Methods of Breaking Seed Dormancy in the Endangered Species *Iliamna corei* (Sherff) Sherff (Malvaceae), with Special Attention to Heating

Jerry M. Baskin

Carol C. Baskin

School of Biological Sciences
University of Kentucky
Lexington, Kentucky 40506-0225 USA
jmbask0@ukcc.uky.edu

ABSTRACT: *Iliamna corei* (Sherff) Sherff, an herbaceous perennial plant listed by the U.S. Fish and Wildlife Service as endangered, is known only from a single site, on Peters Mountain in Giles County, Virginia. Seed dormancy in this species is due to a water-impermeable seed coat. Dormancy was broken in a high percentage of seeds by mechanical scarification, dipping in boiling water, dry-heating, and soaking in concentrated sulfuric acid. However, soaking in absolute ethanol, shifting from low to high temperature regimes, or alternate freezing and thawing did not break seed dormancy. Fire was effective in breaking dormancy of seeds on the soil surface, but not in those covered with 3 cm of soil. Seeds matured and sown in 1989 in greenhouse flats and burned each June from 1990 to 1995 had germinated to the following percentages by September 1995: buried and nonburned—2%, nonburied and nonburned—3%, buried and burned—3%, and nonburied and burned—39%. After five heating (to 80–90 °C)/incubation (25/15 °C) cycles, germination in flats from the burning experiment had increased to the following: buried and nonburned—60%, nonburied and nonburned—61%, buried and burned—45%, and nonburied and burned—71%. Furthermore, at least 65% of 1,800 seeds were viable and germinable after more than 3 years in the "seed bank." Thus, seeds of *I. corei* (1) require fire to germinate, (2) are capable of forming a long-lived seed bank, and (3) exhibit a continuum with regard to degree of seed coat dormancy. These results and those of others on the biology of *I. corei* and two of its closely related species, *I. remota* Greene and *I. rivularis* (Dougl.) Greene, were used to modify Buttrick's (1992) conceptual model of the population dynamics of *I. corei* in relation to fire and canopy development.

Index terms: endangered plant species, fire ecology of seed germination, *Iliamna*, hard seed coat dormancy

INTRODUCTION

Iliamna corei (Sherff) Sherff (Sherff 1949), Peters Mountain mallow, is a long-lived, clump-forming, herbaceous polycarpic perennial endemic to a single site, on Peters Mountain, Giles County, Virginia, in the Ridge and Valley physiographic province (Wieboldt 1991, Williams et al. 1992). The species is insect pollinated and self-incompatible, and it reproduces vegetatively via production of short rhizomes (Williams et al. 1992; T. Wieboldt, Virginia Polytechnic Institute and State University, Blacksburg, pers. com.). It grows at an elevation of approximately 800 m above sea level in an open oak-hickory-pine forest in shallow pockets of soil on Clinch sandstone (Silurian). This federal endangered species never has been collected from any other locality (U.S. Fish and Wildlife Service 1990). *Iliamna corei* is related closely to *I. remota* Greene (Stewart and Porter 1995, Stewart et al. 1996), which, before it was introduced along railroads and highways in Illinois, Indiana, and Virginia, was endemic to Langham Island in the Kankakee River near Altorf, Illinois (Williams et al. 1992). These two eastern U.S. taxa are related closely to *I. rivularis* (Dougl.) Greene of the western United States (Stewart and Porter 1995).

When members of the West Virginia University Botanical Expedition discovered *I. corei* on Peters Mountain in 1927, the population consisted of about 50 plants (clumps) (Strausbaugh and Core 1932); by 1988 the number had declined to 3 plants (U.S. Fish and Wildife Service 1990). Although a sizeable seed bank of this species was found in litter near the three remaining plants (U.S. Fish and Wildlife Service 1990), no seeds ever had been reported to germinate at the site by the time we began our study in 1989. Thus, the purpose of the present study was to identify possible methods to break dormancy in seeds of *I. corei*; this involved testing the seeds' responses to a variety of methods commonly applied to hard-seeded species. Such knowledge has application in ex situ conservation and in in situ conservation management. Special attention was given to possible treatments that might elucidate fire-dependent germination, as has been observed in the field for *I. rivularis* (Steele and Geier-Hayes 1989), *I. remota* (Schweg-

man 1990), and, after using information obtained in the early stages of the present study, for *I. corei* (Caljouw et al. 1994, Caljouw and Lipscomb 1995).

MATERIALS AND METHODS

Seed Source

All seeds used in this study were produced by plants of *I. corei* grown in cultivation at Virginia Polytechnic Institute and State University, Blacksburg, Virginia. The seed source for these cultivated plants was the seed bank of *I. corei* in the leaf litter at the Peters Mountain site (see Wieboldt 1991). Seeds were stored dry in paper bags under ambient laboratory conditions from time of collection until they were used in experiments.

Most of the studies described below were repeated one or two times, in whole or in part, with similar results. Thus, except for the two tests on the effect of continuous soaking in concentrated sulfuric acid on seed dormancy break, results of only one trial are presented.

Effect of Mechanical Scarification on Imbibition

Since other members of the Malvaceae are known to be hard-seeded (i.e., seed coats are impermeable to water), we tested the effect of mechanical scarification on imbibition of water by the seeds. In January 1993, three replications each of 100 scarified (with a single-edge razor blade) and nonscarified 1992 seeds were placed on moist filter paper in 10-cm-diameter Petri dishes kept on a laboratory bench at ca. 23–25 °C. After 0, 0.25, 0.50, 0.75, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4, 5, 6, 8, 10, and 24 h, seeds were removed from the moist filter paper, blotted dry, weighed to the nearest 0.1 mg, and returned to the Petri dishes. Cumulative mean (± SE) percentage increase in weight was calculated.

