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SEED SOAKING AND AGE PLAY A FACTOR IN HEAT-STIMULATED GERMINATION OF TWO MARITIME CHAPARRAL *CEANOTHUS* (RHAMNACEAE) SPECIES

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ABSTRACT

Recent studies have shown that changes in fire seasonality can have detrimental effects on maritime chaparral species. Although very little research has been done on the topic, a majority of the focus has been on soft-seeded species, and only a few studies have explored the effects of wet season fires on obligate seeding species. Using laboratory conditions, we examined the effects of seed soaking prior to heat exposure on the germination and imbibition of two uncommon maritime chaparral species from Parker Flats Reserve in Monterey, CA: *Ceanothus cuneatus* var. *rigidus* and *Ceanothus dentatus* (Rhamnaceae). These species responded differently to soaking. *Ceanothus cuneatus* var. *rigidus* experienced increased germination by ~16–25% at the high heat intensity (100ºC) compared to the control, and *C. dentatus* experienced decreased germination by ~10% at the lower heat intensity (80ºC). Seed age was also found to be a factor for *C. c.* var. *rigidus*, with older seeds (3 yrs) showing no significant benefits from soaking. Overall, *C. c.* var. *rigidus* appears to require high temperatures for germination, while *C. dentatus* showed no difference between the high (100ºC) and low (80ºC) heat intensities. Results from the imbibition experiment provide further evidence that the difference in germination among treatments was due to the effects of soaking and temperature on breaking physical dormancy. Therefore, the soaking of seeds prior to fires that do not produce high soil temperatures may lead to poor germination and poor recruitment of both *C. c.* var. *rigidus* and *C. dentatus* seed bank.

Keywords: *Ceanothus*, fire, germination, maritime chaparral, Rhamnaceae, season, seed, soak.

INTRODUCTION

California's maritime chaparral, a rare habitat, is characterized by having sclerophyllous shrubs, few trees, xeric conditions, and is found in coastal sites at low elevations (Hanes 1977; Keeley 1987; Keeley and Keeley 1988; Deveny and Fox 2006). Located in a Mediterranean climate region, this habitat receives the majority of its rainfall in the spring and winter and experiences drought conditions in the summer (Miller 1981; Barbour and Major 1988; Keeley and Keeley 1988). The low soil moisture, high temperatures and dry vegetation during the dry season (June–November) provide ideal conditions for fire, which occurs with an average frequency of ~40 yrs (Byrne et al. 1977; Green 1981; Minnich 1988). Most fires in chaparral communities naturally occur during the dry season (Beyers and Wakeman 1997). However, prescribed burns are typically conducted during the wet season (December–May) to maximize control of burning (Green 1981; Parker and Rogers 1988). The temporal shift of fire from dry to wet season may affect community composition due to changes in fire characteristics that are brought about by differences in pre-fire conditions (Kauffman and Martin 1991).

Fire intensity is notably one of the most influential factors in determining species establishment post-fire (Moreno and Oechel 1991). Species utilizing a resprouting strategy, where recruitment is primarily via lignotubers or vegetative structures, generally benefit from low intensity fires (Odion and Davis 2000; Buhk et al. 2007), whereas obligate seeding species, which rely solely on seed bank for recruitment, tend to benefit from high intensity fires (Keeley 1987; Moreno and Oechel 1991). Since it is presumed that wet season fires burn at lower intensities, soil seed banks may not reach high enough temperatures for adequate germination (Parker 1989). Therefore, wet season fires may greatly reduce the germination and recruitment of obligate seeding species, and in turn greatly affect community composition post-fire.

Pre-fire soil moisture is another factor that can affect seed germination. Le Fer and Parker (2005) found that soil moisture at the time of heating affects the germination of soft- and hard-coated seeds differently. Multiple studies have shown a reduction in heat tolerance of soft-coated seeds with increased

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soil moisture, which in some cases, may be attributed to the absorption of water prior to heat (Sweeney 1956; Parker 1987; Parker and Rogers 1988; Parker 1990; Moreno and Oechel 1991; Le Fer 1998; Le Fer and Parker 2005). However for hard-coated seeds, soil moisture does not appear to be detrimental for many species, and for one species (*Ceanothus cuneatus* (Hook) Nutt.), 15% soil moisture at 90°C, significantly increased germination (Le Fer and Parker 2005).

Many *Ceanothus* species employ an obligate or facultative seeding strategy, and so have been used as model species for studying plants that rely heavily on seed banks for recruitment. However, *Ceanothus* species tend to have smaller seed banks than other chaparral species (Keeley 1977, 1987; Zammit and Zedler 1988; Parker and Kelly 1989; Zammit and Zedler 1994). Although *Ceanothus* seed banks may survive 50–100 yrs, many populations will only see fire once within the lifetime of each cohort or individual plant. Fires that do not produce adequate germination for *Ceanothus* could lead to a substantial or absolute loss of the species from an area.

