

RESEARCH ARTICLE

The Seed Ecology of  
*Iliamna longisepala*  
(Torr.) Wiggins,  
an East Cascade  
Endemic

Richy J. Harrod<sup>1</sup>

Okanogan-Wenatchee National Forests  
215 Melody Lane  
Wenatchee, WA 98801 USA

Charles B. Halpern

College of Forest Resources  
Box 352100  
University of Washington  
Seattle, WA 98195-2100 USA

<sup>1</sup> Corresponding author:  
rharrod@fs.fed.us; 509-664-9331

**ABSTRACT:** We examined the seed ecology of *Iliamna longisepala* as an aid to developing a conservation strategy for this rare endemic forb of northcentral Washington. We conducted field, greenhouse, and laboratory studies to quantify: (1) densities of buried viable seed among sites with different histories of burning, (2) post-fire spatial distributions of germinants relative to reproductive plants and burn severity, (3) seed production and its annual variation, and (4) germination requirements. Density of seed in the soil was not significantly related to history of burning, but sites that experienced fire 10 years before sampling averaged 10 times as many seeds as sites that burned recently and four times as many seeds as sites that had not burned within 50 years. Density of viable seeds in the soil did not correlate with density of reproductive plants. In a field experiment, germinants appeared after fall burning, but not after spring burning. Germinants were most abundant within 10 m of reproductive plants and were concentrated in areas of high burn severity. Seed production per plant was significantly correlated to crown diameter, but production varied dramatically from year to year. Experimental germination trials were largely unsuccessful due to low (8%) viability of seeds collected from mature plants. However, field studies illustrate that fire is sufficient to break the dormancy of seeds that have accumulated in the soil. Long-term exclusion of fire may lead to local extinction of populations as the longevity of reproductive plants and seeds are exceeded. However, burning more frequently than every 10 years could deplete local seed reserves.

**Index terms:** fire effects, prescribed burning, rare plant, seed ecology

INTRODUCTION

Effective conservation of a rare plant requires an understanding of how habitat requirements, life history, and responses to disturbance shape the population dynamics of a species (Menges 1986, Schemske et al. 1994). For some rare species, fire may determine population patterns in space and time. This appears to be the case with *Iliamna longisepala* (Torr.) Wiggins (Malvaceae), an endemic herb of northcentral Washington. Prior to initiating this work, our observations suggested a strong, positive effect of wildland fire on the density and vigor of *I. longisepala* populations (Kuhlmann and Harrod, unpubl. data). Managers have expressed interest in using prescribed fire as a tool to maintain or enhance populations, but informed decisions are limited by a paucity of information on the effects of fire. In this paper, we report on four studies that explore various aspects of the seed ecology of *I. longisepala*. These contribute to a broader set of experiments (Harrod 2003) that address the population dynamics and possible conservation strategies for this apparent fire-dependent species.

Plant species can survive in frequently disturbed environments by forming a persistent seed bank (Cohen 1966). There may not be a strong correlation between plant abundance and density of viable seed in the soil (Oosting and Humphreys

1940, Pickett and McDonnell 1989). As a result, a species that is relatively rare in the aboveground community may become dominant after disturbance. We suspected that *I. longisepala* maintains a viable seed bank because it has limited dispersal ability and plant density increases markedly after fire (Kuhlmann and Harrod, unpubl. data). However, knowledge of the frequency of disturbance and the ability of *I. longisepala* to develop a seed bank between disturbance events may be important for understanding its population dynamics.

Fire exclusion has greatly modified historical patterns of disturbance in dry, ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forests in the eastern Cascade Range, from a regime of frequent, low severity fire, to one of infrequent, high severity fire (Agee 1994, Everett et al. 2000). For *I. longisepala*, these changes may have important consequences for the density and persistence of viable seed and ultimately for conservation of the species. The first of our four studies explores the density of *I. longisepala* seed in the soil and how it relates to disturbance history and to the abundance of mature, flowering plants. We compare the density of buried viable seed among sites that have burned at different times in the past and that support different densities of reproductive plants.

Numerous factors can influence the spatial

distributions of buried seeds and how they respond to disturbance. For many species, seeds are often aggregated in the soil (Baskin and Baskin 1998). For species with limited dispersal, seeds are often found in close proximity to parent plants (Major and Pyott 1966, Edwards and Whelan 1995). Post-fire recruitment may reflect these initial distributions, but it may also be influenced by patterns of heating during fire (Davis et al. 1989). The second of our four studies examines the distribution of *I. longisepala* germinants relative to reproductive plants and to variation in fire severity during experimental burning.