Effect of Mechanical Scarification on Dormancy Break

Seeds produced in 1989 were mechanically scarified with a single-edge razor blade and tested in light (14-h daily photoperi-

od, cool white fluorescent light, 20 μmoles $m^{-2} s^{-1}$, 400–700 nm) and in constant darkness (dishes wrapped with two layers of aluminum foil) at 12 h/12 h daily alternating temperature regimes of 15 °C/6° C, 20 °C/10 °C, 25 °C/15 °C, 30 °C/15 °C, and 35 °C/20 °C. The light period in this test and in the others described below extended from 1 h before the beginning of the high temperature part of the regime to 1 h after it ended. Each seed was scarified individually, and three replications of 50 seeds each were used for each test condition. Seeds were incubated on moist white quartz sand in 5.5-cm-diameter Petri dishes. Final results of each test were taken after 7 days. Protrusion of the radicle was the criterion for germination in this and all subsequent experiments. Seeds were tested in November 1989.

Effect of Continuous Soaking in Concentrated Sulfuric Acid on Dormancy Break

Seeds produced in 1992 were soaked in concentrated sulfuric acid (H_2SO_4) for 0 min (control), 5 min, 30 min, 1 h, 2 h, 4 h, 6 h, 7 h, 8 h, 9 h, and 10 h. After soaking, the seeds were rinsed with tap water, placed on moist sand in 5.5-cm-diameter Petri dishes, and incubated for 2 weeks at 30 °C /15 °C in light. There were three replications of 50 seeds per treatment. This study was begun on September 8, 1993, and was repeated beginning on September 27, 1993.

Effect of Intermittent Soaking in Concentrated Sulfuric Acid on Dormancy Break

On February 7, 1994, 1,950 seeds produced in 1992 were soaked for 1 h in concentrated H SO. After acid-soaking and rinsing with tap water, 50 seeds each were placed in forty-two 5.5-cm-diameter Petri dishes (39 acid-treated, 3 water controls) and incubated at 30 °C/15 °C in light. This 1-h soaking/4-day incubation cycle was repeated 12 times (Figure 1). Thus, three replications of 50 seeds each were soaked and incubated for 0 (water control), 1, 2, 3, . . . 13 times. In addition to the water control, there was a control for each acid-soaking/incubation cycle. That is, after each cycle three dishes of acid-soaked seeds were left behind as a control for the next cycle, and thus they were incubated on moist sand during the remainder of the 52-day experiment. All 42 dishes were checked for germinated seeds at 4-day intervals throughout the study.

Effect of Dry Heat on Dormancy Break

In May 1989, three replications of fifty 1988-produced seeds were subjected to constant temperature of 50 °C–140 °C at 10 °C intervals in a laboratory drying oven for 1, 15, 30, and 60 min. This range of temperatures includes those that have been reported to break dormancy in other hard-
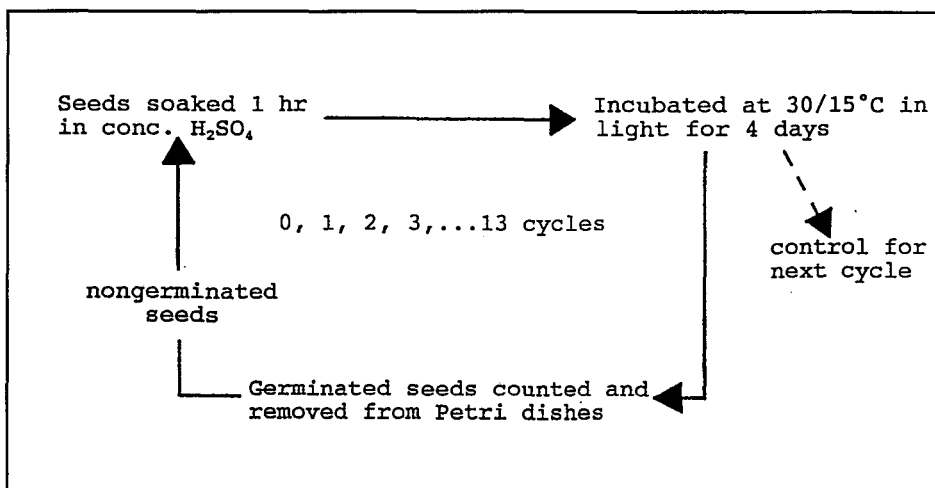

Figure 1. Diagram illustrating procedure used to test the effect of intermittent soaking in concentrated sulfuric acid on dormancy break in seeds of *Iliamna corei*.

seeded species (Martin et al. 1975, Mott and McKeon 1979, Jeffrey et al. 1988, Bossard 1993, Teketay 1996) and to occur within the 1- to 3-cm soil depth range during a fire (Beadle 1940, Sweeney 1956, Floyd 1966, Shea et al. 1979, Auld 1986). After the dry heat treatments, seeds were incubated on moist sand in 5.5-cm-diameter Petri dishes at 30 °C/15 °C in light; they were checked for germination after 14 days. Seeds incubated at 30 °C/15 °C in light without a heat treatment served as the control.

Effect of Dipping Seeds in Boiling Water on Dormancy Break

On May 15, 1992, batches of 1991 seeds were dipped in boiling water for 0, 1, 3, 5, 10, 20, 30, 40, or 60 sec. After boiling, three replications of 50 seeds each for each boiling time and for a control (seeds not dipped in boiling water) were placed on moist sand in Petri dishes. The number of germinated seeds was determined after 14 days of incubation at 30 °C /15 °C in light.

Effect of Soaking in Absolute Ethanol on Dormancy Break

On May 19, 1992, batches of 1991 seeds were soaked in absolute ethanol for 24, 48, 72, or 96 h, followed by rinsing in distilled water. Then, three replications of 50 seeds each for each of the four soaking times in ethanol and for a control (seeds not soaked in ethanol) were placed on moist sand in Petri dishes. Number of seeds that germinated was determined after 14 days of incubation at 30 °C /15 °C in light.