Of the previous field studies on germination and recruitment of *Ceanothus* species during wet season fire, the responses have varied from no response (Moreno and Oechel 1994; Beyers and Wakeman 1997), to reduced germination (Parker and Kelly 1989), or even a dramatic post-fire loss of a species from the landscape (Kelly and Parker 1984; Parker and Rogers 1988; Parker 1990). These varied responses indicate that responses to fire seasonality are complex and may even affect congeners differently. Since *Ceanothus* species replace lost volatilized nitrogen by means of fixation as well as provide habitat and food for mammals, birds, and insects, it is crucial to understand how wet-season fires affect the seed bank of obligate-seeding species such as *Ceanothus*, especially for rare species (Cronemiller 1959; Deveny and Fox 2006).

Ceanothus cuneatus var. *rigidus* (Nutt.) Hoover and *Ceanothus dentatus* Torr. & A.Gray are obligate seeders and are endemic to California. *Ceanothus cuneatus* var. *rigidus* has a limited distribution of only three counties in California and is considered to have a "limited distribution" (CNPS 2008; USDA 2008). It lives on sand hills, flats, closed-cone pine forests, chaparral, and coastal scrub (Hickman 1993). *Ceanothus dentatus* is also found on sand hill flats and mountain slopes and has been observed to naturally occur in only nine California counties (Hickman 1993; USDA 2008). Both *C. c.* var. *rigidus* and *C. dentatus* have received little attention regarding their fire ecology, with virtually no research done on the latter species.

The three main objectives of our research were to: (1) Determine whether soaking, attributed to the heavy precipitation during the wet season, and exposure to heat affect the germination of *C. c.* var. *rigidus* and *C. dentatus*; (2) determine whether the effects of soaking and heat intensity on the germination of *C. c.* var. *rigidus* and *C. dentatus* were a function of the breaking of physical seed dormancy; and (3) determine rate of imbibition and amount of water absorption once dormancy is broken.

METHODS

Study Site and Seed Collection

Seeds were collected from a 1-ha area in Parker Flats, formerly Fort Ord, in Monterey, CA (36°38′19 N, 121°46′36 W). For *C. c.* var. *rigidus*, ~2000 seeds were collected in 2004 (Cecur04) and ~3000 seeds were collected in 2007 (Cecur07). For *C. dentatus*, ~1700 seeds were collected in 2007 (Cede07). All seeds were collected from the beginning of September to the end of October. Seeds were stored in paper envelopes and kept in dry storage at room temperature (~25°C).

Soil Moisture Experiment

To determine the level of soil moisture that seeds experienced in the field, soil moisture was measured in 2008 immediately following precipitation at eight randomly selected field locations (only five locations were used on 10 and 11 Jan) within a 1600 m^2 plot at Parker Flats. Volumetric water content (VWC) of the soil was measured using time domain reflectometry (Field Scout TDR200; Spectrum Technologies, Inc., Plainfield, IL). Three measurements were taken at each location and then averaged. These measurements were repeated 3–5 h after rain stopped. To determine baseline soil moisture prior to precipitation, on two occasions, VWC was measured when no precipitation had occurred for the previous 9 to 12 d. Precipitation data was obtained from the Department of Water Resources California Data Exchange Center (CDEC 2008).

Imbibition Experiment

Cecur04, Cecur07, and Cede07 seeds were individually tested to determine the amount of water imbibed and to examine how moisture and heat affect

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imbibition. There were 50 replicates of each of three treatments for each group of seeds: (1) heat, (2) soak-heat, (3) control. For the heat and for the soak-heat treatments, seeds were individually placed in Petri dishes and heated at 100°C in a forced convection oven for 5 min. However, for the soak-heat treatment, seeds were soaked in glass vials containing 20 ml of distilled water for 9 h and allowed to air dry for 1 hr prior to heating. Seeds in the control treatment were placed directly into vials containing 20 mL of distilled water with no pretreatment. For all treatments, the seeds were weighed prior to soaking and reweighed after 4.5, 9, 14, 24, 37, 55, 79, and 154 hr of soaking after being blotted dry prior to weighing. Percent water absorption was calculated from seed weight prior to soaking (dry weight) and after soaking ([moist weight – dry weight]/dry weight). The uptake of water by seeds prior to embryo expansion can be categorized into three sequential stages. The first phase, phase I (imbibition), is characterized by rapid absorption of water. Initial absorption then reaches a point where it slows or even ceases: phase II (plateau phase). The last stage, phase III, starts when seeds undergo a second absorption of water which leads to embryo elongation (germination) (Finch-Savage and Leubner-Metzger 2006). The proportion of seeds that imbibed was calculated after 154 hr. For both species in our experiment, seeds that had gained >20% mass were considered imbibed. A >20% increase in mass was chosen based on our observation of all three phases of water uptake for both species, with *C. c.* var. *rigidus* and *C. dentatus* averaging an increase of 60–70% and 80–90%, respectively, before ending phase I (end of imbibition). Also, all seeds that absorbed <20% mass usually continued to experience fluctuations in mass between measurements and never reached phase II.

