

Regulation of the germination of *Rhus coriaria*, a post-fire pioneer, by heat, ash, pH, water potential and ethylene

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Germination of the post-fire pioneer species *Rhus coriaria*, in *Pinus halepensis* forests on Mount Carmel, Israel, is restricted to the ash covered microsities under large burned pine trees, where the germination of other species is strongly inhibited. The aim of this study was to examine the effect of heat, ash cover, pH, water potential (Ψ_{π}) and ethylene on germination of *R. coriaria* seeds, in order to identify the causes of this unique germination pattern. Pre-heating to 120–140°C for 15 min was essential for the induction of seed germination. Germination percentage was increased by ash cover of 1.2 and 2.4 kg m⁻² (1 and 2 cm, respectively) but inhibited by ash cover of 6.0 kg m⁻² (5 cm). Wet pine ash from a recently burned forest had pH of 10 and Ψ_{π} of -0.26 MPa.

Under such conditions the germination of *R. coriaria* was reduced by ca 80%. On the other hand, germination was stimulated by 0.03–0.10 p.p.m. ethylene which was released by wet ash. The post-fire germination of *R. coriaria* is regulated by the balance between the stimulating effects of fire heat and the ethylene released by the ash, and the inhibition caused by the high pH and the low Ψ_{π} caused by the ash. Its mode of dispersal by birds and these ecophysiological attributes direct germination of *R. coriaria* to preferred microsities under the burned canopies of large pine trees. These microsities are characterized by improved nutrition and low competition.

Introduction

Many Mediterranean plant species have physiological characteristics that ensure their ability to regenerate after fire (Naveh 1975). Such plants are classified according to their mode of regeneration, as either resprouters or seeders. Basal parts of the resprouters survive the fire and their shoot is regenerated from buds on the trunk base or subterranean plant parts. These species have non-refractory seeds that do not require a fire-related cue in order to germinate. Seeders are killed by fire, and their populations regenerate from refractory seeds that require a fire-related cue in order to germinate (Trabaud 1987, Keeley 1991, 1994). The germination of seeders is regulated by various fire-related factors such as: heat shock (Thanos et al. 1992, Keeley 1994), light (Mayer and Poljakoff-Mayber 1989), smoke (Brown 1993, Brown and van Staden 1997, Keeley and Fotheringham 1997, 1998), charred wood (Keeley 1991, 1994, Keeley and Bond 1997), ash (Ne'eman et al. 1993), and pH and soil water potential (Ψ_{π}) (Henig-Sever et al. 1996).

Natural forests are comprised of a mosaic of microsities occupied by large trees, small trees, shrubs and gaps with herbaceous species. Consequently, wildfire intensity and ash accumulation vary among microsities according to the biomass present in each location (Christensen 1987). The combination of fire-related factors and variation of seed bank size determine the spatial pattern of the regenerating seeder populations (Izhaki et al. 1992, Ne'eman et al. 1992, Benwell 1998, Ne'eman and Izhaki 1998, Ne'eman and Keeley, unpublished data).

The distribution and size of trees in native *Pinus halepensis* Mill. forests before the fire affected the post-fire germination of *P. halepensis*, *Cistus* spp., and annuals. Under the canopies of large burned pine trees, where the intensity of fire was highest and a thick ash layer has accumulated, seedling density of most species was lower than in the open gaps (Lahav 1988, Kutiel and Kutiel 1989, Ne'eman et al. 1992). *Rhus coriaria* L. was the only species that germinated

Abbreviations – Ψ_{π} : water potential.

and established exclusively within the ash circles under the projection of the burned pines canopy. Its growth was very rapid, reaching a height of 2.5 m and first fruit set as early as 3–4 years after germination (Izhaki et al. 1992, Ne'eman et al. 1992).

R. coriaria L. (Sumack) is a small tree ranging from the Canary Islands across southern Europe and southwestern Asia to Tadzhikistan in central Asia. This species is found in small populations near old village sites in the northern part of Israel. It seems to have been introduced to the East Mediterranean in ancient times for cultivation, as a source of tannins for leather processing (Zohary 1972). *R. coriaria* exhibits vigorous vegetative reproduction, but its germination in undisturbed locations in Israel is very rare. However, seedlings are commonly found after fire nearby existing populations of this species (G. Ne'eman, personal observations).

