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Heated substrate and smoke: Influence on seed emergence and plant growth

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Abstract

Combustion products of burning vegetation can increase seed germination of many species of fire-prone plant communities. We tested the influence of heating sagebrush (*Artemisia tridentata* Nutt.) subcanopy soil, aqueous extracts of artificially burned soil, and sagebrush smoke on the emergence of several range plant species of the sagebrush-steppe. In addition, test seeds were exposed to sagebrush smoke and aqueous slurries of artificially burned sagebrush subcanopy soil to determine their effect on plant growth. As compared to the control, substrates previously heated from 250 to 750° C significantly ($P \leq 0.05$) increased the emergence of Thurber's needlegrass [*Achnatherum thurberianum* (Piper) Barkworth] and needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth]. Sagebrush smoke and aqueous slurries of artificially burned soil significantly increased the emergence of Sierra Nevada needlegrass [*Achnatherum occidentalis* (Thurber) Barkworth], Indian ricegrass [*Achnatherum hymenoides* (Roemer & Schultes) Barkworth], and antelope bitterbrush [*Purshia tridentata* (Pursh) DC.]. Rates of new leaf production and leaf elongation following treatment of seeds with the smoke of burning sagebrush were significantly greater for cheatgrass (*Bromus tectorum* L.), basin wildrye [*Leymus cinereus* (Scribner & Merr.) A. Löve], Idaho fescue (*Festuca idahoensis* Elmer), Sierra Nevada needlegrass, and needle-and-thread as compared to the control. After 83 days of growth, smoke-treated seeds of basin wildrye and needle-and-thread produced significantly greater plant mass than their controls. Smoke treatment of certain seeds before sowing is potentially useful for range plant seedings.

Resumen

Los productos de la combustión de la vegetación en llamas pueden incrementar la germinación de muchas especies de plantas propensas al fuego. Hemos probado la influencia calorífica de la artemisia (*Artemisia tridentata* Nutt.) en el subfollaje, los extractos acuosos del suelo artificialmente quemado ye el humo de la artemisia en la aparición de varias especies de plantas en las estepas de la artemisia (salvia). Además, muestras de semillas fueron expuestas al humo de la artemisia de lodos acuosos compuestos del suelo de la artemisia para determinar el efecto en el crecimiento de plantas. Comparado con el estudio de control, los substratos previamente calentados a temperaturas de 250 a 750° C incrementaron ($P < 0.05$) significativamente la aparición de pasto aguja [*Achnatherum thurberianum* (Piper) Barkworth] y [*Hesperostipa comata* (Trin. & Rupr.) Barkworth]. El humo de la artemisa y los acuosos del suelo artificialmente quemado, han incrementado significativamente la aparición del pasto aguja en la Sierra Nevada [*Achnatherum occidentalis* (Thurber) Barkworth], asi como tambien la aparición del pasto del tipo "arroz' Hindú [*Achnatherum hymenoides* (Roemer & Schultes) Barkworth], y el pasto *Purshia tridentata* (Pursch) DC.]. De acuerdo con las nuevas tazas en la producción y alargamiento de las hojas después que las semillas fueron expuestas al humo de la artemisa artificialmente puesta en combustión, tal producción y alargamiento fueron significativamente favorecedores en la aparición (*Bromus tectorum* L.) del centeno silvestre [*Leymus cinereus* (Scribner & Merr.) A. Löve], de la (Festuca idahoensis Elmer), del pasto aguja de la Sierra Nevada y por último está la aparición del pasto tipo "aguja" "hilo". Todo esto comparado de acuerdo con el control anteriormente mencionado. Después de 83 días de crecimiento, las semillas del centeno silvestre de la cuenca, y el pasto "aguja" e "hilo" que fueron tratadas con humo, produjeron significativamente una gran cantidad de plantas mas que sus grupos de control. Cuando ciertos tipos de semillas son tratadas con humo antes de ser plantadas, el resultado es muy útil en el sembradío de plantas.