Germination Experiment

A lab experiment was conducted to determine how soaking of seeds prior to heat exposure affected the germination of Cecur04, Cecur07, and Cede07. All seeds were subjected to one of two soaking treatments: (1) soak, or (2) no-soak. Within each of these treatments, there were five replicates of each of three heating treatments: (1) no-heat (control = room temperature only), (2) 80°C for 40 min, and (3) 100°C for 5 min. Therefore, each species experienced a total of six treatments. Each replicate was comprised of 50 seeds from which we calculated percent germination. Temperatures for our heat treatments were chosen for maximum germination based on Keeley's (1987) results for *C. cuneatus*. Seeds in the soak category were placed in glass vials containing 5 ml of distilled water for 9 hr. Following soaking, they were allowed to air dry and were then heated within 12 hr. To determine whether duration of soaking was a factor, which could be caused by differences in rainfall, an additional soaking treatment of 4.5 hr was used for Cecur07. However, this was not done for Cecur04 and Cede07 due to a limited number of seeds. Seeds were heated in Pyrex Petri dishes in forced convection ovens. Following heating, two pieces of Whatmans #1 filter paper were positioned in the bottom of plastic Petri dishes. A solution of 0.25 g of charate and 8 ml of distilled water was added to each dish. The seeds were then set directly on top of the charate solution. Charate was made according to Keeley's (1987) protocol.

To initiate germination, all seeds were stratified for 4 wks at 0°C. Seeds were maintained in the dark because light has been found to be inhibitory for another species of *Ceanothus, C. integerrimus* (Keeley 1987). The seeds were then incubated at 25°C for 3 wks with no light. In order to maximize germination, this cycle was repeated once (Le Fer and Parker 2005; Keeley 1987). Seeds were examined once a week under indirect green light for germination (Keeley 1987), and were considered to have germinated when a radicle length ≥2 mm was seen.

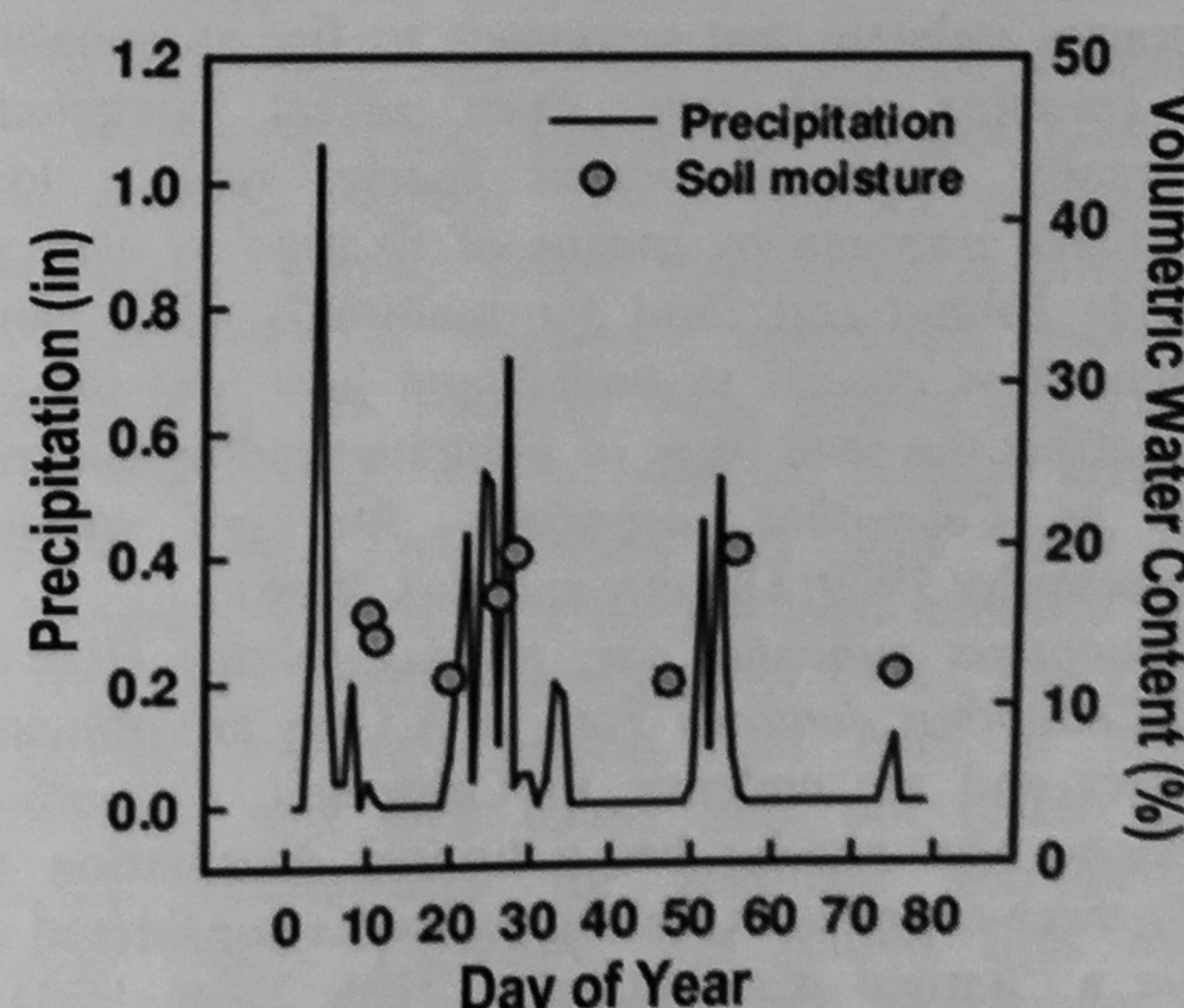

Fig. 1. Average daily precipitation and volumetric water content at Parker Flats Reserve, Monterey, CA. Volumetric water content was taken from 1 Jan 2007 to 31 Mar 2007. Precipitation data was obtained from the Department of Water Resources California Data Exchange Center (*http://cdec.water.ca.gov/*).

