Boiling water scarification plus stratification improves germination of *Iliamna rivularis* (Malvaceae) seeds

Katri Himanen, Markku Nygren, and R Kasten Dumroese

Iliamna rivularis dominating a site in northwestern Montana 2 y after the 2006 Red Eagle Fire in Glacier National Park. Photo by LK Vance

ABSTRACT

Scarification with boiling water plus stratification was most effective in improving germination of *Iliamna rivularis* (Douglas ex Hook.) Greene (Malvaceae) in an experiment that compared 3 treatments. Seeds from 15 sites representing 5 western US states were used in the experiment. Initial response of the seedlots to the treatments was similar, apart from one seedlot. The control treatment (intact seeds) yielded poor germination (1.8%). Mechanical scarification (part of the seedcoat removed) improved germination (average germination 49%), but not as much as the combination of boiling the seeds for 120 s plus stratifying them 28 d at 4 °C (average germination 70%). Germinants from the boiling plus stratification treatment appeared to be more vigorous. Impermeability of the seedcoat is the main factor preventing germination, but the response of embryos to stratification may suggest some physiological dormancy. These treatments can be adapted to nursery production of this species, which has ornamental potential and ecological importance.

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KEY WORDS
streambank wild hollyhock, fire adapted, physical dormancy, seedbank

NOMENCLATURE
USDA NRCS (2012)

CONVERSIONS
1 m = 3.3 ft
1 cm = 0.4 in
1 mm = 0.04 in
1 ml = 0.034 oz
°F = (°C x (9/5)) + 32

Streambank wild hollyhock, or mountain hollyhock (*Iliamna rivularis* (Dougl. ex Hook) Greene [Malvaceae]), is a widespread, herbaceous perennial, native to the US. The taxonomy of the genus has recently undergone change, with the USDA NRCS (2012) now showing 6 accepted *Iliamna* species in the US and Canada. Of those, *Iliamna rivularis* has 2 accepted botanical varieties: *diversa* (A. Nelson) Wiggins found in the Yellowstone area of Idaho, Montana, and Wyoming; and *rivularis* found in British Columbia and Alberta, east of the Cascade Mountains in Washington and Oregon, and the mountainous areas of Idaho, Montana, Wyoming, northern Nevada, Utah, and Colorado, as well as northeastern Illinois and northwestern Indiana (synonym = *I. remota* Greene) and Virginia (synonym = *I. corei* [one county] and *I. remota* [more widespread]). Despite USDA NRCS (2012) lumping *I. remota* and *I. corei* within *I. rivularis*, Slotta and Porter (2006) provide evidence of genetic distinction between the western and eastern US populations, between the populations of *I. remota* in Illinois and Virginia, and between *I. remota* and *I. corei*. Both *I. remota* and *I. corei* are endangered.

In the western US, *I. rivularis* inhabits forest openings, canyons, streambanks, foothills, and disturbed, open areas with moist but well-drained soils (Hitchcock and others 1994) across a wide variety of forest types, including forests dominated by

Figure 1. The attractive flowers of *Iliamna rivularis* occur on an upright raceme (A) in various shades of pink (B) and are 2.5 to 4 cm across; each comprises 5 petals about 2 cm long (C). Photos by R Kasten Dumroese

Figure 2. Flattened seed capsules of *Iliamna rivularis* yield kidney-shaped seeds. Photo by R Kasten Dumroese

Cercocarpus Kunth (Rosaceae)/*Quercus* L. (Fagaceae) (mountain mahogany/oak) and members of the Pinaceae (pine [*Pinus* L.], Douglas-fir [*Pseudotsuga* Carrière], and spruce [*Picea* A. Dietr.]) (Matthews 1993). *Iliamna rivularis* is a bushy, rapidly growing species with alternate, coarse, large (4 to 10 cm long), 5- to 7-lobed maple-like leaves. Attractive pink flowers are 2.5 to 4 cm across and composed of 5 petals about 2 cm long (Figure 1). Flowers occur from June through August on upright racemes (0.5 to 2 m long) supported by a woody caudex (Matthews 1993). Kidney-shaped seeds (approximately 2.0–2.5 mm long) covered with minute hairs are borne in round, flattened capsules (Figure 2; Hitchcock and others 1994). Seeds lack a dispersal mechanism (Matthews 1993) and plants are prodigious seed producers; Brown and DeByle (1989) report 14,300 seeds/m^2 (1300/ft^2) beneath 2-y-old plants. These hard-coated seeds remain viable in the seedbank for long periods of time, perhaps 100 y (Matthews 1993).