Effect of Temperature Shifts on Dormancy Break

In November 1989, samples of 1989-produced seeds were incubated on moist sand in 5.5-cm-diameter Petri dishes in light at 12 h/12 h daily thermoperiods of 5 °C /5 °C, 15 °C /6 °C, 20 °C /10 °C, 25 °C /15 °C, 30 °C /15 °C, 35 °C /20 °C, and 40 °C /20°C. After incubation for 14 weeks, three dishes of seeds (replications) from each temperature regime (except 40 °C /20 °C) were transferred to each temperature regime higher than the one at which they were

incubated for 14 weeks. Three dishes of seeds (controls) remained at each of the six temperatures for the entire study. For example, 18 dishes of seeds were incubated at 15°C/6°C. After 14 weeks at this thermoperiod, three dishes each were transferred to 20 °C /10 °C, 25 °C /15 °C, 30 °C /15 °C, 35 °C /20 °C, and 40°C /20°C, and three dishes (control) remained at 15 °C / 6 °C. Thirty days after the seeds were transferred to the higher temperatures, the number of germinated seeds was determined for all treatments and controls.

Effect of Freezing and Thawing on Dormancy Break

In May 1989, three replications of 50 1988-produced seeds were placed on moist sand in Petri dishes and exposed to a daily thermoperiod of -10°C/+5 °C for 30 days. Seeds were exposed daily to -10 °C for 8 h and to 5 °C for 16 h. Controls for this experiment were kept at 30 °C /15 °C, 5 °C, and -10°C for the 30-day period. After the final freezing and thawing cycle, seeds in this treatment, along with those in the controls at 30 °C /15 °C, 5 °C, and -10 °C, were incubated at 30 °C /15 °C in light for 7 days, at which time the number of germinated seeds was determined.

Effect of Fire on Dormancy Break

In November 1989, 150 1989-produced seeds were sown in each of twelve 20 x 30 x 8-cm-deep metal greenhouse flats containing soil derived from a Pennsylvanian sandstone and collected on the Appalachian Plateau in eastern Kentucky. In half of the flats, seeds were covered with 3 cm of soil, and in the other half they were not covered. Soil in all 12 flats was covered with a 3- to 5-cm layer of dead oak leaves. Flats were kept in a nonheated greenhouse in Lexington, Kentucky, where temperatures are near those out-of-doors (Baskin and Baskin 1985), until September 1995. Soil moisture was kept at or near field capacity, except for a 1-week period before each burn, when the leaf litter and soil in treatments and controls were allowed to dry, and during August and September, when the soil was watered, to field capacity, only once per week. Soil in all 12 flats (treatments and controls) was kept free of

litter from immediately after burning in June until October 1, at which time a 3- to 5-cm layer of dead oak leaves again was added to each flat. Throughout the study, flats were examined weekly for seedlings, which were counted and removed at each checking.

In June 1990, the following treatments and controls were assigned randomly to the 12 flats: (1) buried seeds, burn; (2) buried, no burn (control); (3) nonburied, burn; and (4) nonburied, no burn (control). Flats assigned to the burning treatments were burned each June from 1990 through 1995; controls were not burned during this period. A loose, 3- to 5-cm-thick layer of wheat straw was added to the layer of dead oak leaves before the flats were burned to increase the fuel load and to facilitate burning of leaves. The fires per se lasted about 1-2 min, during which time combustion of the straw/leaf layer was nearly complete.

Effect of Dry Heat on Breaking Dormancy of Seeds That Did Not Germinate in the Burning Experiment

Since only a very few seeds germinated after the 1995 burn, treatment and control flats were heated in a drying oven in an attempt to break dormancy of any seeds remaining in the seed bank. All treatment and control flats were subjected to five dry heat cycles between September 1995 and May 1996. A cycle consisted of heating the dry soil in the flats in a drying oven (to 80–90 °C) for 105 min and then wetting the soil and incubating it at 25 °C /15 °C in light until seed germination ceased, which usually was about 1 month following heating. Soil moisture in the flats was kept at or near field capacity during the incubation period. After the incubation period, the soil was allowed to dry at 25 °C /15 °C for at least 1 week prior to heating in the oven again. The oven was set so that at a depth of approximately 2 cm the soil reached a maximum of 80–90°C after about 60 min. These temperatures previously had been shown to effectively break dormancy in seeds of *I. corei* in the dry heat experiment (see "Results").
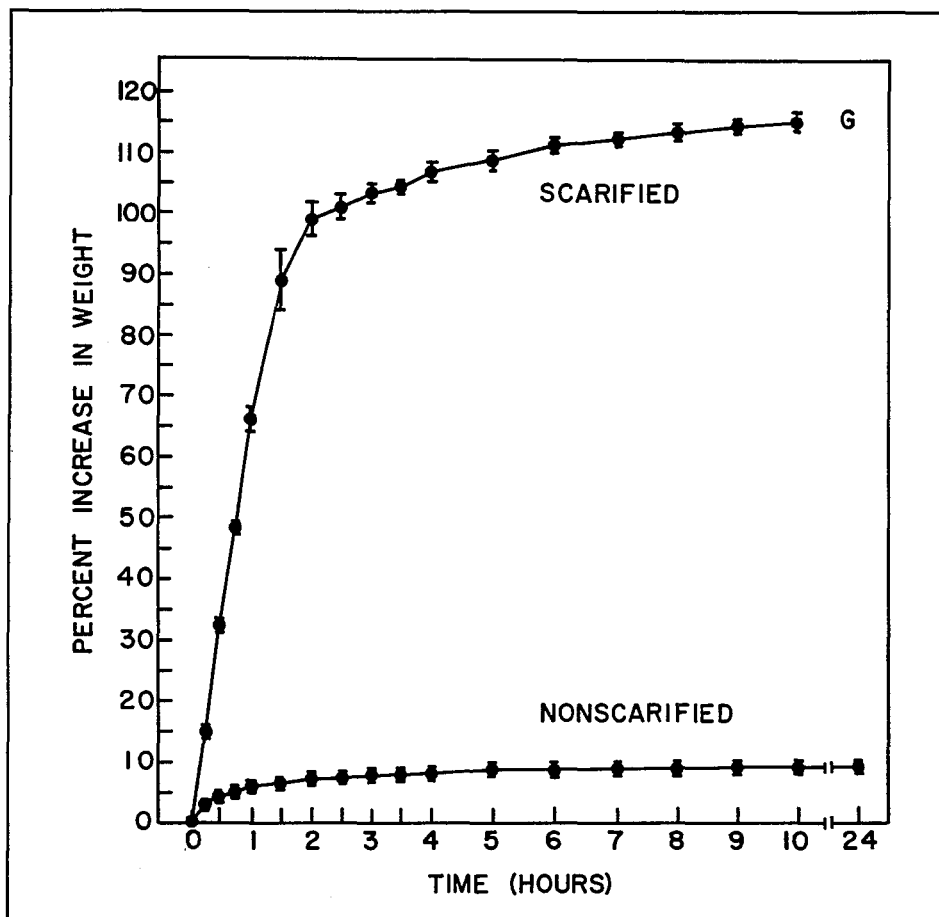
Figure 2. Mean (±SE) increase in weight of scarified and nonscarified 1992 seeds of *Iliamna corei*. G= some seeds had germinated. The study was done in January 1993.

h, respectively. Further, weight of non-scarified seeds had increased only 9±1% after 24 h; by this time, some of the scar-ified seeds had germinated (Figure 2).