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Data Analyses

After 154 hr of soaking, the change in weight recorded for each seed was converted into one of two categories: imbibed (>20% increase in dry weight), or unimbibed (<20% increase in dry weight). A one-tailed *Z*-test was then performed to compare the proportion of seeds that had imbibed between the control, soak, and soak-heat treatments for each species/year (Minitab 15, Minitab Inc., State College, PA).

For the germination experiment, analysis of variance (ANOVA) was used to compare the percent germination of the control, soak, and soak-heat treatments between species/year. A multiple pairwise comparison (Tukey) was then used to determine differences between treatments (Systat vers. 11.0, SPSS Inc., San Jose, CA).

RESULTS

Soil Moisture Experiment

Due to the coarse texture of the soils found at Parker Flats Reserve, soil moisture was relatively low following periods of steady rainfall. Average VWC varied by as much as 13% among locations, and 5% within locations. The highest average VWC following rainfall was 26% and the lowest was 8%. Regardless of the amount of rainfall prior to sampling, average VWC for all sites combined ranged from 12–20% (Fig. 1). For the measurements taken 9 and 12 d after no precipitation occurred, VWC ranged from 7–17% and averaged 12% (Fig. 1). This dramatic drop in soil moisture, of ~10% within roughly a week's time, has also been documented with a soil-monitoring device taking measurements of soil moisture in the field every day during the winter of 2008–2009 at Parker Flats (unpublished data).

Imbibition Experiment

In the control, average seed mass after 9 hr of soaking varied between Cecur04, Cecur07, and Cede07 (Fig. 2–4). For *C. c.* var *rigidus* 07, no seeds had begun to imbibe after 9 hr (Fig. 3). Cecur04, on the other hand, showed an average increase in mass by 10.35% after 9 hr of soaking and 16% of the seeds had already begun to imbibe (Fig. 2). Cede07 also showed an average increase in mass by 6.4% after 9 hr of soaking, with 10% of the seeds having already begun to imbibe (Fig. 4). For all species and years, no more than 24% of the seeds imbibed without the aid of heat, even after 154 hrs of soaking (Fig. 5–7). Regardless of species or year collected, nearly all seeds experienced a drop in mass prior to any increase.