Key Words: burning, fire, grass, rangelands, sagebrush, seeds

In fire-prone plant communities, particular seeds are cued to germinate/emerge as a consequence of wildfire. Persuasive evidence has accumulated that these fire cues are synthesized via combustion of vegetation and/or soil heating and are active in smoke, charred woody material, and aqueous extracts of smoke and burned soil (Keeley et al. 1985; Brown 1993a, 1993b; Baxter et al. 1994; Keeley and Fotheringham 1997). Fire cues encourage the recruitment of new plants when competition is at a minimum and there has been a release of nutrients. There has not been a deep understanding of how fire cues stimulate germination/emergence (Baxter et al. 1995); but recently it has been demonstrated that smoke increases the permeability to solutes of a subdermal seed membrane for some species of the California chaparral (Keeley and Fotheringham 1997). Moreover, some dormant seeds of the California chaparral can be cued to germinate via exposure to nitrogen oxides (Keeley and Fotheringham 1997). Specific mechanisms of fire cue stimulation may be species dependent and

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involve triggering via elevated nutrient content in the soil seedbed, the presence of stimulating gases in the smoke and/or triggering chemicals that permeate the embryo and induce enzymatic changes which triggers germination (Baldwin and Morse 1994; Baxter et al. 1994; Keeley and Fotheringham 1997). Fire cues may also deactivate compounds in the soil or seed coat that are inhibitory to seed germination (Keeley and Nitzberg 1984).

This research was undertaken to determine if emergence of some common plant seeds of the sagebrush steppe are positively influenced by the products of vegetation fires and to isolate attributes in burning vegetation or heated soil which are responsible for elevated germination/emergence. In addition, studies were conducted to determine if chemical compound(s), in the smoke from burning sagebrush and from extracts of heated soil, influence plant growth.

Materials and Methods

Experiment 1: Emergence From Heated Substrates

We measured rates and maximum emergence of several lots of test seeds in heated substrates. Tested seeds included: 'Secar' bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve], Thurber's needlegrass [*Achnatherum thurberianum* (Piper) Barkworth], needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], squirreltail [*Elymus elymoides* (Raf.) Sweazey], antelope bitterbrush [*Purshia tridentata* (Pursh) DC.], and cheatgrass [*Bromus tectorum* L.]. Seeds in this and following experiments were from the same lot, collected at the same time and place. Bitterbrush seeds were pretreated with a 5% hydrogen peroxide solution for 2 hours to reduce dormancy (Everett and Meeuwig 1978).

Substrates were a coarse sandy loam derived from granite parent material and a loam to clay loam derived from mixed extrusive volcanic parent material. Soil was collected beneath sagebrush canopies, 0–10 cm. Each substrate was homogenized and coarse woody debris removed. In increments of 120 g, substrates were artificially burned in a preheated muffle furnace in the laboratory for 10 min at temperatures of 250, 350, 550, and 750° C. The control was unheated substrate. A portion of the control or heated substrates was analyzed for soluble solute content by extracting with water (10 g substrate, 30 ml deionized water, shaken for 1 hour and filtered). Cations and anions in the extracts were quantified using ion chromatography.

Twenty-five seeds of each test species × 4 replicates were placed atop 250 cm^3 of substrate in plastic pots. The seeds were covered with 100 cm^3 of the same substrate, to a depth of approximately 1 cm. Pots were kept moist with deionized water, incubated at 20° C and illuminated with florescent lighting (light output = 420 μmoles m^{-2} sec^{-1} at 15 cm). Emergence was recorded periodically for 4 weeks.

Statistical analyses of emergence rates were facilitated by developing linearized regression equations (log transformation) of emergence as a function of species, substrate (granitic, mixed), and burn treatment (burn temperature = 0, 250, 350, 550, and 750 °C). General Linear Model F-tests were run, for individual species, to determine differences among treatments within substrates. For significant ($P \leq 0.10$) F-tests, a metric (integral of the difference between 2 regression equations) was used to determine treatment differences (Palmquist et al. 1993). Maximum emergence data were analyzed by species using ANOVA with categorical variables of burn temperature (0, 250, 350, 550, and 750 °C) and substrate (granitic, mixed). Duncan's test was performed on treatment-substrate combinations with significant ($P \leq 0.05$) F-tests. Correlations between percent emergence and concentrations of various solutes in the heated substrates were determined to potentially explain significant treatment effects on maximum emergence.