Izhaki et al. (1992) suggested that dispersal of seeds by birds, fire-induced heat shock, and thick ash cover were responsible for selection of that regeneration niche by *R. coriaria*. Still, the ecophysiological mechanisms that targeted germination to this specific niche are not clear. In order to identify the environmental signals responsible for this selection, the direct effects of several fire-related factors on germination of *R. coriaria* were examined. These included heat shock, ash cover, pH, Ψ_{π} , and ethylene.

Materials and methods

Plant material

Seeds were collected on Mount Carmel, Israel, in late summer, immediately after fruit ripening. Fresh seeds were collected and used annually. Seeds were disinfected by immersing them in 3% Na-hypochlorite solution for 15 min followed by thorough rinse in distilled water.

Germination in the laboratory

The effects of heat shock, pH, Ψ_{π} , NO_3^- , and NH_4^+ on seed germination were tested using petri dishes (9 cm) lined with one layer of Whatman no. 1 filter paper, moistened with 5 ml of distilled water or one of the treatment solutions that included buffered pH solutions, Ψ_{π} treatment solutions, and NO_3^- or NH_4^+ solutions. Each petri dish contained 20 seeds, and each treatment was replicated 10 times. The seeds were incubated for germination in a temperature-controlled growth chamber (Biotronette model 845-2, Lab-Line, IL) at $20 \pm 1^\circ\text{C}$, and were exposed daily to 11 h of white light (a mixture of 20 W cool white fluorescent lamps, Sylvania, Danvers, MA and 40 W incandescent lamps with a total photon flux density of $30.3 \mu\text{mol m}^{-2} \text{s}^{-1}$). Radicle emergence from the seed coat was used as the criterion for germination. Germinated seeds were counted and removed once a week, until no more germination was observed for 4 weeks.

In the experiments testing the requirement of heat shock for germination, the treatment was applied by placing seeds for 15 min in a pre-heated oven at temperatures of 100, 120,

140, or 160°C . Unheated seeds served as control. In the experiments testing the effects of pH, Ψ_{π} , NO_3^- , or NH_4^+ and ethylene on germination a heat shock of 120°C for 15 min was given to all the seeds as a standard pre-treatment.

Buffer solutions with adjusted pH values in the range 6–11 were used to examine the effect of pH on germination. For pH 6, 7, 8, and 9 we used 0.05 M Bis-Tris propane buffer solutions, and for pH 10 and 11 we used 0.05 M CAPS [3-(cyclohexylamino)-1 propane sulfonic acid] buffer. Distilled water served as a control. Mannitol solutions were used to examine the effect of Ψ_{π} at -0.1 , -0.2 , -0.3 , -0.4 , -0.5 , -0.7 , -1.0 , -1.2 , and -1.5 MPa on germination. Distilled water served as control. Bis-Tris propane buffer solutions (0.05 M) at pH values of 7 and 9, and 0.05 M CAPS buffer at pH 11 were used to examine the effect of pH on seed respiration. Distilled water (pH 6) served as a control. Seeds oxygen demand was determined in a Warburg apparatus (model VL 85, B. Braun, Germany) at 22°C for the first 6 h after imbibition. Each measurement was replicated five times.

Solutions of KNO_3 , NH_4HCO_3 and a combination of KNO_3^+ NH_4HCO_3 were used to examine the effects of NO_3^- and NH_4^+ ions on seed germination. The solutions contained $200 \mu\text{M}$ NO_3^- and/or $1784 \mu\text{M}$ NH_4^+ . These concentrations were chosen because they were the concentration of the ions found in aqueous extract of pine ash (1:3 ash to water). The treatment solutions had pH values of 7.0, 7.7, and 7.6, respectively. Distilled water served as a control.

For the detection and quantification of ethylene released by wet ash two samples of 1 g dry pine ash were mixed with 4 ml of distilled water in an Erlenmeyer flask (25 ml) sealed by a rubber septum. After incubation for 24 h at 20°C , a sample of 5 ml gas was taken out with a gas-tight syringe (Hamilton, Reno, NV) and injected into a gas chromatograph (model 750, Gow-Mac, USA with a flame ionization detector) using an Alumina capillary column (Chrompack, 50 m long with 0.53 mm inner diameter). Measurements were replicated five times.

The effect of ethylene on germination was tested with batches of ten seeds in 50 ml Erlenmeyer flasks lined with one layer of Whatman no. 1 filter paper, moistened with 2.5 ml of distilled water and sealed with a rubber septum. Ethylene was injected into the flasks with a gas-tight syringe to form a final concentration of 0.01–0.5 ppm, from an ethylene/air mixture of 20 ppm at atmospheric pressure (Gordon Gas, Tel-Aviv, Israel). The experiment included ten replicates.