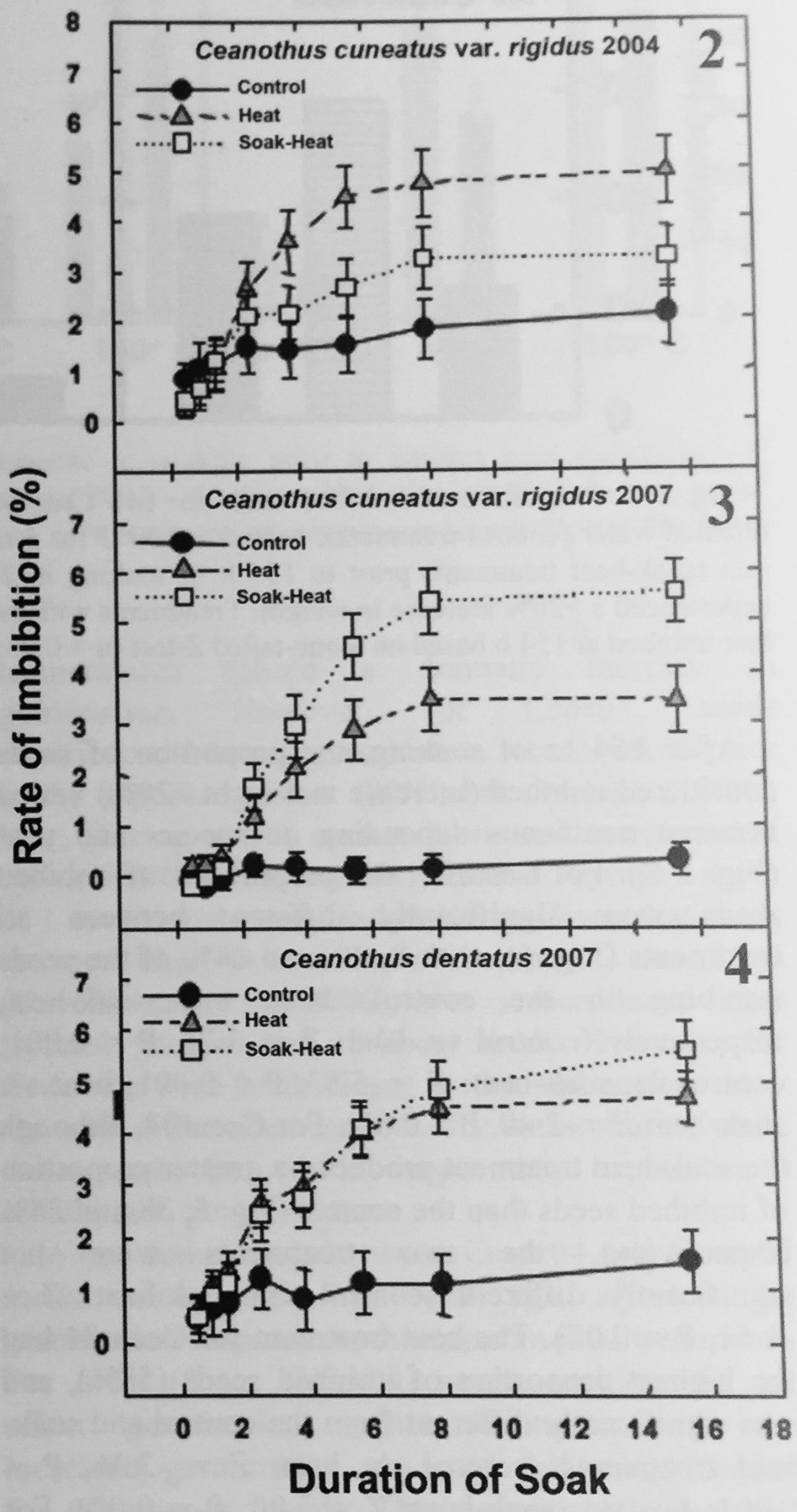

Fig. 2–4. Rate of imbibition for two species of *Ceanothus*.—2. *Ceanothus cuneatus* var. *rigidus* 2004.—3. *Ceanothus cuneatus* var. *rigidus* 2007.—4. *Ceanothus dentatus* 2007. Seeds were placed directly into distilled water (control treatment), heated at 100°C for 5 min (heat treatment) or soaked for 9 h and then heated at 100°C for 5 min (soak-heat treatment) prior to 154 h of soaking in 20 mL of distilled water. At 4.5, 9, 14, 24, 37, 55, 79, and 154 hrs, seeds were removed from water, patted dry, and reweighed (n = 50). Error bars = 1 SE.

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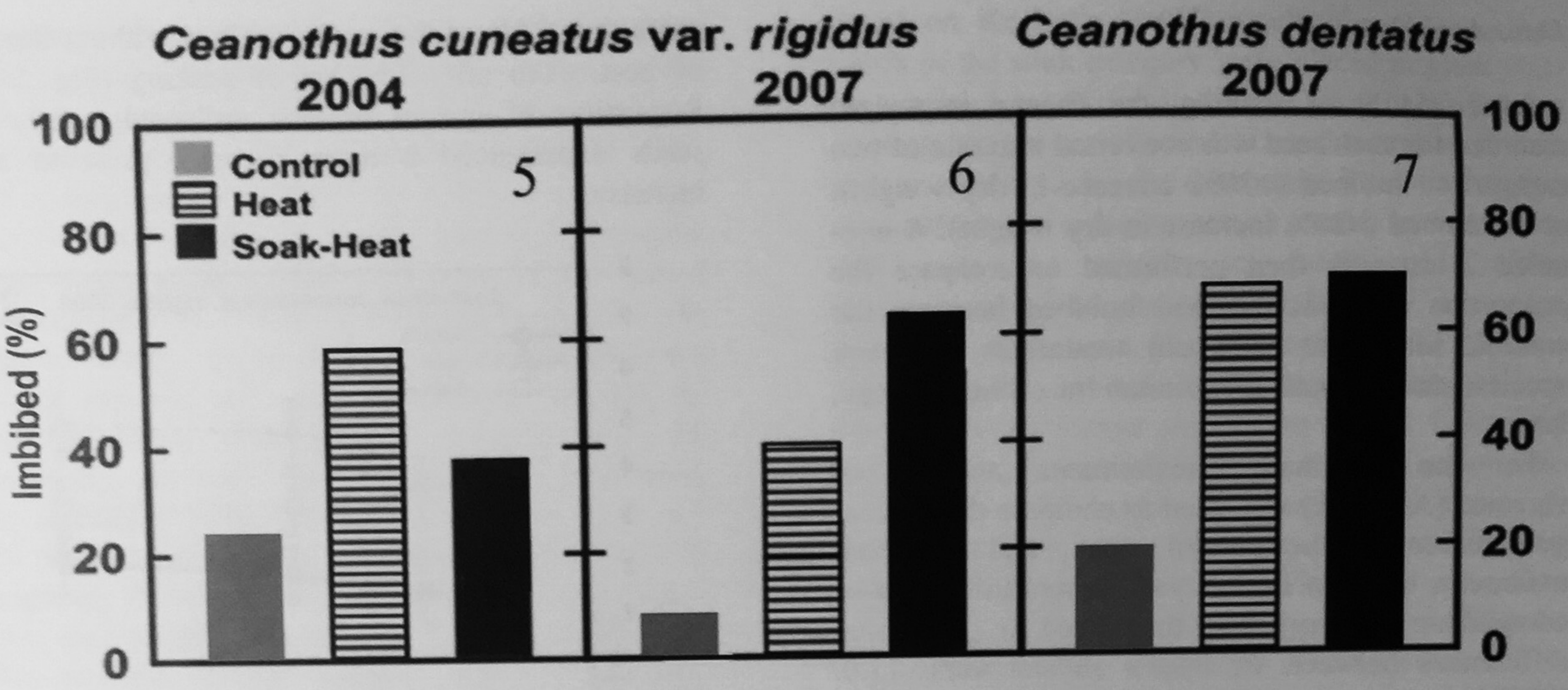