Experiment 2: Influence of Burned Soil and Smoke on Seedling Emergence

We tested the effect of smoke on seedling emergence and isolated factors in burned substrates that influence seedling emergence. Tested seeds included: bluebunch wheatgrass, Thurber's needlegrass, needle-and-thread, squirreltail, antelope bitterbrush, cheatgrass, Sierra Nevada needlegrass [*Achnatherum occidentalis* (Thurber) Barkworth], medusahead wildrye [*Taeniatherum caput-medusae* (L.) Nevski], Sandberg's bluegrass [*Poa secunda* ssp. *secunda* J.S. Presl], Idaho fescue [*Festuca idahoensis* Elmer], Indian ricegrass [*Achnatherum hymenoides* (Roemer & Schultes) Barkworth] and basin wildrye [*Leymus cinereus* (Scribner & Merr.) A. Löve]. Treatments were control, smoke, liquid extract, and direct contact. Dried sagebrush leaves and stems were used for the smoke treatment. A small portion of sagebrush was placed in a 136 liter metal garbage can and ignited. A wire mesh was placed over the can to reduce oxygen flow to the burning sagebrush thereby creating smoke. Seeds of individual species were placed atop a sieve screen and placed about 1-m above the smoking sagebrush and shaken for 1 min. At the height seeds were placed, there was no appreciable elevation in temperature. Liquid extract and direct contact treatments were conducted by heating (lots of 150 g) sagebrush subcanopy soil from a mixed source rock area at 450° C for 10 min. An approximately equal weight of deionized water was added to this heated substrate and the slurry mixed. For the liquid treatment, seeds were placed between sheets of germination paper, sealed and placed in the slurry for 4 hours, then removed. The contact treatment was conducted by placing seeds between a nylon mesh which was also placed in the slurry for 4 hours. After treatment, seeds were planted in plastic pots, 25 seeds per pot × 4 replicates using a coarse loamy sand commercial landscaping substrate. Seeds were covered with 100 cm^3 of the same substrate to a depth of approximately 1 cm. Pots were kept moist with deionized water, incubated at 20 °C and illuminated with florescent lighting (light output = 420 μmoles m^{-2} sec^{-1} at 15 cm). Emergence was recorded periodically for 3 weeks.

Statistical analyses of emergence rates were conducted by developing linearized regression equations (log transformation) of emergence as a function of species and treatment (control, liquid, contact, and smoke). General Linear Model F-tests were run for individual species to determine differences among temperatures within substrates. For significant ($P \leq 0.10$) F-tests, a metric was used to determine treatment differences (Palmquist et al. 1993).

Experiment 3: Influence of Aqueous Extracts of Heated Soil and Smoke on Plant Growth

We determined if solution from heated soil or smoke from burning sagebrush influences plant growth for several species. Species evaluated included: Idaho fescue, Sierra Nevada needlegrass, bluebunch wheatgrass, Thurber's needlegrass, needle-and-thread, squirreltail, antelope bitterbrush, cheatgrass, basin wildrye, and Sandberg's bluegrass. The treatments were control, soak, and smoke. Soak treatments involved soaking seeds for 2 hours within a nylon mesh in an aqueous slurry of soil artificially heated in a muffle furnace at 350° C for 10 min. Soil was obtained from mixed sagebrush subcanopy sites used in experiments 1 and 2. For the smoke treatment, seeds were exposed to smoke of burning sagebrush leaves for 1 min. Five seeds X 6 replicates of each treatment were planted in a loamy sand commercial landscaping substrate. Only 1 emerging seed per pot was allowed to grow. During the course of plant growth, maximum plant height and number of leaves were measured periodically. After 83 days (60 days for bluebunch wheatgrass), plants were harvested, and aboveground and belowground biomass dried at 60° C and weighed.

Statistical analyses of leaf elongation and rate of new leaf production were facilitated by developing linearized regression equations (log transformation) of individual species growth as a function of treatment (control, soak, and smoke). For individual species, General Linear Model F-tests were run to determine differences among treatments within substrates. For significant ($P \leq 0.10$) F-tests, a metric was used to determine treatment differences (Palmquist et al. 1993). Three one-way ANOVA's were conducted on post-harvest aboveground mass, belowground mass, and shoot to root mass ratios. Duncans's new multiple range test was performed for significant ($P \leq 0.05$) F-tests.

Results

Experiment 1

The temperature to which a substrate is heated and the nature of the substrate significantly ($P \leq 0.05$) influenced the rate of and maximum seedling emergence (Figs. 1 and 2). Three findings are noteworthy. Seedlings for all species, except cheatgrass, emerged differently with variation among substrate burn temperatures. Emergence rate and maximum emergence for seedlings of Thurber's needlegrass and needle-and-thread, were significantly greater in heated substrates than controls. Emergence of antelope bitterbrush decreased with increasing substrate burn temperature.

Experiment 2

Aqueous extracts of heated soil and smoke from burning sagebrush significantly influenced the rate of emergence and maximum emergence of seedlings when compared to the control (Fig. 3). Contact with aqueous slurries of heated soil significantly reduced the emergence of medusahead wildrye compared with control and liquid treatments. Smoke treatment significantly reduced the rate of and maximum emergence of needle-and-thread and Idaho fescue compared with the control. Smoke treatment significantly increased emergence of Sierra Nevada needlegrass and Indian ricegrass as compared to the control. Thurber's needlegrass did not emerge in all treatments (data not presented). This lack of emergence was unexpected as the same lot of seed readily emerged from unheated and heated sagebrush subcanopy soil (experiment 1).