Effect of Mechanical Scarification on Dormancy Break

Scarified seeds germinated to 100% at 20 °C/10 °C, 25 °C/15 °C, 30 °C /15 °C, and 35 °C/20°C in light and to 92%–100% at these temperatures in darkness (Table 1). At 15°C/6 °C, 13% and 31% of the seeds germinated in light and darkness, respective-ly. Nonscarified seeds germinated to only 0-1% over the range of test conditions.

Effect of Continuous Soaking in Concentrated Sulfuric Acid on Dormancy Break

In the test begun on September 8, 1993, germination percentagea (± SEs) of 1992 seeds soaked for various periods of time in concentrated H_2SO_4 were as follows: 0 min (control)=0.7±0.5%, 5 min=4.0±0%, 30 min=10.7±0.5%, 1 h=24.0±3.4%, 2 h=19.3±1.4%, 4 h=32±3.6%, 6 h = 37.3±3.8%, 7 h=66.7±4.9%, 8 h = 60.7±1.4%, 9 h=72.7±2.8%, and 10 h = 33.3±5.1%. In the test begun on September 27, 1993, germination of 1992 seeds in-creased from 4±1% in the control to 72±3% in seeds soaked for 10 h.

Survival in "Seed Bank" of 1991-Produced Seeds

In March 1992, 300 1991-produced seeds were added to each of six 20 x 30 x 8-cm-deep metal flats containing soil derived from Pennsylvanian sandstone and col-lected from the Allegheny Plateau in south-eastern Ohio. In three of the flats, seeds were covered with 3 cm of soil, and in the other three flats seeds were not covered. In all six flats, the soil was covered with a 3- to 5-cm layer of dead leaves. Flats were kept in the same nonheated greenhouse as those in the burning experiment. These buried and nonburned seeds were handled using the same procedures as for those in the burned-nonburied and nonburied-non-burned controls in the burning experiment. Between September 1995 and May 1996, the seeds were subjected to the five dry heat/incubation cycles described above.

RESULTS

Effect of Mechanical Scarification on Imbibition

The weight of scarified seeds increased 98±3% in 2 h and 115±2% in 10 h. In contrast, weight of nonscarified seeds in-creased only 7±1% and 9±1% in 2 and 10

Effect of Intermittent Soaking in Concentrated Sulfuric Acid on Dormancy Break

Seeds given 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, and 13 1-h periods of soaking germi-nated to 66%, 79%, 85%, 86%, 87%, 88%, 88%, 88%, 89%, 90%, 90%, 90%, and

Table 1. Effect of mechanical scarification on germination percentages (mean±SE) of 1989 seeds of *Iliamna corei* incubated in light (L) and in darkness (D). Study was conducted in November 1989.

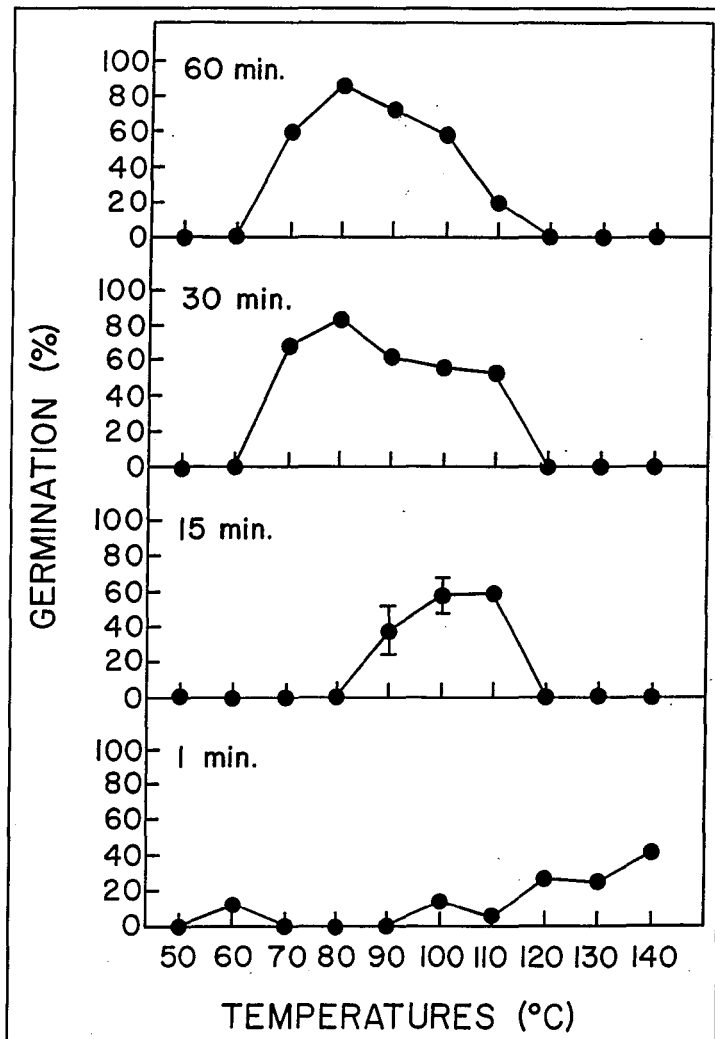| Treatment	Light/Dark	Thermoperiod (°C)				
		15/6	20/10	25/15	30/15	35/20
Scarified	L	13±2	100	100	100	100
Nonscarified	L	0	0	3±2	1±1	1±1
Scarified	D	31±1	94±1	100	100	92±1
Nonscarified	D	0	1±1	1±1	1±1	0