Fig. 5–7. Proportion of imbibed seeds for two *Ceanothus* species after 154 h of soaking. Seeds were placed directly into distilled water (control treatment), heated at 100ºC for 5 min (heat treatment) or soaked for 9 h and then heated at 100ºC for 5 min (soak-heat treatment) prior to 154 h of soaking in 20 mL of distilled water. Seeds were classified as "imbibed" if they experienced a >20% increase in weight. Treatments with the same letter were not significantly different in the proportion of seeds that imbibed at 154 h based on a one-tailed Z-test ($\alpha = 0.05$; n = 50).

After 154 hr of soaking, the proportion of seeds considered imbibed (increase in weight >20%) varied between treatments depending on species and year (Fig. 5–7). For Cecur07, the proportions of imbibed seeds were significantly different between all treatments (Fig. 6), with 8, 40, and 64% of the seeds imbibing in the control, heat, and soak-heat, respectively (control vs. heat: $Z = -3.75$, $P < 0.001$; control vs. soak-heat: $Z = -5.83$, $P < 0.001$; heat vs. soak-heat $Z = -2.40$, $P = 0.01$). For Cecur04, although the soak-heat treatment produced a greater proportion of imbibed seeds than the control (Fig. 5; 38 and 24% respectively), the two treatments were not significantly different (control vs. soak-heat: $Z = -1.51$, $P = 0.07$). The heat treatment for Cecur04 had the highest proportion of imbibed seeds (58%), and was significantly different from the control and soak-heat treatments (control vs. heat: $Z = -3.46$, $P < 0.001$; heat vs. soak-heat: $Z = 2.00$, $P = 0.02$). For Cede07, the soak-heat and heat treatments were not significantly different (Fig. 7; heat vs. soak-heat: $Z = -0.22$, $P = 0.41$) and produced a very similar proportion of imbibed seeds (70 and 68%, respectively). Both of these treatments produced a significantly greater proportion of imbibed seeds than the control (20% imbibed) (control vs. heat: $Z = -4.83$, $P < 0.001$; control vs. soak-heat: $Z = -5.03$, $P < 0.001$). Rate of imbibition and the proportion of imbibed seeds were highly correlated, supporting the significant differences seen between treatments.

For Cecur04 and Cecur07, the mass of most seeds increased 80–90% within one to two measurements of a recorded initial increase associated with imbibition. Following this increase in weight, seeds entered into phase II (plateau phase), where seeds no longer gained weight for at least one to two of the following measurements. For Cede07, phase II was also reached within one or two measurements after initial imbibition occurred. However, the average increase in weight was slightly lower for Cede07, averaging around 60–70%.

Interestingly, Cecur04 and 07 seeds had a thin transparent outer layer that began sloughing off after a few hours of soaking. However, this sloughing was not detected for Cede07 seeds. It is unknown what this layer is or what function it serves, but it may play a factor in the differences in imbibition seen between the two species.

Germination Experiment

Ceanothus cuneatus *var.* rigidus.—Cecur04 and Cecur07 experienced a significant increase in germination only when subjected to the highest heat intensity of 100ºC (Fig. 8 and 9; Cecur04 $F = 20.55$, $P < 0.001$; Cecur07 $F = 74.76$, $P < 0.001$). However, for Cecur07, heat only increased germination when seeds were soaked prior to heating (Fig. 9; partial soak Tukey $P < 0.001$, and full soak Tukey $P = 0.02$). When compared to the control, partial-soak increased