All species in the *I. rivularis* taxon, including *I. corei* and *I. remota*, depend on site disturbance to supply niches necessary for seed germination (Matthews 1993; Baskin and Baskin 1997). Wildfire is the chief disturbance mechanism for *I. corei* (Baskin and Baskin 1997) and western *I. rivularis* (Steele and Geier-Hayes 1992, 1993). In the western US, large stands of *I. rivularis* frequently appear in full-sun conditions after prescribed and wild fires (Steele and Geier-Hayes 1992, 1993; Ferguson and others 2005). Absent before fire, germination usually occurs the first year after fire, with this seral, shade-intolerant species often forming dense stands and remaining a conspicuous part of the understory for several years until new trees and shrubs shade them out (Kramer 1984; Steele and Geier-Hayes 1993; Stickney and Campbell 2000). It can also be an important post-fire food source for ungulates (Kay 1993).

Iliamna rivularis, because of its rapid colonization of burned sites and persistence until replaced by taller woody vegetation, has potential to be used after wildfire to mitigate erosion and to initiate post-fire succession. For these same reasons, it may also have utility for other forest restoration plantings, including road obliteration on federal land where rapid development of a plant canopy is desired (Foltz and others 2007). In addition, this species is a recommended landscape plant because of its outstanding beauty, ease of propagation, and success in landscapes (Meyer 2005).

For wide-scale use to be efficient and economic, timely, prompt, and thorough germination of large quantities of seeds is necessary. As with other species in the Malvaceae (Page and others 1966; Egley and Paul 1981; Alberts and Mandel 2004; Dunn 2011; Kildisheva and others 2011), *I. rivularis* has a water-impermeable seedcoat that invokes physical dormancy. A special feature of these seeds, the water gap, can become permeable following exposure to temperature flux, drying, or scarification, thus allowing imbibition (Baskin and Baskin 2001; Baskin 2003). Mechanical scarification, usually accomplished opposite the water gap and employing piercing, nicking, or abrasion, has been used to improve germination of physically dormant seeds (Baskin and Baskin 2001) including *I. corei* (Baskin and Baskin 1997). This technique can be laborious and expensive, especially when large numbers of seeds are required. Scarification with boiling water, which softens and dislodges the water gap, is commonly used in other hard-seeded plants (Baskin and Baskin 2001) including those in the Malvaceae (for example, *Callirhoe involucrata* (Torr. & A. Gray) A. Gray [Alberts and Mandel 2004]) and could be used effectively on large numbers of seeds. Wick and others (2008) report good germination of *I. rivularis* after a 10 s dip in boiling water followed by 30 to 60 d stratification at 3 °C. Our study objective was to find a seed treatment to promote rapid and uniform germination of *I. rivularis* seeds collected across the western US.

MATERIAL AND METHODS

Seedlots

Iliamna rivularis seeds were collected from 15 sites in Utah (7), Idaho (3), Wyoming (3), Montana (1) in July to September 2005, and Washington (1) in August to September 2008 (Table 1; Figure 3). Most seedlots contained approximately 2000 seeds and were stored in an envelope at room temperature (about 22 °C) until the study was initiated in June 2009. To have some representation across the range of *I. rivularis*, we located a Washington seedlot (Scotty Creek) and decided to include it despite it being younger and stored frozen by the collector for 11 mo before it was sent to us for experimentation. For each seedlot, we determined seeds/kg by weighing 8 random replicates of 100 seeds. By X-raying a random sample of 100 seeds from each seedlot, we estimated the portion of nonviable seeds