Experiment 3

Rate of leaf elongation and maximum leaf length were significantly influenced when seeds were pre-treated with smoke or by immersing in an aqueous slurry of heated soil (Fig. 4). For the initial 30 days of growth, smoke-treated seeds of Basin wildrye, Sierra Nevada needlegrass, and needle-and-thread had significantly greater leaf elongation rates as compared to the soak or control treatments, afterwhich leaf elongation rates of the soak and control were greater.

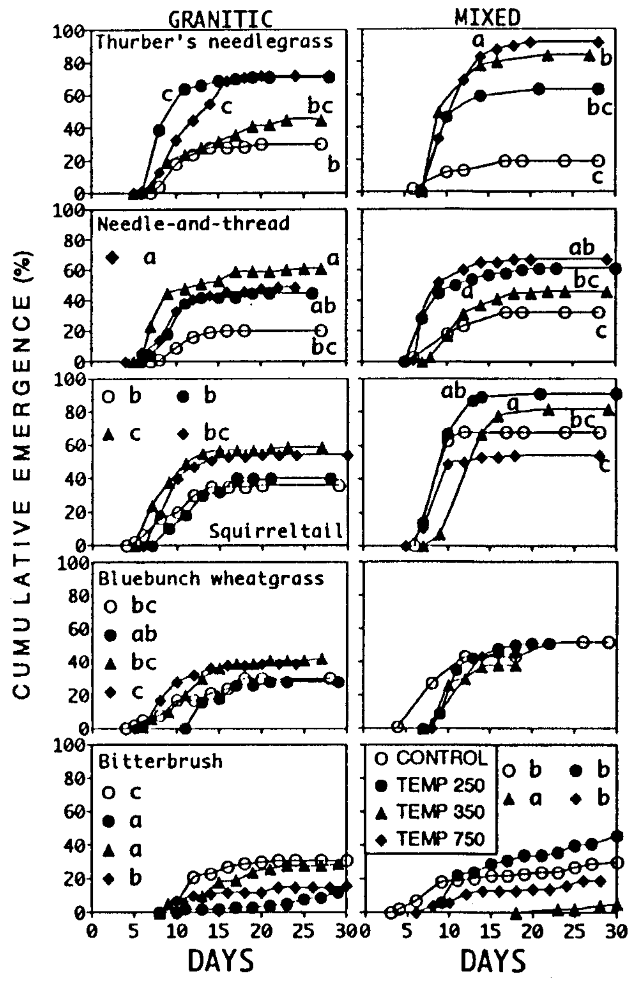

Fig. 1. Cumulative seedling emergence for test seeds sown in granitic and mixed extrusive volcanic substrates obtained from sagebrush subcanopy positions. The substrates were either unheated (control) or previously heated in a muffle furnace at temperatures of 250, 350, and 750° C and allowed to cool before sowing seeds. Significant differences among treatments are shown by letters adjacent to treatment lines or denoted by letters next to treatment symbols.

For individual measurement dates, the number of leaves for cheatgrass, Idaho fescue, Sierra Nevada needlegrass and needle-and-thread was significantly greater for the smoke treatment compared with the control or soak treatments (Fig. 5). Even after 75 days of growth, rate of leaf formation was greater for most smoke treatments than the control or soak treatments. As compared to the control, only leaf production of cheatgrass was significantly reduced by the soak treatment.

After harvest of plants on day 83 (day 63 for bluebunch wheatgrass), significant treatment effects were noted for aboveground