Garden bed experiment

Ash was collected immediately after a wildfire in a *P. halepensis* forest near Amirim, Upper Galilee, Israel in June 1993 from ten sites where tree trunks were charred but needles and small twigs were completely burned. The ash samples were mixed and sieved (2 mm) to remove pieces of charred wood and stones. A sample of the ash was mixed with distilled water (1:2, w/v, ash to water) for pH and Ψ_{π} measurements. The pH was measured with a pH meter (model PBS 730, El-Hama Instruments, Mevo-Hama, Israel). Ψ_{π} was measured with a vapor pressure osmometer (model 5500, Wescor Inc., Logan, UT).

Seeds were sown in the botanical garden at Oranim, Tivon Israel, in beds of local gray Rendzina soil covered by 1 cm (1.2 kg m^{-2}), 2 cm (2.4 kg m^{-2}), or 5 cm (6 kg m^{-2}) of ash. Beds with no ash cover and beds covered with 5 cm of vermiculite (5.8 kg m^{-2}) served as controls. Each treatment included ten replicates of $20 \times 20 \text{ cm}$ beds, 100 seeds per bed. The treatments were randomized among the 50 garden beds. The seeds were sown at the beginning of the rainy season in November 1993, and were not watered except for the natural rainfall. Emergence of the cotyledons was the criterion for germination. Seedlings were counted and removed once a week until May 1994.

The transmission of sunlight through wet ash and vermiculite was determined by putting a 1 cm layer of ash or vermiculite irrigated to field capacity, in a petri dish over the sensor of a light meter (model LI-189, Li-Cor, Lincoln, NB).

Data analysis

The results were analyzed by one-way ANOVA on transformed (arcsin square root) data of final percentage of germination. The results of significant effects were followed by a Tukey multiple range test ($P < 0.05$) to compare individual treatments. All analyses were performed using SYSTAT 5 for windows (Wilkinson et al. 1992).

Results

A heat shock was essential for germination of *R. coriaria* seeds. Maximal germination percentage ($45 \pm 7\%$ in the light) was attained after a treatment at 120°C . Germination of such heat-treated seeds in the dark was significantly lower at $26 \pm 5\%$ ($F_{1,18} = 45.9$, $P < 0.001$). Heat treatments of 100°C and 140°C resulted in germination of $29.5 \pm 7.1\%$ and $33.5 \pm 4.4\%$, respectively. Seeds did not germinate at all without a heat treatment or after a heat shock of 160°C .

Saturated paste of the pine ash used for these experiments had a pH of 10 and a Ψ_π of -0.26 MPa . Full sunlight ($1900 \mu\text{mol m}^{-2} \text{ s}^{-1}$) was blocked completely by a 1 cm layer of both wet ash and wet vermiculite. The effects of ash cover on germination percentage were highly significant ($F_{4,45} = 103.3$, $P < 0.0001$). An ash layer of 1 cm (1.2 kg m^{-2}) and 2 cm (2.4 kg m^{-2}) increased (2.5- and 2.7-fold, respectively) the germination percentage relative to uncovered seeds. An ash layer of 5 cm (6.0 kg m^{-2}) caused a 0.3-fold decrease, but vermiculite cover of 5 cm did not have any significant effect on germination (Fig. 1).

A gradual, but significant ($F_{6,63} = 62.7$, $P < 0.0001$), decrease in final percentage of germination with increasing pH was observed (Fig. 2). The germination in buffer solutions at pH 6 and 7 was not significantly different from the germination in water, indicating that buffer solution itself had no adverse effect on germination. At pH 10 (the pH of wet pine ash), germination of *R. coriaria* was reduced by 80% relative to the distilled water control.

