001	7 ± 2	3 ± 1	***	78 ± 4
Emmaenanthe penduliflora, Pop. no. 1	0.445 ± 0.006	8 ± 1	63 ± 1		67 ± 1
Romneya coulteri, Pop. no. 1	0.835 ± 0.004	6 ± 0	46 ± 2		47 ± 1
Phacelia grandiflora	0.130 ± 0.004	9 ± 1	40 ± 4		43 ± 4
Caulanthus heterophyllus	0.393 ± 0.005	6 ± 2	109 ± 10		116 ± 9
Silene multinervia	0.153 ± 0.004	14 ± 2	65 ± 7		66 ± 8
Camissonia californica	0.241 ± 0.005	7 ± 1	41 ± 4		41 ± 4
Dicentra chrysantha‖					
Room	0.782 ± 0.022	7 ± 1	30 ± 3		28 ± 4
Soil	0.783 ± 0.028	7 ± 1	35 ± 4		33 ± 2

*** $P < 0.001$, significant difference between treatments.
† Air-dry seed mass.
‡ As percentage of dry mass.
§ Percentage at steady-state Phase II imbibition curves.
‖ Both room-stored and soil-stored seeds were tested; see Fig. 6 for explanation.

Although the mechanism of smoke-triggered germination is not known for any species, the responses observed here indicate that these smoke-induced species differ in the number of barriers that must be overcome to induce germination. These differences are most clearly illustrated when comparing three species with very deeply dormant seeds; *Emmenanthe, Romneya,* and *Dicentra.* For example, freshly collected seeds of both *Emmenanthe* and *Romneya* germinate readily when treated with smoke, whereas *Dicentra* seeds require extended outdoor burial in soil prior to smoke treatment (Fig. 6). The smoke-induced germination of soil-stored *Dicentra* (but not of room-stored) seeds is of profound significance because of its very deep dormancy. Previous studies have tested tens of thousands of room-stored seeds with heat, charred wood, smoke, and all possible combinations but failed to induce germination of even a single seed (Keeley 1991). It appears that prior to smoke exposure, *Dicentra* seeds require an extended period of moist afterripening or interaction with some component of the soil environment, a phenomenon that is shared with other hard-to-germinate species such as *Dendromecon* and *Trichostema.*

The treatments required to induce germination in the absence of smoke also indicate that species differ in the numbers and types of barriers to germination. For example, physical scarification alone is sufficient to induce germination in *Emmenanthe,* whereas in *Romneya* scarification must be coupled with GA (gibberellic acid), but in *Dicentra,* scarification plus GA (even with soil-stored seed) is insufficient (Table 3). Differences are evident with other treatments as well, e.g., *Emmenanthe* germinates completely with brief pulses of nitrogen dioxide, nitric acid, sulfuric acid, or hydrogen peroxide, none of which induced germination in *Romneya* or soil-stored *Dicentra.*

Hypothesized mechanisms behind smoke-induced germination include: (1) increased solute permeability of the subdermal cuticle may enhance the uptake of ions or gases that induce germination, (2) increased solute permeability of the subdermal cuticle may result in the leaching out of internal inhibitors, (3) nitrates in smoke may trigger germination, (4) acids in smoke may lead to internal acidification, and (5) induction of enzymes or growth regulators by chemicals in smoke.

A potential role for either hypothesis 1 or 2 is suggested by the smoke-induced changes in solute permeability of the semi-permeable subdermal cuticle of most species thus far examined. Further support is suggested by the induction of germination following physical scarification of the seed coat in several smoke-stimulated species (Table 3). However, it is possible that the mechanism behind scarification-induced germination is unrelated to smoke-induced germination. The observation that high oxygen tensions alone could induce substantial germination in *Caulanthus* and *Camissonia* suggests that there may be seed-coat-associated barriers to oxygen uptake in these species that are not present in other species.