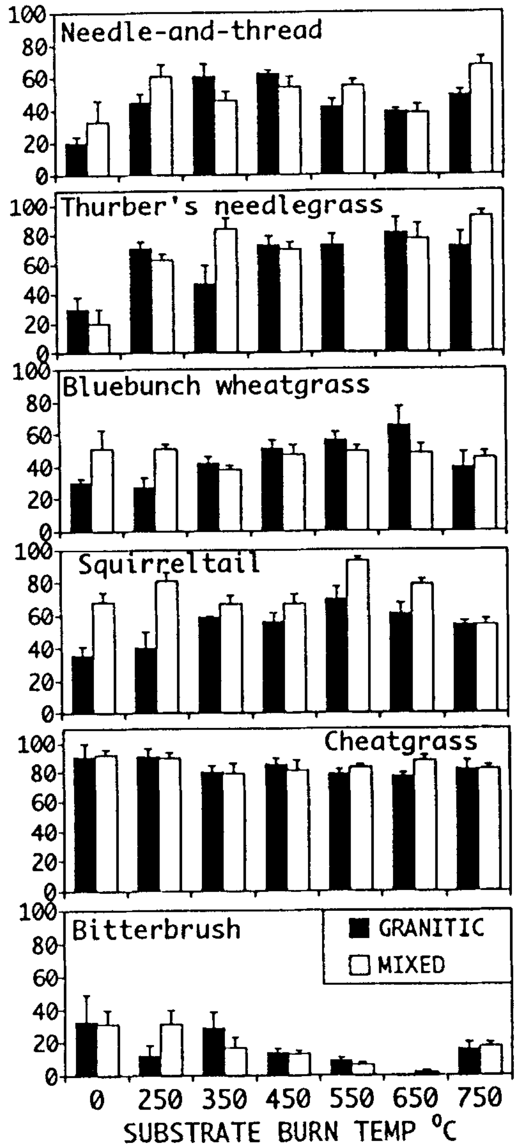

Fig. 2. Maximum percent emergence for the test seeds sown in granitic and mixed substrates. Except for cheatgrass, all seeds tested have a significant (P ≤ 0.05) substrate x temperature interaction. The data for Thurber's needlegrass at 550° C for the mixed substrate are not shown because germination trials were inadvertently ended too soon.

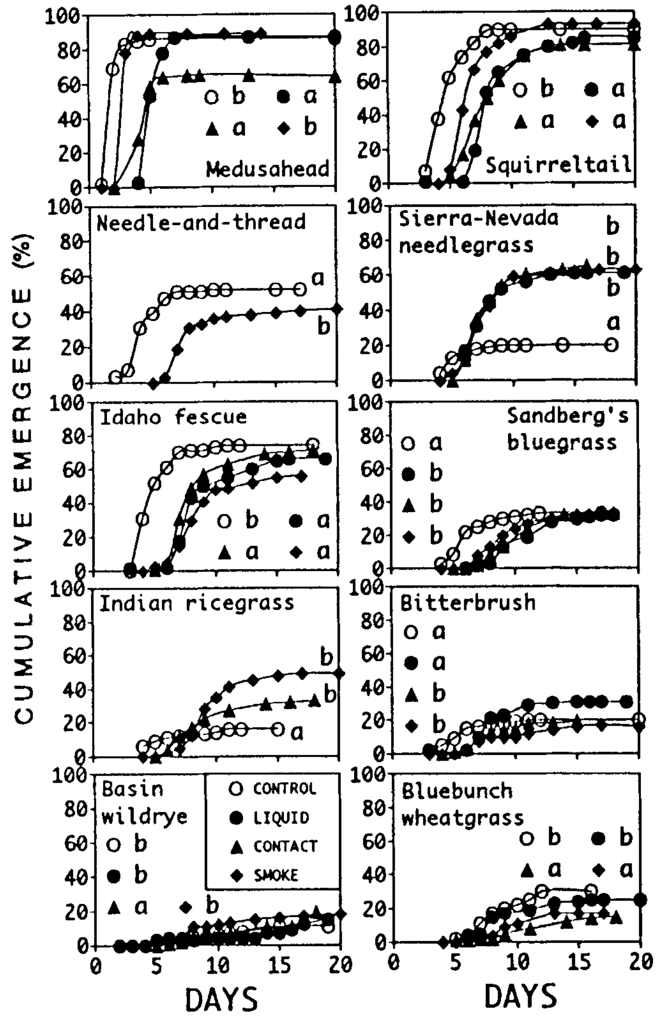

Fig. 3. Cumulative percent seedling emergence for test seeds sown in commercial coarse loamy sand landscaping substrate. Treatments were control, liquid in which seeds were exposed only to the aqueous extract of artificially burned soil through germination paper, contact in which seeds were in contact with an aqueous slurry of artificially burned soil through a mesh, and smoke in which seeds were exposed to the smoke of burning sagebrush for 1 min. Because of lack of sufficient seed in the seed lot, liquid and contact treatments were not done on needle-and-thread nor contact treatment for Indian ricegrass. Significant differences among treatments are shown by letters adjacent to treatment lines or denoted by letters next to treatment symbols.

mass, belowground mass, and shoot to root mass ratios (Fig. 6). The smoke treatment significantly increased the aboveground biomass of Sierra Nevada needlegrass, basin wildrye, and needle-and-thread relative to the control. The soak treatment produced less aboveground mass than the control treatment except for bluebunch wheatgrass. The smoke treatment significantly increased belowground mass of cheatgrass, basin wildrye, bluebunch wheatgrass, and needle-and-thread as compared to the control. As occurred in experiment 2, Thurber's needlegrass did not emerge at greater than 2% in any treatment.