TABLE 1

Iliamna rivularis *seedlots[z] used in the study.*

Location	County	State	Latitude, Longitude	Elevation (m)[y]	Collection date(s)	Seeds per kg [x]	Nonviable (%)
Tinney Flat, Santaquin Canyon	Utah	Utah	39.901671, –111.726923	1890	11 Jul 2005	327,896 (±890)	18 (12–27)
Eureka	Juab	Utah	39.954754, –112.118912	2286	Aug 2005	494,896 (±1147)	13 (8–21)
Squaw Peak Road	Utah	Utah	40.259338, –111.577872	2280	22 Aug, 12 Sep 2005	298,809 (±485)	7 (3–14)
Timpooneke Road near summit	Utah	Utah	40.425792, –111.685002	2438	14 Sep 2005	335,570 (±416)	7 (3–14)
Silver Lake Road	Utah	Utah	40.516024, –111.655842	2377	31 Aug 2005	325,177 (±476)	3 (1–9)
Wolf Creek Pass, Highway 35	Wasatch	Utah	40.518166, –111.076814	2286	15 Aug– 3 Sep 2005	362,746 (±389)	6 (3–13)
Bountiful Peak	Davis	Utah	40.983952, –111.802855	2263	24 Aug 2005	347,343 (±585)	3 (1–9)
Periodic Springs	Lincoln	Wyoming	42.749781, –110.860769	2092	16 Aug, 9 Sep 2005	347,584 (±596)	2 (1–7)
Nordic Inn, Highway 89, Alpine	Lincoln	Wyoming	43.175103, –111.005742	1730	8 Sep 2005	490,076 (±1236)	6 (3–13)
Grand Targhee Campground	Teton	Wyoming	43.756625, –111.920719	2119	8 Sep 2005	333,904 (±728)	5 (2–11)
McCoy Creek Road	Bonneville	Idaho	43.179967, –111.127467	1736	16 Aug 2005	350,816 (±908)	5 (2–11)
Rainey Creek	Bonneville	Idaho	43.570733, –111.215217	2060	8 Sep 2005	246,268 (±143)	0 (0–4)
Highway 20, Road 042	Clark & Freemont	Idaho	44.518233, –111.620189	2298	8 Sep 2005	341,837 (±770)	4 (2–10)
Red Eagle Burn	Glacier	Montana	48.694586, –113.431091	1524	15 Aug 2008	274,395 (±270)	1 (0–5)
Scotty Creek	Chelan	Washington	47.240122, –120.391443	671	26 Aug 2008	413,074 (±772)	3 (1–9)

Notes: For seeds per kg and for the portion of nonviable seeds, 95% confidence intervals are presented in parentheses.

[z] Seedlots were collected by the USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah, except that Ted Alway collected Scotty Creek and Tara Luna collected Red Eagle Burn.

[y] Conversion: 1 m = 3.3 ft

[x] Conversion: (seeds per kg) x 0.4535 = seeds per lb

(seeds with embryo and endosperm missing or appearing not to be intact).

Germination Conditions

To ensure uniform germination conditions, we used a germination cabinet (GC 10/11, FLOHR instruments, Netherlands) set to 20 °C, 16 h day length, and 98% relative humidity unless otherwise noted. Each treatment replicate was placed inside Petri plates (8.5 cm diameter) containing 2 layers of blotter paper (Munktell no. 1701, Falun, Sweden) moistened with 5 ml of tap water. A seed was considered germinated when the radicle and both cotyledons had emerged from the seedcoat (ISTA 2005).

Preliminary Tests

We conducted 3 preliminary tests. First, we tested the effect of mechanical and boiling water scarification on imbibition of water in the Bountiful Peak seedlot because this lot contained the most seeds; this allowed us opportunity to reserve sufficient seeds for the final test described below. Control seeds were not treated. Mechanical scarification was achieved by removing a small piece of the seedcoat from the radicle end with a scalpel

Figure 3. Locations of the 15 seedlots used in this study.

(under microscopic examination), carefully avoiding the embryo and endosperm; seeds were immediately placed into Petri plates. To scarify seeds with boiling water, we placed seeds inside a tea sieve and submerged them in boiling water for 10 or 120 s, after which they were dipped into cool water, surface dried, and set into Petri plates. Fresh weight increase of 10 seeds from each treatment was measured at intervals during imbibition. Control seeds did not imbibe water during the first 72 h, whereas the average weight increase of mechanically scarified and seeds scarified by boiling for 10 or 120 s was 150%, 28%, and 114%, respectively (Figure 4).

Second, we tested the effect of germination temperature on seeds from Bountiful Peak and McCoy Creek treated 3 ways: control (as described above), boiling water scarification (120 s as described above), and boiling plus 30 d stratification. For the boiling water scarification plus stratification treatment, seeds were treated as described above, but Petri plates were sealed with Parafilm and placed in a cooler (4 °C) for 28 d. Seeds were germinated either at constant 20 °C (16 h day) or in 15 °C (16 h day) alternated with 6 °C (8 h darkness), the later temperatures more consistent with springtime (Van Assche and others 2003). After 21 d incubation in 15/6 °C, no control seeds or seeds that were boiled had germinated in either of the seedlots. For Bountiful Peak and McCoy Creek in 20 °C, the germination capacity of control seeds was 0 and 1% and for the boiled seeds 10% and 4%, respectively. However, boiling combined with stratification was effective in improving germination of both seedlots, with germination capacity of 75 and 56 in Bountiful Peak and McCoy Creek, respectively, in 20 °C. Germination capacity was 43 percentage points lower in 15/6 °C for Bountiful Peak and 48 points lower for McCoy Creek compared to the steady 20 °C (Figure 5).