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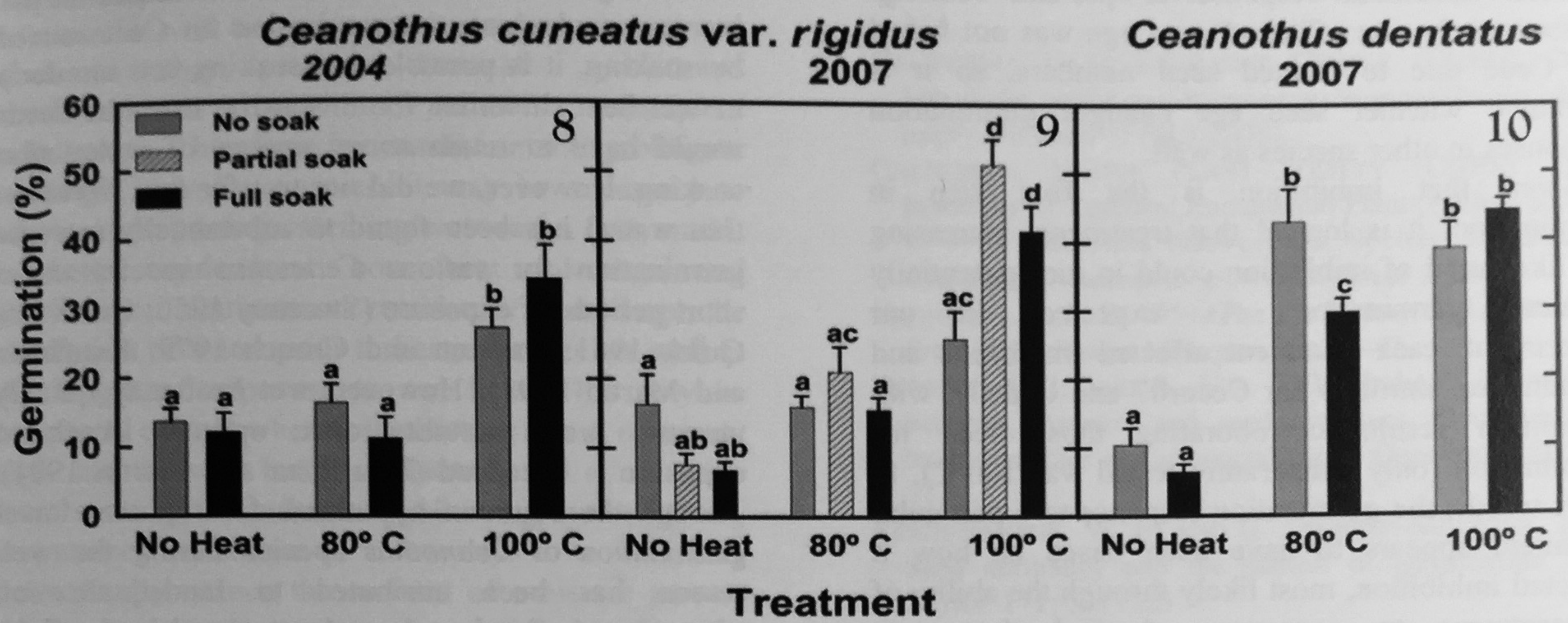

Fig. 8–10. Percent germination of two *Ceanothus* species in response to soaking prior to various heat intensities.—8. *Ceanothus cuneatus* var. *rigidus* 2004.—9. *Ceanothus cuneatus* var. *rigidus* 2007.—10. *Ceanothus dentatus* 2007. In each panel, treatments with the same letter were not significantly different based on a Tukey pairwise comparison ($\alpha = 0.05$; $n = 50$). Error bars = 1 SE.

germination by 25%, while full soak increased germination by 16% at the 100°C treatment (Fig. 9). Although partial soak seeds produced higher germination in both the 80°C and the 100°C treatments the difference were not statistically different ($P = 0.10$). Soaking had no significant effect on the germination of Cecur04 seeds at all heat intensities (Fig. 8; $F = 0.003$, $P = 0.96$). However, for all unsoaked treatments, Cecur04 and Cecur07 responded similarly when subjected to the same heat intensity (control: 14 and 16%; 80°C: 16 and16%; and 100°C: 27 and 26% for Cecur04 and Cecur07, respectively).

Ceanothus dentatus.—Soaking of Cede07 seeds reduced germination by ~10% at the 80°C treatment (Fig. 10; $F = 5.35$, $P = 0.04$), while at 100°C it had no significant effect ($P = 0.74$). For Cede07 seeds that were not soaked, both the 80 and 100°C treatments dramatically increased germination. When compared to the control, heat increased the germination of unsoaked seeds by 43 and 39% for the 80 and 100°C treatment respectively, with no significant difference between the two heat intensities (Fig. 10; $P = 0.92$).

DISCUSSION

We found that seeds of each species of *Ceanothus* responded differently to the experimental treatments of soaking and heat, which were used to simulate the effects of precipitation and fire in the field. For Cecur07, soaking prior to the exposure of high temperatures caused a dramatic increase in germination. However, for Cede07, seeds experienced lowered germination when soaked prior to the exposure of low (80°C) but not high (100°C) heat. During a wet season burn, soil temperatures above 100°C would not likely extend beyond a depth of 1 cm (Moreno and Oechel 1991). Given that seeds are most likely to be found in the upper 2 cm of soil (Deveny and Fox 2006), wet season burns may increase germination of Cecur seeds. However, for Cede, the seed bank closer to the soil surface may show no difference in wet vs. dry season burns, while those seeds that reside deeper may experience a reduction in germination.

In our comparison between Cecur04 and Cecur07 seeds, we found that seed age affected the germination response to the experimental treatments. For older (3 yr; Cecur04) seeds, soaking did not affect germination, which contrasts with the increased germination observed following soaking for the younger seeds. The majority of *Ceanothus* seed bank is comprised of persistent seeds that range from 1 to ~100 yrs old (Keeley 1975; Deveny and Fox 2006). Consequently, the majority of seeds that would be recruited post fire would be from the persistent seed bank. Just as seed depth can play a factor in seed scarification (Zammit and Zedler 1994), seed age may play a role as well. How the effects of seed age in dry lab storage conditions relate to those experienced in the wild is not known, but most likely they differ significantly. However, it is possible that under natural conditions a similar trend may be taking place, with older seeds showing a

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reduced beneficial response to pre-fire soaking. Unfortunately, the effect of seed age was not tested for Cede due to limited seed numbers, so it is unknown whether seed age changes germination responses in other species as well.