Discussion

Smoke from burning vegetation stimulates germination for a proportion of seeds in fire-prone plant communities (Keeley and Pizzorno 1986; De Lange and Boucher 1990; Brown 1993a, 1993b; Baldwin and Morse 1994; Keeley and Fotheringham 1997). Moreover, the agent(s) in smoke responsible for stimulating germination are present in aqueous extracts of smoke (Brown 1993b). The biochemically active compounds in smoke and aqueous extracts of charred wood are widespread in burning vegetation. There appears, however, to be a relationship between germination enhancement of plant-derived smoke and the temperature to which the vegetation is heated (Baxter et al. 1994; Keeley and

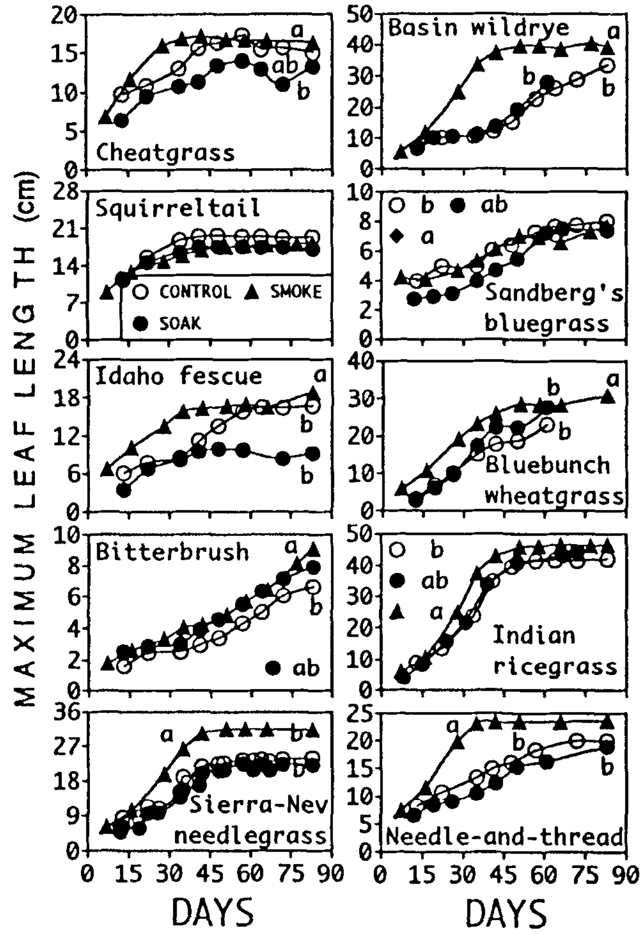

Fig. 4. Maximum leaf length for several test seeds sown in commercial landscape substrate. Treatments were control, soak in which seeds in a mesh were soaked for 2 hours in aqueous slurry of artificially burned sagebrush subcanopy soil, and smoke seeds exposed to smoke of burning sagebrush for 1 min. The decreases in maximum leaf length at approximately day 70 for the soak treatment of cheatgrass and Idaho fescue are due to death of the longest leaf. Significant differences among treatments are shown by letters adjacent to treatment lines or denoted by letters next to treatment symbols. The Y-axis scales are different to clarify treatment differences.