The time course of seed respiration during the first 6 h of germination at pH 6 was the same as in water (Fig. 3), indicating that the buffer solution by itself had no adverse effect on seed metabolism. At pH 9 the respiration was low

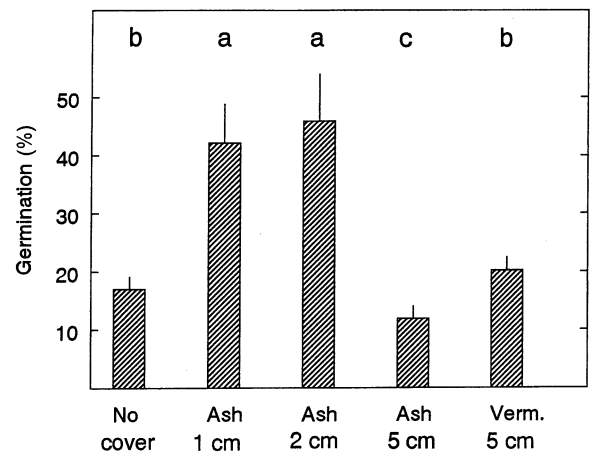


Fig. 1. The effect of ash and vermiculite cover on germination of heat-treated seeds of *Rhus coriaria* in garden beds (averages of ten replicates + SD). Bars labeled with the same letter are not significantly different according to Tukey multiple range test ($P < 0.05$).

and did not increase during the measurement period. At pH 11 respiration of the seeds ceased altogether after 1.5 h.

Low Ψ_π treatments also had a significant effect on germination percentage ($F_{9,90} = 77.12$, $P < 0.0001$). At -0.26 MPa , which is the Ψ_π value of pine ash paste, *Rhus* germination was reduced by about 50% relative to the control, germination was completely inhibited at Ψ_π values lower than -0.3 MPa (Fig. 4).

Unlike what was found before for another seeder species in that ecosystem (*Pinus halepensis*), NO_3^- and NH_4^+ in the concentration released by the ash had no effect on the germination of *R. coriaria* seeds.

Ethylene is one of the compounds that are released by ash after wetting and is known to affect plant development at very low concentration. During 24 h of incubation 1 g of ash produced on average ($n = 5$) 0.69 nl of ethylene. Our results showed that ethylene significantly enhanced germination of *R. coriaria* ($F_{6,63} = 34.14$, $P < 0.0001$) (Fig. 5). The optimum concentration was 0.05 ppm.

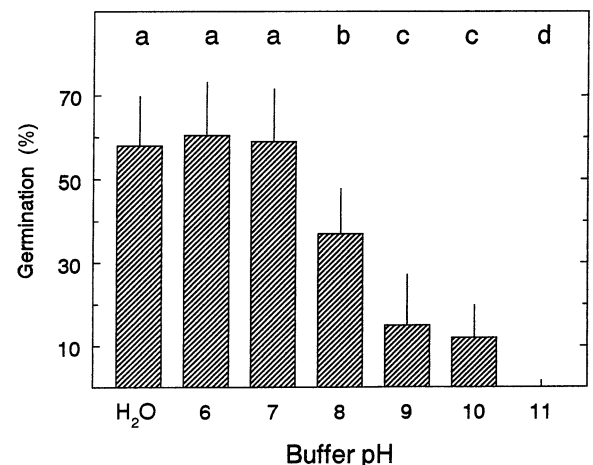


Fig. 2. Effect of pH on germination of heat treated seeds of *Rhus coriaria* (averages of ten replicates + SD). Bars labeled with the same letter are not significantly different according to Tukey multiple range test ($P < 0.05$).

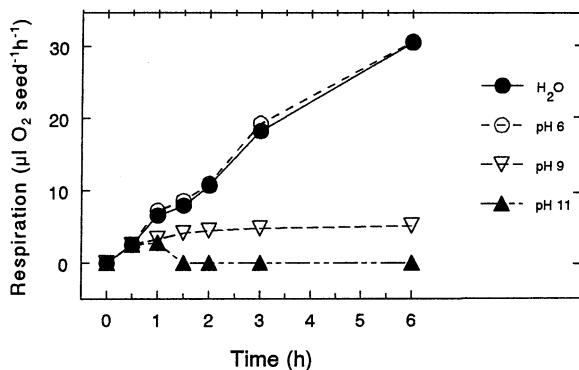


Fig. 3. Time course of respiration of heat treated seeds of *Rhus coriaria* in distilled water (pH 6) and in buffered solutions of higher pH values, during the first 6 h of germination (averages of five replicates).