Hypothesis 3 is suggested by the observation that high nitrate levels stimulate germination in many species (Hendricks and Taylorson 1974), and may cue germination of weedy species to gaps (Pons 1989), but its role in the induction of postfire chaparral is doubtful. We were able to duplicate the prior report of nitrate-stimulated germination by Thanos and Rundel (1995), but only under conditions that failed to support their conclusion that nitrate is the principle factor triggering germination in postfire species. For both potassium ni-

trate and nitric acid, *Emmenanthe* and *Silene multinervia* germination was induced at pH < 6 but not at pH 7 or 8. Since nitrate is the base of a strong acid, it is present at equal concentrations across this pH range, thus the nitrate ion alone is not responsible for germination. This is consistent with the fact that chaparral seeds are not dark inhibited (Fig. 3), whereas nitrate is generally stimulatory in dark-inhibited species (Hilhorst and Karssen 1989). This suggests a possible role for nitrate may exist in coastal sage-type subshrubs where charred-wood-stimulated germination has previously only been demonstrated for seeds in the dark (Keeley 1991). The response of *Emmenanthe* and *Silene multinervia* to other forms of nitrogen, and the diverse nitrogen transformations possible following vegetation fires (Raison 1979, Bartlett 1981, O'Neill 1985), suggest that the role of nitrogenous compounds may be rather complex.

Nitrogen dioxide is a significant component of wood smoke (Browne 1958, Lobert and Warnatz 1993) and appears to be an important ecological trigger in the germination of *Emmenanthe* and *Silene multinervia*, and to a lesser extent of *Caulanthus* and *Phacelia grandiflora* (Fig. 9). Numerous experiments with different concentrations and durations of exposure of both NO_2 and NO failed to induce any germination in *Romneya* or *Dicentra*. However, such treatment was capable of cracking the *Romneya* seed coat. In light of the fact that *Romneya* germination was induced by scarification plus gibberellic acid (Table 3), we hypothesize that nitrogen dioxide in combination with other gases in smoke may trigger germination.

This difference in response to nitrogen dioxide, coupled with the failure to respond to either nitrate or nitric acid at any pH suggests that *Romneya* has a very different mechanism than *Emmenanthe* or *Silene multinervia*. Nitrite at pH 6 did induce high germination in *Romneya*, a pattern consistent with the dormancy-breaking model proposed by Cohn (1996). He maintains that dormancy-breaking chemicals are active only in their associated form because of their enhanced uptake ability. Nitrate is thought to be ineffective because it is dissociated, except at extremely low pH. Nitrite, on the other hand is present as nitrous acid across a broad pH spectrum. While Cohn (1989, 1996) has accumulated evidence that chemicals are most effective in their associated form, it is unknown whether the disassociated form, which is likely under cellular conditions, induces germination or whether internal acidification is responsible.

Surprisingly, ethylene, a known growth regulator in germination and an important component of biomass smoke, does not stimulate germination in any of the smoke-induced species tested here. The same has been reported for smoke-stimulated species in other ecosystems (de Lange and Boucher 1990, Baldwin et al. 1994, Baxter et al. 1994). Likewise, carbon dioxide is quantitatively the most important component of smoke (Levine 1991) and is known to stimulate germination (Bewley and Black 1982), but it had no stimulatory effect on any of our smoke-stimulated species. Other gases that do not appear to play a role in germination of these species include carbon monoxide, nitrous oxide, and methane.

In conclusion, the widespread occurrence in phylogenetically distant families (both within chaparral and between chaparral and other mediterranean-type ecosystems) suggests the hypothesis that smoke-induced germination is the result of convergent evolution. The apparent lack of homology in physiological mechanisms triggered by smoke also supports this conclusion. The recent observation that smoke may induce germination in succulent species from both fire-prone and non-fire-prone ecosystems (Pierce et al. 1995) suggests that the active components of smoke may be rather generally available in ecosystems and smoke-stimulated species may have been pre-adapted to these germination cues. Seedling recruitment restricted to post-fire sites, plus different germination behavior in desert populations of *Emmenanthe* (Jones and Schlesinger 1980) argues strongly for the ''current utility'' (sensu Pagel 1994) of the smoke-stimulated response in chaparral.

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