Third, we exposed seeds from 4 seedlots (Bountiful Peak, Periodic Springs, McCoy Creek, and Scotty Creek) to 4 treatments described above: control, mechanical scarification, boiling water scarification (120 s), boiling water scarification plus

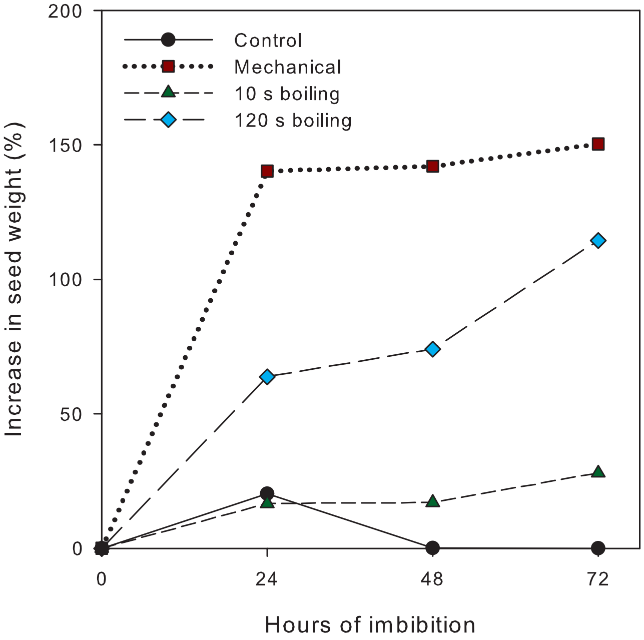

Figure 4. Percentage increase in seed weight of seeds from Bountiful Peak 72 h after no treatment (control), mechanical scarification, or exposure to boiling water for 10 or 120 s.

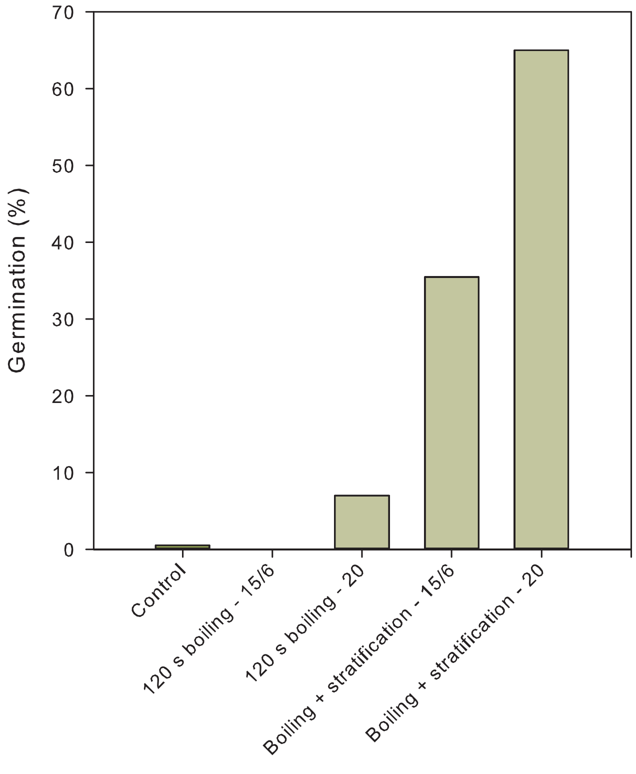

Figure 5. The average germination percentage for Bountiful Peak and McCoy Creek Road exposed to no treatment (control) and germinated at 20 °C; 120 s boiling water and germinated at 20 °C or alternating 15/6 °C; or 120 s boiling water followed by 28 d stratification at 3 °C and germinated at 20 °C or alternating 15/6 °C.

stratification (120 s, 28 d stratification at 4 °C). Four replicates of 25 seeds were germinated for 21 d in 20 °C for each seedlot × treatment combination. Control seeds germinated poorly, and simple boiling resulted in slow germination and low germination capacity (Table 2). Boiling plus stratification yielded the best germination except for Scotty Creek, for which mechanical scarification proved to be most effective.