Figure 3. Effect on dormancy break of dry heating 1988 seeds of *Iliamna corei* for 1 to 60 min at various temperatures. Only 1% of the seeds germinated in the nonheated control. SEs of less than 5% are not shown. Study was done in May 1989.
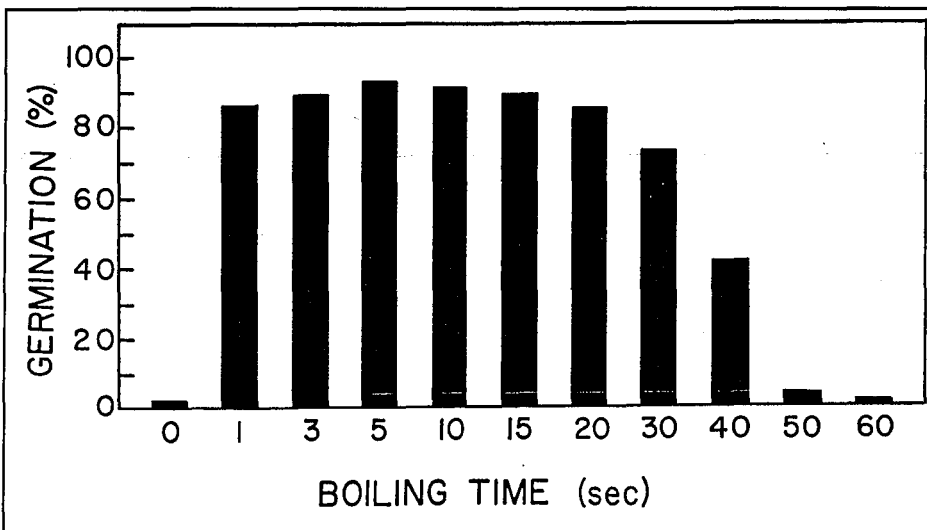
90%, respectively. Only 2% of the seeds in the water control germinated. In the left-behind controls, 99% of the seeds that germinated during a soaking/incubation cycle had done so after 4 days of incubation at 30 °C/15 °C. That is, very few additional seeds germinated in these controls throughout the rest of the 52-day experiment.

Effect of Dry Heat on Dormancy Break

Constant temperatures of 70 °C, 80 °C, 90 °C, 100 °C, and 110 °C were effective in breaking dormancy in a high percentage of the 1988 seeds of *I. corei* (Figure 3). Whereas the optimal temperature for seed coat breakdown in the 30- and 60-min exposures was 80 °C, in the 15-min exposure 100 °C and 110 °C were optimal. Seeds heated for 15, 30, and 60 min at 120 °C, 130 °C, or 140 °C did not germinate; they were killed. On the other hand, 43% of the seeds germinated after exposure to 140 °C for 1 min. Only 2% of the seeds in the water-control germinated.

Effect of Dipping Seeds in Boiling Water on Dormancy Break

Seeds dipped in boiling water for 1 to 20 sec germinated to 85%–93%, but boiling longer than 20 sec caused a decline in germination percentage (Figure 4). Dipping seeds in boiling water for 50 sec or longer killed most of them. Only 1% of the control seeds germinated.

Effect of Soaking Seeds in Absolute Ethanol on Dormancy Break

Soaking seeds in ethanol was totally ineffective in overcoming hard seed coat dormancy. Germination percentages for seeds soaked for 0 (control), 24, 48, 72, and 96 h were 1%, 2%, 1%, 1%, and 2%, respectively; seeds that did not germinate also did not imbibe water.

Effect of Temperature Shifts on Dormancy Break

Shifting seeds from lower to higher temperatures was totally ineffective in breaking hard seed coat dormancy. Only 0%-2% of the seeds germinated regardless of treatment, and none of those that did not germinate imbibed water.

Effect of Freezing and Thawing on Dormancy Break

Freeze/thaw cycles were totally ineffective in breaking hard seed coat dormancy. No seeds imbibed or germinated in treatment or in control.

Figure 4. Effect on dormancy break of dipping 1991 seeds of *Iliamna corei* in boiling water for 1 to 60 sec. All SE bars were ±2% or less. Study was done in May 1992.

Effect of Fire on Dormancy Break

Burning was effective in breaking dormancy only in seeds on the soil surface (Table 2). However, even six annual June burns (1990–1995) resulted in only 39% germination for the seeds in the nonburied-burned treatment.

Effect of Dry Heat on Breaking Dormancy of Seeds That Did Not Germinate in the Burning Experiment

Dry heat was quite effective in breaking hard seed coat dormancy in both burned and nonburned flats (Table 3). Five dry-heating treatments increased germination from 2% to 60% and 3% to 61% in the buried-nonburned and nonburied-nonburned controls, respectively, and from 3% to 45% and 39% to 71% in the buried-burned and nonburied-burned treatments, respectively.

Survival in "Seed Bank" of 1991-Produced Seeds

A high percentage of both buried and nonburied 1991 seeds survived in the "seed bank" from March 1992 to September 1995. After five dry-heating/incubation cycles, 70% and 64% of the buried and nonburied seeds, respectively, had germinated (Table 4).

Table 2. Effect of fire on cumulative germination percentages (mean±SE) of 1989 seeds of *Iliamna corei.*

Year	Buried Nonburned	Nonburied Nonburned	Buried Burned	Nonburied Burned
1989	0	0	0	0
1990	1±1	3±1	1±1	10±7
1991	2±1	3±1	1±1	12±7
1992	2±1	3±1	2±1	20±7
1993	2±1	3±1	2±1	30±6
1994	2±1	3±1	2±1	39±6
1995	2±1	3±1	3±1	39±6

Table 3. Effect of dry heat on cumulative germination percentages (mean±SE) of 1989 seeds of *Iliamna corei* remaining in the seed bank of the burning experiment in September 1995.