Discussion

R. coriaria in Israel exhibits vigorous vegetative reproduction forming dense clones as do other *Rhus* species world wide (Lovett-Doust and Lovett-Doust 1988, Luken 1990). This species is a post-fire seeder, and germination from soil-stored seed bank occurs only after fire events (Izhaki et al. 1992). In Japan *R. trichocarpa* and *R. javanica* are facultative seeders regenerating both by resprouting and germination (Nakagoshi et al. 1987). American *R. laurina* and *R. integrifolia* regenerate after fire mainly by resprouting and by some seedling establishment, but their seedlings can be established in the absence of fire as well (DeSouza et al. 1986, Thomas and Davis 1989, Lloret and Zedler 1991).

Heat and charred wood induced germination in some *Rhus* species (*R. triloba* and others) from the Californian chaparral (Keeley 1991, Bell et al. 1993). Seeds of certain *Rhus* species require scarification by concentrated sulfuric acid for germination in vitro (Lloret and Zedler 1991, Tipton 1992). Other species (*R. virens*, *R. aromatic* and *R. trilobata*) require an additional stratification period (Tipton 1992). Fresh seeds of *R. coriaria* are dormant and require a heat treatment for induction of germination, but they do not require an additional stratification period.

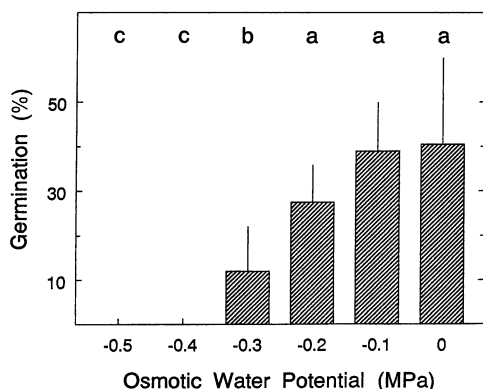


Fig. 4. Effect of water potential on germination of heat treated seeds of *Rhus coriaria* (averages of ten replicates + SD). Bars labeled with the same letter are not significantly different according to Tukey multiple range test ($P < 0.05$).

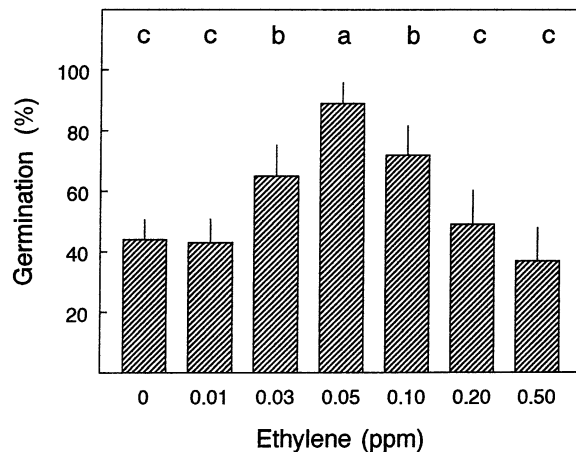


Fig. 5. Effect of ethylene on germination of heat treated seeds of *Rhus coriaria* (averages of ten replicates + SD). Bars labeled with the same letter are not significantly different according to Tukey multiple range test ($P < 0.05$).

R. coriaria has fleshy fruits and its seeds are dispersed by birds. They were found to comprise an important component of the seed rain and of the seed bank under trees in a Mediterranean type vegetation in southern France. However, *Rhus* seedlings were not observed in the study area in which no fire took place (Debussche and Isenmann 1994). The present results that show that heat shock is essential for germination of *R. coriaria* seeds explain this observation.

The requirement of a heat shock in order to induce germination causes the seed bank of this species to build up in the soil between fire events. The fire releases the whole seed stock from dormancy at the same time and a large number of recruits appear simultaneously in the burned area. Species displaying such behavior were classified by Keeley (1991) as seeders. Most plants showing this syndrome have small refractory dry seeds that are dispersed by abiotic factors (wind, water, and gravity), or by granivorous animals (insects, birds, and rodents). *R. coriaria* has a peculiar dispersal mode within this syndrome. Its fleshy fruits are eaten by birds that disperse the seeds by defecation. This mode of seed dispersal targets them particularly to locations beneath large trees in the forest frequented by the birds. As long as these trees are viable, there is little chance for establishment of young recruits in such locations. On the other hand, once these large trees are killed by fire, the locations underneath their burned canopies are prime sites for regeneration (Ne'eman et al. 1992).