Germination Experiment

Based on our preliminary tests, we subjected all 15 seedlots to 3 treatments described above (control, mechanical scarification, and boiling water scarification plus stratification [120 s plus 28 d stratification at 4 °C]) and germinated them at constant 20 °C (16 h day). We replicated each treatment 4 times with 25 seeds per replication; replicates were randomly selected from the whole seedlot by using an electronic seed counter (Unit Counter Model 600, Elmor, Switzerland). Seed germination was monitored 21 d.

Statistical Design and Analyses

To test the effect of treatments and seedlot on germination, we employed a 3 treatment × 15 seedlot × 4 replicate design in which replicates were nested within seedlot. Therefore our data consisted of 4500 seeds from 180 germination plates. Because viability was high for most seedlots (≥ 93%), germination percentages were determined on the basis of all seeds in the test. Germination energy and germination capacity (total number of seeds germinating out of 25 on days 7 and 21, respectively) were analyzed using a hierarchical generalized linear mixed model with logistic link function (GenStat 13) in which the treatment was the fixed model term and the seedlot and replicate were the random terms. The fit of the model was evaluated by examining the deviance and the standardized residuals. When initially modeling the germination of all seedlots, Scotty Creek yielded large residuals. Therefore the germination of this particular lot was analyzed separately. To compare the treatment effects statistically, we calculated 95% confidence intervals for the estimated true differences between individual treatments. If the confidence interval did not include zero, differences were deemed statistically significant at the 5% risk level (Collett 2003).

RESULTS

Seeds per kg ranged from 246,248 at Idaho's Highway 20 site to 494,896 for Eureka, Utah, with an average of 352,692. Radiography suggested that 18% of the Tinney Flat seeds, and 13% of the Eureka seeds were nonviable, with the other 13 seedlots showing more than 93% viability (Table 1).

Treatment significantly (P <0.001) affected germination capacity, that is, the final germination percentage on day 21. At the end of the 3-wk incubation period, the average germination

TABLE 2

Germination percentages (± standard error) of Iliamna rivularis *seeds after treatments in preliminary test 3.*

		Percentage germination			
Seedlot	**Days of observation**	**Control**	**Mechanical scarification**	**Boiling 120 s**	**Boiling 120 s + stratification**
Bountiful Peak	7	0	16 ± 3.7	0	39 ± 4.9
	21	2 ± 1.4	44 ± 5.0	21 ± 4.1	61 ± 4.9
Periodic Springs	7	0	14 ± 3.5	1 ± 1.0	73 ± 4.4
	21	1 ± 1.1	41 ± 4.9	24 ± 4.3	89 ± 3.1
McCoy Creek Road	7	0	17 ± 3.8	0	47 ± 5.0
	21	6 ± 2.4	25 ± 4.3	6 ± 2.4	74 ± 4.4
Scotty Creek	7	1 ± 1.1	46 ± 5.0	0	0
	21	1 ± 1.1	85 ± 3.6	16 ± 3.8	16 ± 3.8

capacity (± standard error) of the control seeds across all seedlots (excluding Scotty Creek) was 1.8 ± 0.4% (Figure 6). For these seedlots, average germination capacity for mechanically scarified and boiled plus stratified seeds was 49 ± 3.4% and 70 ± 3.1%, respectively (Figure 6). Boiling water scarification followed by 28 d of stratification increased germination capacity 17.7 to 24.6 percentage points compared with mechanical scarification in all seedlots excluding Scotty Creek, a significant ($P \leq 0.05$) amount. For Scotty Creek, mechanical scarification yielded a germination capacity of 85 ± 3.6%, which is 69 percentage points higher than the germination capacity after boiling and stratification.