Seed production is fundamental to maintaining or replenishing the seed bank after fire-induced germination or mortality. Seed production tends to vary with plant size and vigor (Kelly 1984, Harrod et al. 1997). Thus, if seed production can be estimated from easily measured plant morphological traits, it may be possible for managers to predict when seed banks of fire-dependent species have been sufficiently augmented for prescribed fire to stimulate population growth. Although mature plants of *I.*

*longisepala* have the potential to produce large numbers of seeds, we have observed considerable annual variability in fruit production. This year-to-year variation may reflect annual weather patterns (Coffin and Lauenroth 1992) or other processes. Our third study explores the relationship between seed production and plant morphological traits (e.g., number of stems, plant height, or crown width) and documents annual variation in seed production within plants.

A seed bank strategy requires that seeds remain dormant, but germinate in response to an environmental cue such as heating during fire (Harper 1977, Baskin and Baskin 1998) or leachates from charred wood, ash, or smoke (Keeley et al. 1985). Effects of fire on seed germination have been studied in a number of common species (Baskin and Baskin 1998), and fire-mediated germination has been inferred for three congeners of *I. longisepala* – *I. rivularis* (Dougl.) Greene, *I. remota* Greene, and *I. corei* (Sherff) Sherff (Brown and DeByle 1989, Steele and Geier-Hayes 1989, Williams et al. 1992, Baskin and Baskin 1997). Prelimi-

nary observations suggest that seeds of *I. longisepala* require fire to break dormancy (Kuhlmann and Harrod, unpubl. data), but its particular germination requirements have not been identified definitively. In our final study, we compare germination rates among combinations of treatments that vary temperature, duration of heating, presence of ash, and/or depth of seed burial within the soil.

## STUDY AREA AND SPECIES DESCRIPTION

Historically, our study area was characterized by a high-frequency, low-severity fire regime that maintained an open, park-like forest dominated by *P. ponderosa* (Agee 1993, 1994). However, after decades of fire exclusion, some forests were burned by intense, stand-replacing wildfires. We selected 10 sites representing three disturbance histories (Table 1) for our studies. Wildland fire burned three sites in 1994 and four sites in 1988. Where populations of *I. longisepala* were present in these areas, plant density tends to be high. The remain-

Table 1. Burn history (year of most recent fire), plant association, density of *I. longisepala* plants, and physical characteristics of the study sites.

Study site	Most recent fire (year) <sup>a</sup>	Plant association <sup>b</sup>	<i>Iliamna</i> density (no. m <sup>-2</sup> )	Elevation (m)	Aspect (deg)	Slope (%)	Soil texture <sup>c</sup>
Mad River	1994	1	1.24	515	190	35	LS
Potato Creek	1994	1	0.52	515	240	10	GFSL
Tumwater Mtn.	1994	1	1.44	800	135	35	SL
Burch Mtn.	1988	2	1.6	1135	105	25	SSL
Mills Canyon	1988	2	0.14	605	70	70	SSL
Swakane Canyon	1988	3	0.12	725	200	35	SSL
Rattlesnake Spr.	1988	3	1.12	1350	150	40	SFSL
Deer Park Spr.	–	3	0.12	1210	135	45	LS
Red Hill	–	4	0.04	725	90	60	SL
Mission Creek	–	4	0.1	545	200	30	SL

<sup>a</sup> Dash (–) indicates no fire in the last 50 yr.

<sup>b</sup> Plant associations according to Lillybridge et al. (1995): 1 = *Pseudotsuga menziesii* / *Symphoricarpos albus* / *Calamagrostis rubescens*, 2 = *Pinus ponderosa* / *Agropyron spicatum*, 3 = *Pseudotsuga menziesii* / *Calamagrostis rubescens* / *Agropyron spicatum*, 4 = *Pinus ponderosa* / *Purshia tridentata* / *Agropyron spicatum*.