Number of Dry Heat Treatments	Buried Nonburned	Nonburied Nonburned	Buried Burned	Nonburied Burned
0	2±1[a]	3±1[a]	3±1[a]	39±6[a]
1	38±1	34±2	37±12	61±6
2	52±3	45±6	42±12	67±10
3	59±6	58±9	45±11	68±10
4	59±6	60±10	45±11	70±10
5	60±5	61±10	45±11	71±10

[a]Percent of seeds that had germinated in the burning experiment (from Table 2) by September 1995.

DISCUSSION

As has been shown for species of Malvaceae and several other plant families (Rolston 1978; Baskin and Baskin 1988, 1989), the seed coat of *I. corei* is impermeable to water (Figure 2). The water-impermeable seed coat can be rendered permeable to water by mechanical scarification (Table 1), soaking in concentrated sulfuric acid (data in text), dry heating (Figure 3, Table 3, Table 4), dipping in boiling water (Figure 4), and burning (Table 2). Furthermore, once the seed coat becomes permeable a high percentage of the seeds germinate over a wide range of temperatures in light and in darkness (Table 1); thus, the embryo is nondormant. Mechanical scarification, soaking in concentrated H_2SO_4, dipping in boiling water, and dry heating are well-known methods of breaking hard

seed coat dormancy under laboratory conditions (Crocker and Barton 1957, Rolston 1978). However, other treatments, including soaking in absolute ethanol, shifting from low to high temperature regimes, alternate freezing and thawing (Crocker and Barton 1957, Rolston 1978), and dry storage at ambient laboratory conditions (Baskin and Baskin 1984, Morrison et al. 1992), that have been shown to be effective in breaking hard seed coat dormancy in some species (Rolston 1978) were ineffective in *I. corei.*

Various factors in the natural environment have been shown, or postulated, to break dormancy in hard-seeded species. These include microbial action (e.g., Fenner 1985, Mayer and Poljakoff-Mayber 1989, Bew-

Table 4. Effect of dry heat on cumulative germination percentages (mean±SE) of 1991 seeds of *Iliamna corei* in the seed bank in September 1995.

Number of Dry Heat Treatments	Buried	Nonburied
0	0[a]	2± 0[a]
1	60±12	49±11
2	67±8	49±11
3	69±7	62±10
4	70±7	63±10
5	70±7	64±10

[a] Percentage of seeds that germinated between March 1992 and September 1995

ley and Black 1994), mechanical scarification (Went 1955, Fenner 1985, Mayer and Poljakoff-Mayber 1989, Bewley and Black 1994), passage of seeds through the digestive tract of animals (Swank 1944, Krefting and Roe 1949, Lamprey 1967, Hoffman et al. 1989), fire (Floyd 1966, Shea et al. 1979, Abrams and Dickmann 1982), freezing and thawing (Midgley 1926, Dunn 1939, Martin 1945, Barton 1947), natural fluctuating temperatures (Quinlivan 1966, 1968; Vasquez-Yanes and Orozco-Segovia 1982; Dillon and Forcella 1985), and drying (Baskin and Baskin 1974). However, we are unaware of any good evidence that hard seed coat dormancy is broken in nature by microbial action, mechanical scarification, or passage through the digestive tract of birds or other animals. Furthermore, shifting seeds of *I. corei* from low to high temperatures was completely ineffective in breaking dormancy in seeds of this species, as was storing them dry for 5.5 years at ambient laboratory conditions (Baskin and Baskin, unpubl. data).

Thus, we conclude that fire is the only one of these factors that breaks hard seed coat dormancy in *I. corei* in nature. All three methods used to heat the seeds (burning, dry heating, boiling) effectively broke dormancy. Further, the temperatures that broke dormancy by dry heating (ca. 70°C –110°C) and boiling (100°C) include those that have been recorded in the 1- to 3-cm-soil-depth range during fires (e.g., Floyd 1966, Shea et al. 1979, Auld 1986). However, burn temperatures have not been recorded in *I. corei* habitat.

A cohort of seeds of *I. corei* varies in degree of hard seed coat dormancy, as shown by results of the experiment testing the effects on dormancy break of soaking in concentrated H_2SO_4, dry heating, and dipping in boiling water. The number of hours of soaking required to break dormancy varied from 1 to 10 among seeds in a 1992 cohort (data in text). A substantial number of seeds that did not germinate in the 1989 cohort that was burned in 1990–1995 did so after one heating in a drying oven, but others required two, three, or more heatings (Table 3). Dormancy in some of the 1988 seeds in the laboratory dry

heat experiment (Figure 3) was broken, for example, by heating them for 30 or 60 min at 70 °C, whereas others did not germinate until after they were heated for 30 or 60 min at 80 °C (Figure 2). Finally, although a high percentage of the 1991 seeds dipped in boiling water for 1 sec germinated, a few did not germinate until they were dipped for 3 or 5 sec. In all these tests, very low percentages (ca. 2%) of the seeds germinated without treatment. Thus, a few seeds in the cohorts were not dormant at all, which often is the case in hard-seeded species (e.g., Morrison et al. 1992). This continuum of hardseededness (sensu Thanos and Georghiou 1988) in *I. corei* may be caused by seeds maturing under different environmental conditions (e.g., James and Bancroft 1951, Evenari et al. 1966, El Bagoury 1975) or in different positions on the mother plant (Taylor and Palmer 1979).

Degree of hard seed coat dormancy also varies within cohorts over time. For example, 1992 seeds soaked in concentrated H_2SO_4 for 1 h in September 1993 and 1 h in February 1994 germinated to 29% (Baskin and Baskin, unpubl. data) and 66% (data in text), respectively. Furthermore, only 50% of the seeds tested in September

1993 germinated after soaking for 4 h in concentrated H_2SO_4 (Baskin and Baskin, unpubl. data).