Given that imbibition is the first step in germination, it is logical that treatments increasing the likelihood of imbibition could in turn potentially increase germination. As expected, in our experiment, each treatment affected imbibition and germination similarly for Cecur07 and Cede07, with imbibition results corroborating those seen for germination (only temperature tested was 100°C). In other words, the germination response to a particular treatment appears to have been based on how it affected imbibition, most likely through the ability of a treatment to overcome physical dormancy. However, for Cecur04, soaking prior to high intensity heat exposure (100°C) significantly lowered the likelihood of imbibition when compared to heat alone, yet slightly increased germination, although not significantly. This is paradoxical to what would be expected since imbibition is the precursor to germination and not the opposite, and the causes for these differences are unknown.

Although Cecur04/07 and Cede07 were found to have similar rates of absorption, the total percent increase in weight differed between the two species (80–90% and 60–70% respectively). Given that both species have the ability to absorb a great deal of water in a relatively short period of time (>50% increase in dry weight in 9hr), it is possible that some seeds of both species could begin imbibition during periods of winter precipitation. Some species have been found to experience a significant loss in heat tolerance with the absorption of water prior to heat exposure (Parker and Rogers 1988; van Klinken and Flack 2005). Whether the absorption of water or the differences in the amount absorbed between the two species affects their tolerance to heat is unknown. Older seeds of Cecur were more likely (16% compared to 0%, Cecur04 vs. Cecur07, respectively) to imbibe without heat scarification. If soaking prior to fire is found to decrease heat tolerance, older seeds may be at a greater risk. Cede07 seeds were also more likely to imbibe without heat when compared to fresh Cecur07 seeds (10% compared to 0%). The greater likelihood of Cede07 to absorb water prior to heat exposure may explain the drop in germination of soaked Cede07 seeds in the 80°C treatment. Why Cede07 experienced a drop in germination at the 80°C and not the 100°C treatment is not known but may have to do with the longer exposure to heat in the former treatment (40 min vs. 5 min, respectively).

Although we do not know the direct causes for the increase or decrease in germination for Cede caused by soaking, it is possible that soaking acts similarly to wet heat. In order for this to be true, the seeds would have to retain some amount of water after soaking. However, we did not test for this. Wet-heat (hot water) has been found to substantially increase germination for various *Ceanothus* species under short periods of exposure (Sweeney 1956; Quick and Quick 1961; Radwan and Crouch 1977; Kauffman and Martin 1991). However, wet heat may quickly increase seed mortality once optimal length of exposure is exceeded (Kauffman and Martin 1991). Though the common hypothesis for reported lower germination of *Ceanothus* species during the wet-season has been attributed to inadequate soil temperatures, this has never been tested in the field. A lab experiment by Campbell et al. (1996) has shown that wet soils are capable of reaching 95°C and can increase thermal conductivity. Therefore, it may be necessary to further explore the role that wet heat plays during wet-season fires, especially when duration of exposure is considered.

While wet heat and seed age may play a greater role in fire-related seed-dormancy release than previously believed, research has extensively shown that dry-heat intensity is still likely the most critical factor in the germination of *Ceanothus* spp. (Stone and Juhren 1953; Quick and Quick 1961; Keeley 1987, 1991; Kauffman and Martin 1991; Moreno and Oechel 1994; Zammit and Zedler 1994; Le Fer and Parker 2005). In our study, the germination of Cecur04, 07 and Cede07 seeds responded positively to high dry-heat intensities. However, we found that the optimal temperatures for germination differed between the two species studied. Cecur required temperatures above 80°C, with ideal temperatures above 100°C. This is similar to what has been documented by other studies using *C. cuneatus* (Keeley 1987; Le Fer and Parker 2005). *Ceanothus dentatus*, however, showed no difference between the 80 and 100°C treatments. Unfortunately we did not test the wider range of temperatures needed to adequately determine those necessary for optimal germination of each species. Due to the lack of literature on *C. dentatus*, it is unknown whether this species produces similarly high germination rates at temperatures lower than 80°C or higher than 100°C.

The effects of soaking (winter precipitation) on *Ceanothus* seeds prior to heat exposure is complicated, and may be dependent on a number of factors such as heat intensity, seed soaking, age of seed bank, and species. Since individuals of obligate-seeding *Ceanothus* species receive only one opportunity to recruit from the seed bank within their lifetime, it will be necessary to make management decisions that produce adequate recruitment conditions in order to maintain subsequent populations. Therefore, for stands containing obligate seeding *Ceanothus* species, it may be necessary to take caution when prescribing wet season fires until it is better understood how heat tolerance and scarification requirements correlate with seed age, the absorption of water prior to heat exposure, as well as the length of exposure to wet heat. This may be especially critical when soil moisture is still relatively high and the seed bank is relatively old. Until these factors are better understood, allowing the soil to dry down over the course of a few days to a week may dramatically reduce the amount of moisture present during a prescribed winter burn, and therefore the effects associated with wet heat.

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