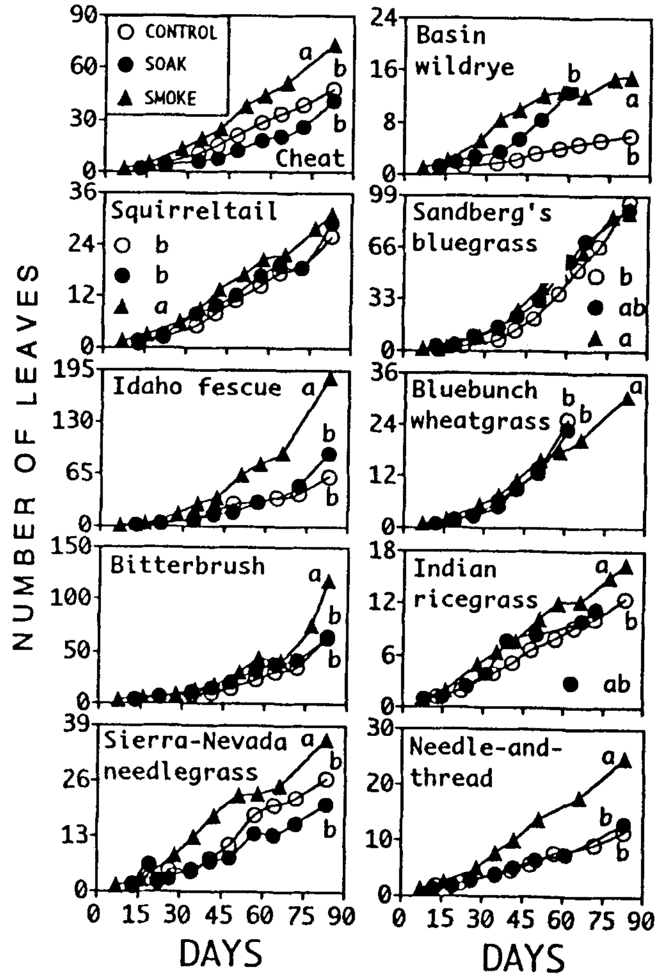

Fig. 5. Number of leaves for the test plants. Treatments are the same as explained in figure 4. The Y-axis scales are different to clarify treatment differences.

Pizzorno 1986). Smoke pretreatment of seeds before sowing may enhance establishment success (Baxter and van Staden 1994).

Our studies show that smoke and compound(s) present in aqueous extracts of heated soils increases the emergence of common plant species of the sagebrush-steppe of the western United States. The exact nature of these germination cue(s) however, was not clarified. The expression of fire cues has been related to increased permeability of a seed membrane to solutes in some California chaparral species (Keeley and Fotheringham 1997). Variable emergence depending on the temperature to which a soil is heated and the nature of the substrate (experiment 1) suggests multiple cues. Acetate and formate occur in high levels in post-wildfire soil (Blank et al. 1994) and are known to influence seed germination (Gal 1938; Cohn et al. 1987). There was, however, no significant correlation between percent seedling emergence and soil content of acetate for those species which increased their emergence in heated substrates (Table 1, experiment 1) which suggests other triggering cues are involved. Using a highly efficient anion exchange liquid chromatography column, with gradient separation, our lab has discerned over 30 organic anions in aqueous extracts of soil heated between 250 to 450° C, most of which have not yet been identified. These unknown compounds or combinations of compounds could be cuing agents. Baldwin et al. (1994) tested the effects of compounds in smoke on the germination of *Nicotiana attenuata*, a species known to be stimulated by smoke. They determined that none of the compounds, including organic acids, phenols, aldehydes, ketones, and carbohydrates, stimulated germination. They were, however, able to stimulate germination via exposure of seeds to several unidentified gas chromatography fractions of smoke at estimated concentrations of less than 1 pg seed^{-1}. Emergence-promotive effects may also be due to gases released from soil heating and in sagebrush smoke, such as CO, N_2O, and NO_2 known to induce germination in some seeds (Hardy et al. 1996; Keeley and Fotheringham 1997).

The emergence of Thurber's needlegrass warrants separate discussion. Seedlings of this species emerged at low rates from freshly collected sagebrush subcanopy soil. When soil was heated to