Figure 5 (modified from Buttrick 1992) is a general conceptual model showing the role of fire and forest canopy development in the population dynamics of *Iliamna* species. Fire in this model stimulates seeds in the seed bank to germinate and opens up the forest canopy. Full sunlight enhances seedling survival, growth, flowering, and reproduction of the shade-intolerant *Iliamna* plants (Lyon 1971, Brown and DeByle 1989, Steele and Geier-Hayes 1989, Schwegman 1990, Williams *et al.* 1992). After a fire, succession leads to canopy closure and thus eventually to loss of vigor and death of the plants (Lyon 1971, Brown and DeByle 1989, Steele and Geier-Hayes 1989). During intervals between fires, the population of growing plants may decline to low numbers, or even to zero. However, it appears that a high percentage of the seeds can survive in the soil for a long period of time. Up to at least 58% of the *I. corei* seeds planted in 1989 in the nonburned controls in the burning experiment survived until 1995 (Table 3). Further, at least 62% of the seeds sown on the soil surface and 70% of those bur-
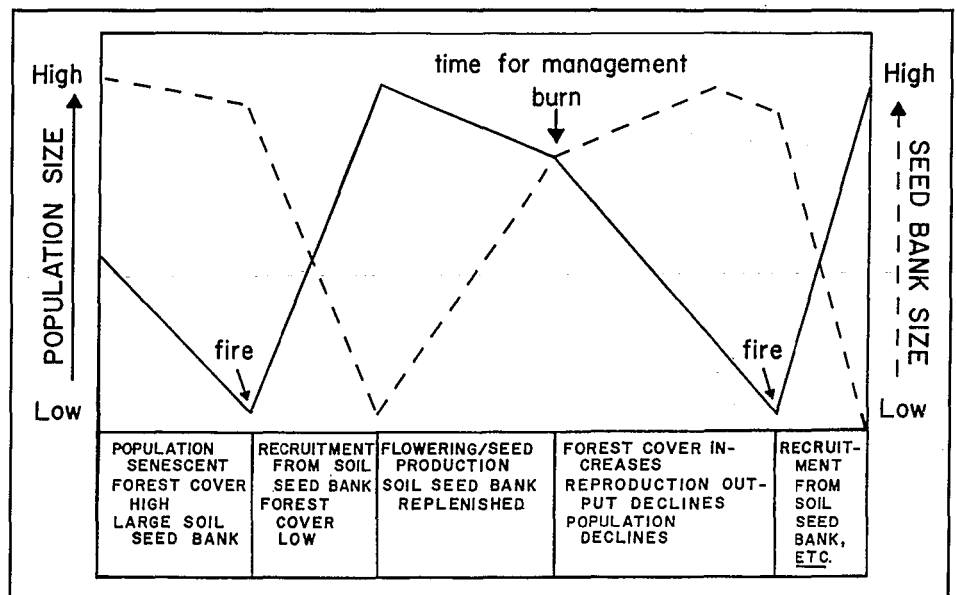

Figure 5. Conceptual model of population and seed bank dynamics of *Iliamna* spp. in relation to natural fire and canopy development (modified from Buttrick 1992). Stage in population cycle at which we suggest site should be burned is indicated by "time for management burn," but predicted results of the burn (discussed in text) are not shown.

ied 3 cm below the soil surface in March 1992 still were alive in September 1995 (Table 4). Kramer and Johnson (1987) found seeds of *I. rivularis* in the seed bank of *Abies grandis/Acer glabrum* and *Abies grandis/Vaccinium globulare* habitat types with stand ages ≥ 64 and ≥62 years, respectively. Seeds of *I. remota* can survive in the soil for at least 10 years (Schwegman 1990).

The model shows that a high percentage of the seeds at a population site survive from a reproductive episode until the next fire, at which time most of them germinate. Although no field data are available on the proportion of seeds in the seedbank that germinate after a forest fire, flushes of *Iliamna corei* (Caljouw et al. 1994, Edwards 1995), *I. remota* (Schwegman 1984), and *I. rivularis* (Steele and Geier-Hayes 1989) may be very large following a burn. For example, 492 seeds in the natural seed bank of *I. corei* on Peters Mountain germinated following a management burn on May 7, 1993 in a "roughly 10m x 15m" plot (Caljouw et al. 1994), and 194 germinated in a "roughly 5m x 8m" plot following a management burn on May 13, 1994 (Edwards 1995). Further, dormancy was broken by only one dry-heat treatment in 55%–81% of the *I. corei* seeds remaining in the seed bank for about 6 years in the burning experiment (Table 3) and in 70%-76% of those remaining in the seed bank for more than 3 years in the seed survival study (Table 4). According to Schwegman (1984) "dense stands of [*I. remota*] seedlings were noted on July 18. . ." at "hot spots" caused by burning of brush piles during a management burn on April 2. Figure 17 of Steele and Geier-Hayes (1989: 37) shows hundreds of juveniles of *I. rivularis* in the vicinity of a charred stump. According to the caption for the figure, "This area was clearcut and severely burned 2 years ago. *Iliamna* germinated profusely from seed buried in the soil and now dominates the site." Seeds of many other species in various plant families with hard seeds also have been observed to germinate in the field after fire (Cremer and Mount 1965, Floyd 1976, Orme and Leege 1976, Purdie and Slatyer 1976, Shea et al. 1979, Dell 1980, Kamada et al. 1987, Hartnett and Richardson 1989).

Two conclusions from our study contribute to the "validation" of Buttrick's (1992) model: (1) Fire is the only plausible natural seed dormancy-breaking factor for *I. corei*, and (2) the species can form a long-lived seed bank. Although Buttrick's model implies that germination of *I. corei* is fire dependent and that seeds in the seed bank can live a long time, heretofore no data were available to support these assumptions.

A small proportion of viable seeds on the soil surface germinated after each fire in our study (Table 2); this may have resulted from a lack of a uniformly high temperature over the entire surface of the flats, or because there were differences in the heat requirement for dormancy break among the seeds, or both. The seeds were not killed by the fire, since many more of them germinated after they were dry-heated at the end of the burning experiment. Furthermore, the fire was not hot enough to break dormancy in seeds 3 cm below the soil surface (Table 2).