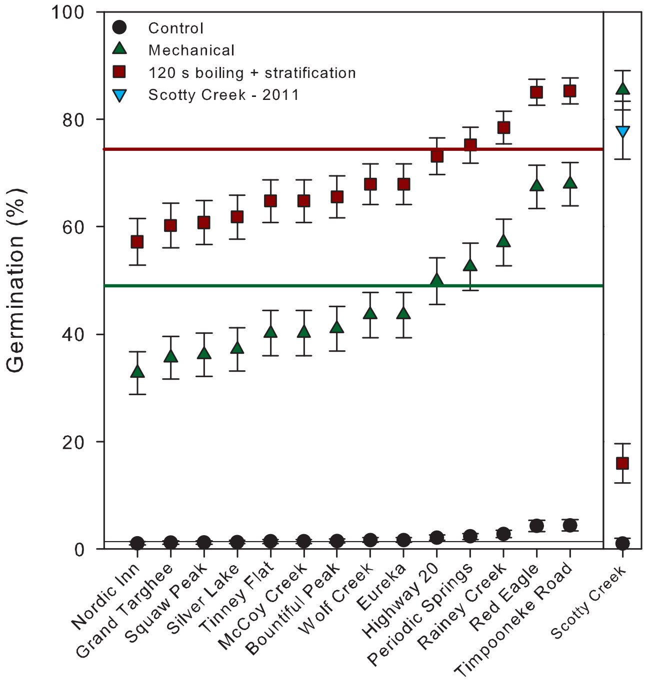

Figure 6. Germination percentages of control (black circles), mechanically scarified (green triangles), and boiling water scarified plus stratified (red squares) seeds after 3-wk incubation. Average germination percentages were 1.8% (black line), 49% (green line), and 70% (red line) for all seedlots except Scotty Creek. The estimate of germination percentage for Scotty Creek is calculated by a separate model. The blue triangle presents germination of Scotty Creek in a second germination test after 2 y of storage.

Treatments had a similar effect on germination energy, that is, germination percentage on day 7 ($P < 0.001$) in both models. The mean germination energy of control seeds was 0.2 ± 0.1% for all seedlots excluding Scotty Creek. For mechanically scarified and boiled plus stratified seeds, average germination energy was 20 ± 1.8% and 49 ± 2.5%, respectively, which is significant at the 5% risk level on day 7 in both models.

Fungal growth originating from the seeds was observed on Petri plates in most seedlots in control and mechanical scarification treatments. The fungi grew quite aggressively, but they seemed to attack mostly seeds that did not start to germinate during the 3-wk incubation period.

DISCUSSION

Our first preliminary study clearly showed that nearly all *I. rivularis* seeds are impermeable to water because they did not imbibe even when kept in moist conditions for several weeks; the few exceptions may have had damaged seedcoats, or perhaps a small fraction of the population does have permeable seeds, as is reported for *I. corei* (Baskin and Baskin 1997) and other species (Silvertown 1984; Baskin and Baskin 2001; Michael and others 2006). Therefore, untreated seeds yielded a very low germination percentage, similar to many other studies on seeds with a similar dormancy mechanism in several families (Van Assche and others 2003; Baskin and others 2004; Jayasuriya and others 2007; Kildisheva and others 2011). This physical dormancy prevents seeds from germinating at a time when the completion of germination or the survival of seedlings is unlikely, even though conditions would be temporarily favorable for germination (Baskin and Baskin 2001).

When physical dormancy is broken naturally, a water gap, also known as the lens, residing in the middle of the seed is opened by an environmental cue such as heat (Baskin and Baskin 2001; Baskin 2003). As the gap is opened, water flows into the seed in a controlled manner (Baskin and others 2004). In our study, the seeds of all the tested seedlots responded to boiling, that is, moist heat. This was expected because the regeneration of this species is dependent on site disturbance mainly caused by fire (Matthews 1993; Baskin and Baskin 1997). Similar treatment effects have been documented on *I. corei* (Baskin and Baskin 1997). For *I. corei*, dipping in boiling water and dry-heating broke the physical dormancy, but with boiling water scarification the best results were achieved with boiling time of 1 to 20 s with no stratification (Baskin and Baskin 1997), contrary to our results with *I. rivularis*. In our preliminary experiment we noticed that the imbibition rate of *I. rivularis* seeds was much slower after 10 s boiling compared to boiling for 120 s. In our findings, 120 s boiling did not negatively affect the germinability or viability of the seeds, although Baskin and Baskin (1997) report a decreased germination percentage after ≤ 30 s boiling for *I. corei*. These findings support the view presented by Slotta and Porter (2006) that *I. rivularis* and *I. corei* are in fact separate species, or at least that the seed dormancy characteristics or the regeneration ecology of these taxa differ from each other.

In our first preliminary experiment, the imbibition of seeds from Bountiful Peak occurred more readily following mechanical rather than boiling water scarification, similar to results with *Sphaeralcea munroana* (Douglas) Spach [Malvaceae] (Kildisheva and others 2011) and *Dodonaea viscosa* (L.) Jacq. [Sapindaceae] (Baskin and others 2004). This difference in imbibition rate probably relates to the size of the water-permeable opening — the artificial nick being several times larger than the natural water gap (Baskin and others 2004). This kind of uncontrolled water uptake may lead to damage in the embryo tissue or disrupt germination in some other way. If this is the case, the lower germination energy and capacity we noted after mechanical scarification compared to boiling plus stratification may not indicate that dormancy was not broken, but rather that the mechanical scarification is harmful to the seeds. Manning and Van Staden (1987) concluded that seedlings resulting from seeds scarified with boiling water were more vigorous than those obtained from mechanical scarification because the lens also acts as a regulator of water uptake. Our qualitative assessment of *I. rivularis* seedlings concurred.