<sup>c</sup> LS = loamy skeletal (<25% rocks in profile), GFSL = gravelly fine sandy loam, SL = sandy loam, SSL = stoney sandy loam, SFSL = stoney fine sandy loam (USDA 1995).

ing three sites had not experienced wildfire in the recent past (>50 yr); here densities of *I. longisepala* are comparatively low. Sites burned in 1994 and 1988 had little residual overstory cover and were dominated by *Ceanothus velutinus* Dougl. and various grass species (*Agropyron spicatum* (Pursh) Scribn. & Smith, *Calamagrostis rubescens* Buckl., and *Bromus tectorum* L.). Unburned sites were dominated by an overstory of *P. ponderosa* and *P. menziesii* and *C. rubescens* and *Purshia tridentata* (Pursh) DC were abundant in the understory. All sites belong to the *P. menziesii* forest series and represent hot, dry-shrub or cool, dry-grass plant associations (Lillybridge et al. 1995) (Table 1). Plant nomenclature follows Hitchcock and Cronquist (1973).

All sites lie on the eastern slope of the Cascade Range within the Wenatchee and Entiat River watersheds in the Okanogan-Wenatchee National Forests, Washington (Figure 1). Elevations range from 515 to 1360 m, aspects are generally southerly, and slopes are <70%. Soils are sandy to loamy (Table 1). The climate is continental due to the rain shadow produced by the Cascade Mountains; annual precipitation averages <50 cm and occurs mostly in the form of snow (Lillybridge et al. 1995).

*Iliamna longisepala* is considered a sensitive species in Washington State and has a global rank of imperiled by The Nature Conservancy (WNHP 1997). It occurs from just south of Lake Chelan to near Liberty, east to the Columbia River (a few populations occur east of the Columbia River

in Douglas County), and west to about Lake Wenatchee. Nearly all locations are on public lands administered by the U.S. Forest Service.

*Iliamna longisepala* is a long-lived herbaceous, tap-rooted perennial that can reach a height of 1-2 m. Leaves are maple-like, broadly cordate, and 5-7 lobed (Hitchcock et al. 1969). Plants have dark pink flowers which produce an average of ~30 hard coated seeds per fruit (Kuhlmann and Harrod, unpubl. data). The species appears to depend on out-crossing (mean of 1.8 vs. 23.6 seeds/fruit in selfed vs. out-crossed plants, respectively; Harrod, unpubl. data). Plants are typically found in upland sites dominated by perennial herbs and grasses with a scattered overstory of *P. ponderosa* or *P. menziesii*. In some locations, plants oc-