Heat shock is a common fire-related factor that activates the germination process in seeds of many Mediterranean species (Trabaud 1987, Thanos et al. 1992). Germination induction of *R. coriaria* seeds by heat shock (120–140°C) results probably from cracking of the hard seed coat by the heat allowing water penetration into the seed. Water impermeability is a common explanation for the mechanism of germination inhibition by hard seed coats (Werker 1980/81, Egle 1989). Similar hardseededness, classified as a specific type of primary seed dormancy, was found in 12 families of flowering plants (e.g. Werker 1980/81, Koller and Hadas 1981, Tran and Cavanagh 1984, Egle 1989).

Charred wood and smoke are other fire-related cues that stimulate germination of fire following species as was found in California (Keeley and Bond 1997, Keeley and Fotheringham 1997, 1998), South Africa (Brown and van Staden 1997) and Australia (Dixon et al. 1995, Roche et al. 1997a,b). However, charred wood failed to affect the germination of several Mediterranean species (Keeley and Baer-Keeley 1999). *R. coriaria* seeds that were exposed to cold smoke for 5–30 min did not germinate (G. Ne'eman unpublished data).

Ash is also an important fire-related factor that affects the germination of various species. In most of the studied cases, deep layers of ash inhibited germination (Lahav 1988, Thomas and Wein 1990, Ne'eman et al. 1993, Gonzalez-Rabanal and Casal 1995). Our results showed that ash layer of 5 cm inhibited germination of *R. coriaria* seeds but a similar vermiculite cover, which like ash blocked all sunlight, had no significant effect on germination. This indicated that germination inhibition by the thick ash layer resulted from its chemical properties. From the data presented in Figs. 2–4, it is concluded that the high pH and low Ψ_{π} in the soil underneath the ash layer are the factors responsible for the inhibition of germination of *R. coriaria* seeds by thick ash layers. The negative influence of pH on seed respiration suggests that the influence on germination results from a toxic effect on the seed metabolism. Similar inhibitory effect of high pH on germination of *P. halepensis*, *Cistus salvifolius* L., *Cistus creticus* L. and some annual species was demonstrated in our previous study (Henig-Sever et al. 1996).

Mannitol was used as the osmoticum in this study because preliminary experiments have shown that even low concentration of polyethylene glycol (PEG 6000) had a negative effect on germination of these seeds (see also Leshem 1966). Stoop et al. (1996) have listed a number of plant species that were found to metabolize mannitol. *Rhus* or any other member of its family (Anacardiaceae) were not included in this list. Mannitol was shown by Riov and Yang (1982) to increase ethylene production in leaf disks of citrus, but it was not metabolized by the cells. So in this, as in other cases, mannitol affected the tissue through its contribution to the osmotic potential of the solution.

In contrast to the inhibitory effect, we demonstrated here for the first time the stimulation of *R. coriaria* germination by thin ash covers (1 and 2 cm, 1.2 and 2.4 kg m⁻²). In a previous study (Henig-Sever et al. 1996), we described the stimulatory effect of NO₃⁻ and NH₄⁺ on germination of *P. halepensis*. However, we found no effect of NO₃⁻ and NH₄⁺ in concentration equivalent to those released by ash, on germination of *R. coriaria* seeds. The stimulatory effect could be ascribed to ethylene, which is an important component of smoke released by burning plant material (Abeles 1973). This plant hormone is known to induce and stimulate germination of several species (Abeles 1973, Mayer and Poljakoff-Mayber 1989, Corbineau and Come 1995) including hard-coated seeds (Vieira and Barros 1994, Corbineau and Come 1995, Sutcliffe and Whitehead 1995). Interestingly, ethylene does not stimulate germination of many smoke-induced species that were tested (Keeley and Fotheringham 1998, but see Sutcliffe and Whitehead 1995 and

Brown and van Staden 1997). From our results (Fig. 5) it can be concluded that ethylene in low concentration stimulated *R. coriaria* germination. We propose that ethylene released from wet ash is the active component that stimulates *R. coriaria* germination by thin ash covers.

Regulation of the post-fire germination of *R. coriaria* is a result of a balance between the effects of inhibiting factors (the high pH and the low osmotic potential), and stimulation by ethylene. This regulation mechanism explains the special spatial pattern of *R. coriaria* recruitment after fire (Izhaki et al. 1992). The seeds are deposited, before the fire, by defecating birds under large trees rather than in the open area. In these locations the seed bank is smaller, and overall post-fire seedling density is low. The final result is that *R. coriaria* seedlings germinate and grow in the sparsely occupied niche under big burned pine trees, where low competition and high mineral nutrition enable their rapid growth.

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