Conversely, our preliminary test 3 showed that the seeds of the tested lots (Bountiful Peak, Periodic Springs, and McCoy Creek) responded poorly to boiling although boiling plus stratification clearly promoted germination. This suggests that *I. rivularis* may exhibit physiological dormancy in addition to a physical one, again contrary to findings on *I. corei* (Baskin and Baskin 1997). The idea of double dormancy is supported by the more robust and vigorous germinants seen after the stratification treatment compared with germinants from mechanically scarified seeds. A similar dormancy mechanism has been reported on other *Sphaeralcea* species of the Malvaceae (Smith and Kratsch 2009). It may also indicate that boiling only partially opens the lens and that subsequent time spent during stratification may finally allow sufficient water to enter the seed to support germination. This is supported by our first preliminary experiment that showed water flux was dependent on the duration of exposure to boiling water. This may also explain why Wick and others (2008) report good germination of a Montana seedlot when 10 s of boiling was followed by 28 d of stratification.

Although having impermeable seedcoats, several species of the Fabaceae show seasonal cycles in their germination capacity by responding to alternating germination temperatures simulating spring after stratification (Van Assche and others 2003). For example, *Medicago lupulina* L. and *Melilotus albus* Medik. seeds germinated well in alternating 15/6 °C and in 10/20 °C temperatures although germination capacity was poor in constant 10 or 23 °C temperatures (Van Assche and others 2003). Our preliminary experiment, however, suggests that *I. rivularis* seeds do not respond to 15/6 °C germination temperature in a similar way. This alternating temperature may not be the right environmental cue for this species.

In general, seeds collected in 2005 (all lots except Red Eagle and Scotty Creek) and 2008 (Red Eagle) responded similarly to the treatments, whereas Scotty Creek, also collected in 2008, did not. Seeds from Scotty Creek may have responded differently for several reasons, including: 1) it is from the east slope of the Cascade Mountains rather than the Rocky Mountains; 2) it was growing at the lowest elevation of any source; and 3) it was the only seedlot frozen.

Curiously, when we re-tested Scotty Creek during the preparation of this manuscript (2 y after the original tests; 2011), after it had been stored at room temperature in a paper envelope, we found that it behaved similarly to the other 14 seedlots (germination percentage at day 7 [± SE] after boiling plus stratification was 41 ± 6.2% and the germination capacity at day 21 was 78 ± 5.4%). This suggests some physiological change in the seeds during storage; enhanced germination after 2 y storage suggests the seeds were initially more dormant. It may be that seeds of *I. rivularis* have non-deep physiological dormancy (Baskin and others 2004), characterized by initially deeper dormancy that dissipates with air-dry storage (Baskin and Baskin 2001). Similarly, Heather and others (2010) found that some seeds of 2 species of *Polygonella* Michx. (Polygonaceae) had non-deep physiological dormancy that was alleviated by postharvest storage. Their conclusion that it may be more fruitful to focus on after-ripening treatments than on dormancy mitigation treatments seems applicable to *I. rivularis* as well.

Both mechanical scarification and boiling water scarification followed by stratification promoted germination of *I. rivularis* on a large number of seedlots from a wide geographical range in the Rocky Mountains. To make mechanical scarification work on a production scale, special equipment is needed and the method of scarification needs to be advanced. Seeds could, for example, be scarified by using a machine that rolls or blows seeds against an abrasive surface. The advantage of mechanical scarification is that no stratification is needed; however, boiling plus stratification is easier to apply to large amounts of seeds and no special equipment is needed to complete the treatment. Boiling appeared to reduce fungi from the seeds that could otherwise cause problems during stratification or at the time of germination. Our results also suggest that seedlots of this species may show different responses to treatments, and these responses may change over time. Therefore, taking into account the collection and handling history of a seedlot when interpreting the results of a test is crucial; and testing a small fraction of the seedlot before implementing a treatment on larger amounts of seeds is recommended.