Our version of the model differs from Buttrick's version in two ways. First, it graphically illustrates the dynamics of the seed bank population. After replenishment of the seed bank, there is a gradual decline in the number of seeds in the soil/litter, and then a rapid decline following a fire. The most rapid buildup of the seed population takes place before there is a significant increase in tree canopy cover. This is followed by a slower buildup of the seed bank during canopy development, and then a slow decline after canopy closure. Buttrick's model says only that the seed bank is large in the senescent phase of the plant population cycles, declines after a fire when population recruitment occurs, and is replenished via seed production by the recruits.

The second way in which the modified version of the model differs from the original is that in the former, population growth and decline do not fit a bell-shaped curve. Immediately following a fire, there is rapid recruitment of the aboveground population, and then a slow decline of that population during the open-canopy phase of the cycle. After some period of time, a point is reached in percentage of canopy closure that "triggers" an increase in mortality of plants. Finally, by the next fire the aboveground population has declined to very low numbers, or perhaps to zero; in the latter case, *I. corei* would be present at the site only as seeds in the seed bank. Thus, compared to Buttrick's model our version contains more details on, and more tightly couples, population dynamics of seeds in the seed bank and aboveground plants.

Obviously, a plan for in situ management of *I corei* must include burning the population site. The question is, at what time interval should it be burned? This question cannot be answered in terms of number of years between burns. However, we suggest that the site should be burned when mortality rate of plants starts to increase and rate of seed accumulation starts to decrease (labeled "time for management burn" in Figure 5). A fire at this point should promote increases in the minimum and maximum number of seeds and plants reached in the population cycles, and perhaps lower the amplitudes of the cycles. Therefore, the cycles would be "reset" to maintain larger populations of both seeds and plants than presently occur at the site. Under this management plan, monitoring data on survival and reproductive output (number of seeds produced) of plants will help the preserve manager decide when, or when not, to burn, without having prior knowledge of the burning interval in years required to preserve the *I. corei* population. As such, the model (Figure 5) will serve as a guide for management of this federally endangered species (Buttrick 1992).

It is important to note that fire does not kill plants of *I. corei* (Edwards 1995). Schwegman (1990) also reported that mature plants of *I. remota* "typically are not injured by fire." In the northern Rocky Mountains, *I. rivularis* can recolonize burned areas by regrowth of shoots from caudices of plants growing on the site at the time of the fire and by seeds in a long-lived seed bank (Stickney 1985, 1986). Stickney (1986) used the term "survivors" for " those species with established plants on the site at the time of the fire that were capable of regrowth after burning."

It appears, then, that the life history adaptations of these three *Iliamna* species to fire are nearly identical. Furthermore, all of them are early successional and shade-intolerant clump-forming polycarpic perennials. They are examples of narrowly endemic (*I. corei, I. remota*) and geographically widespread (*I. rivularis*) congeners with very similar autecologies. As such, information about the biology of *I. rivularis* can be useful in developing a conservation strategy for *I. corei* and *I. remota* (see Baskin and Baskin 1986). However, the high degree of overlap in their autecologies precludes identifying possible proximal causes of endemism in *I. corei* or *I. remota*.

In 1927, the number of *I. corei* plants (clumps) at the population site on Peters Mountain consisted of "no more than 50 plants" (Strausbaugh and Core 1932). Keener and Hardin (1962) estimated that there were about 40 clumps of *I. corei* at the site in 1962, and they found the population "still flourishing thirty-five years after its initial discovery." Whereas the population size decreased by 20% or less between 1927 and 1962, it declined from 40 to 11 clumps (72.5% decrease) between 1962 and 1978 and from 11 to 3 (72.7% decrease) between 1978 and 1988. Thus, the population exhibited a slow rate of decline for at least 35 years, after which the rate increased sharply (U.S. Fish and Wildlife Service 1990).

This rate of decline in the *I. corei* population is much slower than the rates reported by Lyon (1971) and Brown and DeByle (1989) for populations of *I. rivularis* in the northern Rocky Mountains in Idaho. There, population sizes and biomass of *I. rivularis* reach a peak in about 2 (Debyle and Brown 1989) to 6 (Lyon 1971) years following a fire. Except for seeds in the seed bank, the populations decrease to very low numbers, or the species may even disappear from the site, in 6 (Debyle and Brown 1989) to 20 (Lyon 1971) years. Seeds in the seed bank do not germinate until the next burn, at which time the cycle starts again. The short period of time that *I. rivularis* grows vigorously on a burned site before it starts to decline is due to the rapid resprouting of shrubs (e.g., *Cean-*

othus velutinus Hook., *Ribes* spp.) that shade it (Lyon 1971, Stickney 1986, Brown and DeByle 1989).

Caljouw et al. (1994) determined that in the vicinity of the *I. corei* population the mean fire return interval between 1941 (beginning of fire records) and 1992 was only 6 years. They also reported that the area was logged extensively in the 1920s. Thus, perhaps between 1927 and 1962 the site of *I. corei* was burned or otherwise disturbed several times. These disturbances would have resulted in (1) rejuvenation of the population from seeds in the seed bank (burning only), (2) maintenance of an open habitat that allowed at least 80% (40) of the approximately 50 plants present at the site in 1927 to persist in a vigorous condition for 35 years or more (disturbance by logging or windthrow, but not by fire), or (3) a combination of rejuvenation from seeds and persistence of some of the plants present at the site in 1927 (disturbance by logging or windthrow and by fire). On the other hand, rate of decline of the *I. corei* population may be slow because succession to canopy closure in its rocky habitat (U.S. Fish and Wildlife Service 1990) is slow. In the latter case, burning or other types of management would be needed only at infrequent intervals to keep the population in a healthy condition. If this is the case, then after the tree canopy at the *I. corei* site on Peters Mountain is opened up and a healthy population of this species is reestablished as a result of the recovery efforts now in progress, occasional burns, the frequency of which will be determined by monitoring (see above), should maintain a healthy population of this federal endangered species.

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Jerry M. Baskin is a Professor of Biological Sciences at the University of Kentucky. His research interests include seed germination ecology, biology of rare plants, and plant geography.

Carol C. Baskin is an Adjunct Professor in the School of Biological Sciences at the University of Kentucky. Her interests include the life cycle ecology of herbaceous plants, with particular reference to seed germination ecology.

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