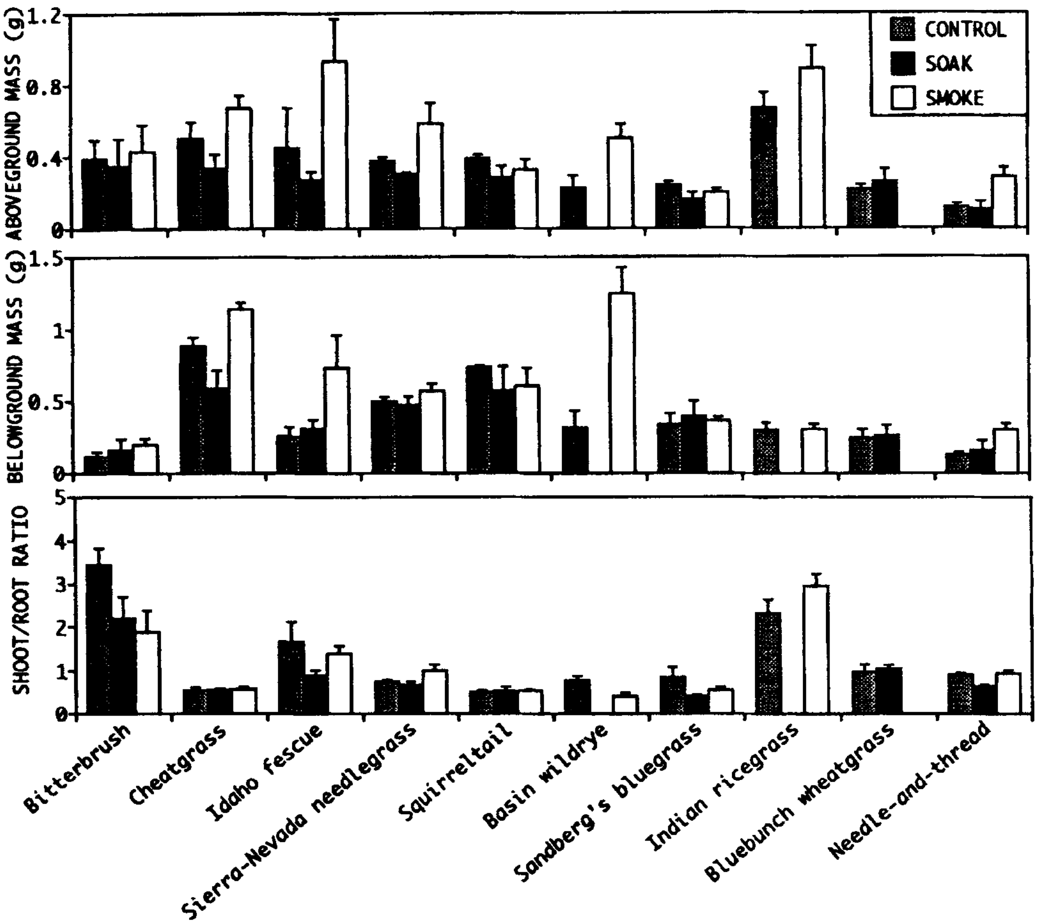

Fig. 6. Aboveground mass, belowground mass, and shoot to root mass ratios following harvest after 83 day growth (day 63 for bluebunch wheatgrass) for the test species. Because of inadvertent early harvest, data are not included for soak treatment of basin wildrye and Indian ricegrass and for the smoke treatment of needle-and-thread.

temperatures between 250 and 750° C, emergence increased significantly. Such results suggest, as reported by Keeley and Nitzberg (1984), that plant material in the soil has produced germination cue(s) at elevated temperatures. Less than 1% of Thurber's needlegrass seedlings emerged when seeds were exposed to sagebrush smoke and planted in the commercial landscaping substrate similar in texture to the granitic substrate. These results suggest that the responsible cuing agent(s) are synthesized in heated soil, but not in sagebrush smoke. The biological nature of the substrate itself may influence the germination ecology of Thurber's needlegrass; there may be a synergism between the soil substrate and the cuing agent(s) in sagebrush smoke. Smoke treated seeds may also require sowing in a biologically active substrate to express germination cues present in smoke.

Exposing particular seeds to smoke of burning sagebrush significantly increases seedling growth rate relative to controls. To our knowledge this is a new unreported aspect of fire ecology. The mechanism(s) responsible for enhanced growth is/are perplexing. Smoke is known to be a fungicide and bactericide (Parmeter and Uhreholdt 1975). Pathogenic fungi or bacteria on

Table 1. Solute concentration in aqueous extracts of the heated substrates.

Substrate	Temp	NH_4^+	Na^+	K^+	Mg^{+2}	Ca^{+2}	Acetate	NO_3^-	HPO_4^{-2}	SO_4^{-2}
	(°C)					(mg kg^{-1} soil)				
Granitic	0	0.6	9.3	31.7	1.8	11.0	dl	4.7	5.9	2.4
	250	0.7	1.0	32.4	2.1	11.0	2.0	4.4	7.2	1.5
	350	1.7	0.4	44.1	4.9	24.1	12.8	4.0	9.8	6.9
	550	5.1	3.3	47.2	7.5	44.6	33.8	1.3	7.6	20.1
	750	0.3	11.3	14.6	3.6	44.0	dl	dl	1.8	37.0
Mixed	0	0.8	8.0	39.3	5.2	17.2	dl	5.6	5.2	4.8
	250	1.6	4.4	62.0	9.5	31.0	11.7	10.2	7.9	9.1
	350	7.3	6.3	97.2	25.8	79.9	63.2	8.0	14.1	35.8
	550	2.8	1.8	61.0	10.6	70.2	43.7	0.6	6.1	50.5
	750	0.3	2.7	51.0	15.4	64.7	dl	0.6	dl	70.5

the seedcoat may have been killed thereby allowing greater seedling growth rates. Moreover, exposure to smoke may deposit nutrients on seeds which then elevates seedling growth rates. This possibility seems unlikely, however, because seedlings from smoke-treated seeds displayed elevated growth rates relative to the controls when plants were of sufficient size to have exhausted smoke-deposited nutrients. An intriguing possibility is that active compounds in smoke influence enzyme systems which control growth rate.

Elevated leaf production and root mass induced by smoke treatment of seeds suggests potential utility in range seeding operation. Although our research was conducted in the greenhouse, a plant which grows faster and taller with a more robust root system has competitive and survivorship value in natural environments. These laboratory growth experiments need to be duplicated in the field.

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