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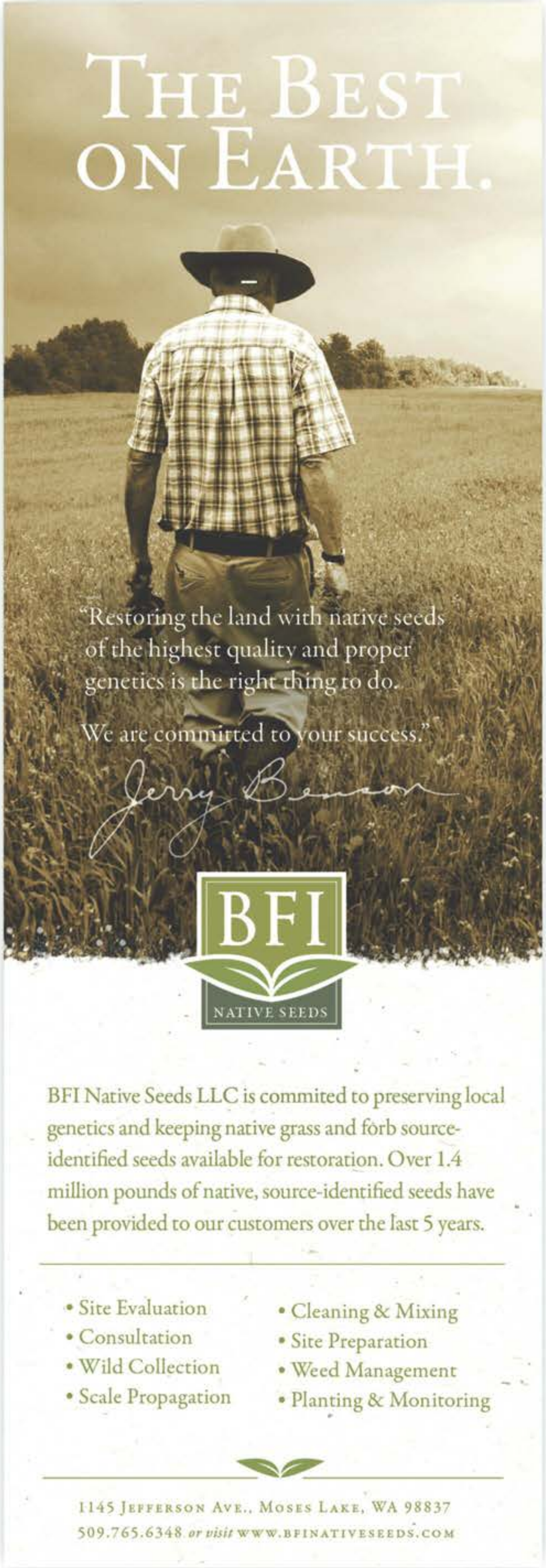

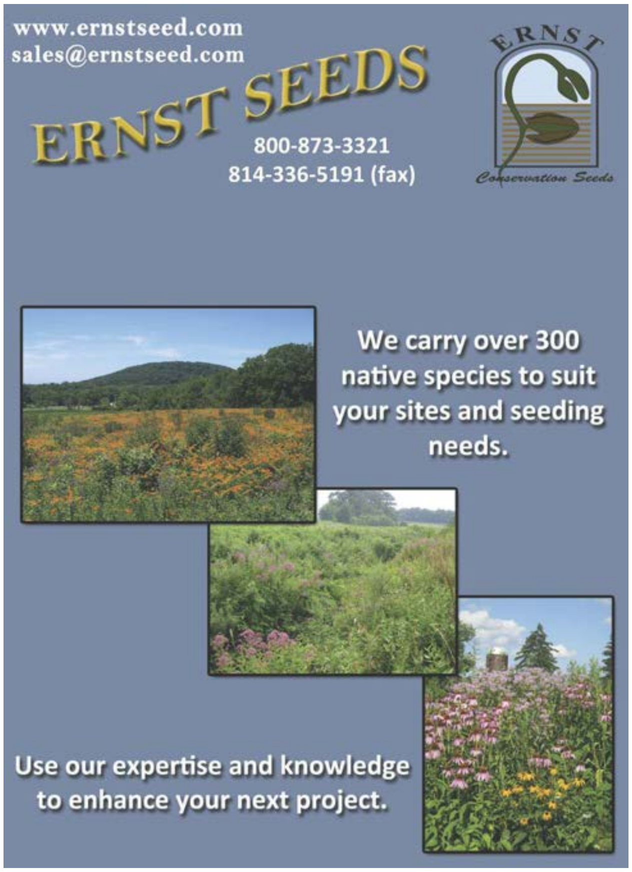

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