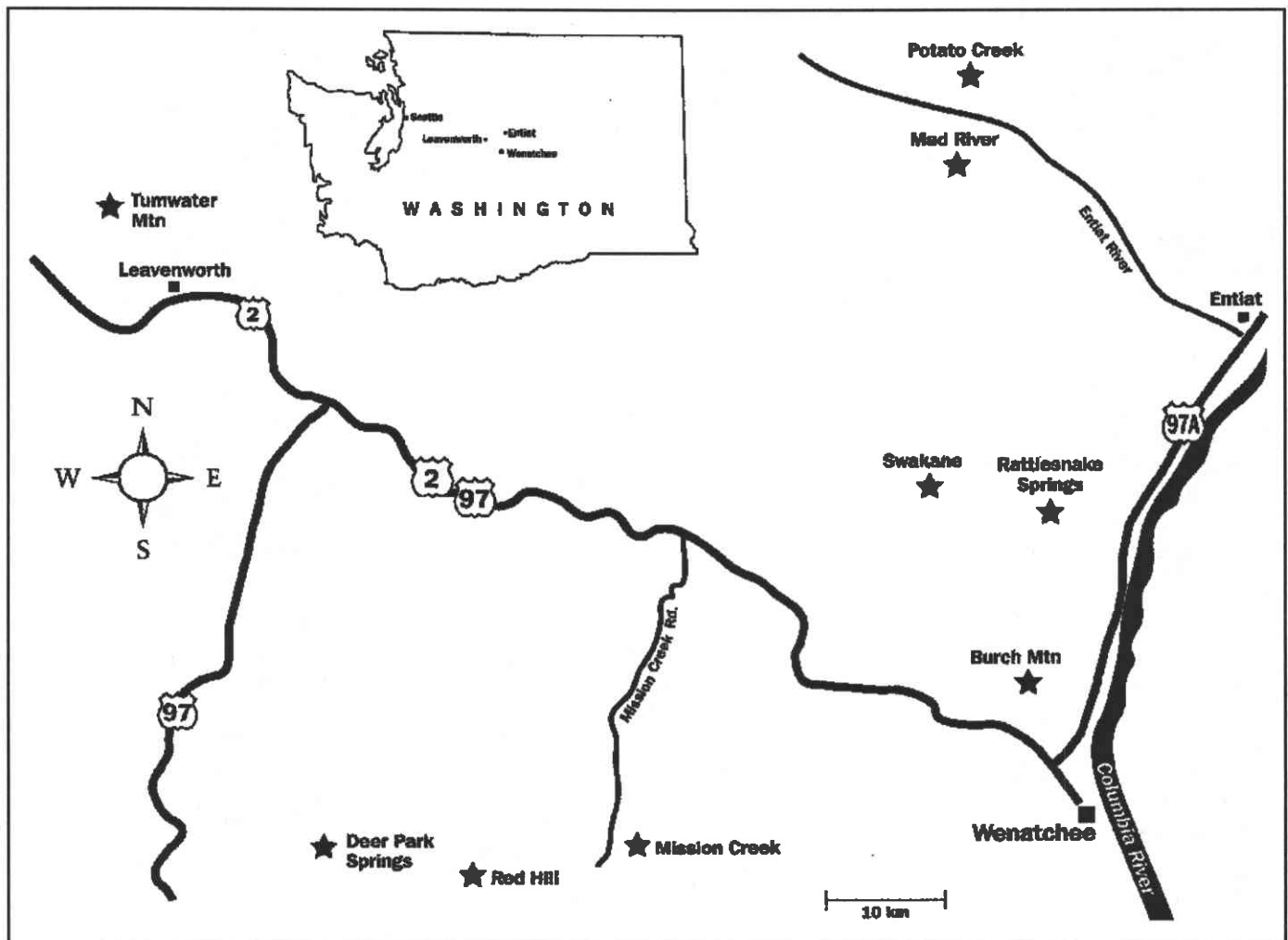


Figure 1. Locations of the study sites. See Table 1 for details.

cur on road-cut banks or old skid trails.

## METHODS

### Study 1. Soil Seed Bank Density

To quantify the density of buried viable seed in the soil and its relationship to disturbance history, we used both the seedling emergence method (Simpson et al. 1989, Gross 1990) and direct seed counts. Direct counts were made because few seedlings emerged from untreated or heated soils (see below).

Between 27 March and 10 May 1998, soils were collected from nine sites representing the three histories of burning: burned in 1994, burned in 1988, or not recently burned (Table 1). Sites were randomly selected from a larger pool of sites that met the following criteria: supporting extant populations of *I. longisepala* with at least one flowering individual, located in a relatively undisturbed plant community (no roads or skid trails), and <1 km from a road. Near the center of the population at each site, we established a 10-m x 10-m plot, grided into 100, 1-m x 1-m subplots. Soil samples were collected from the centers of 50 randomly selected subplots per plot (yielding a total of 450 total samples) using a bulb planter (surface area of 23.8 cm<sup>2</sup>) that removed an 11-cm-deep core (litter plus soil). Samples were bagged individually and stored in a cooler for 1-2 days until they were transported to the greenhouse.

Between 1 April and 13 May 1998, soil samples were placed in 15-cm x 20-cm germination flats and arranged in random positions on two greenhouse tables. Soil depth averaged 2 cm. Samples were watered daily from above and were exposed to a photoperiod of 16 hr light (natural lighting supplemented with 1000-watt, metal-halide lamps) and 8 hr dark. Flats were observed for the presence of germinants twice weekly until July 1998.

Few germinants emerged and all samples were then dried, stored for ~5 mo at room temperature, and heated in a drying oven to simulate temperatures experienced

during fire (Baskin and Baskin 1997). Specifically, a drying oven was preheated to 200°C; each sample was then heated in a ceramic dish for ~20 min, at which point the temperature at 1 cm depth was ~100°C. Heated samples were randomly assigned to germination flats in the greenhouse on 26 January 1999, and observed until 25 May 1999. Because of limited greenhouse space, we used 335 randomly selected samples of the original 450.

Seedling emergence was again low; and in April 1999, a second set of soil samples was collected from sites representing the three burn histories. A 5-m x 5-m plot was divided into 1-m x 1-m subplots near the center of each *I. longisepala* population and an 11-cm-deep sample was collected with a bulb planter (as above) from each subplot (yielding 25 samples per site). The number of flowering plants in each subplot was also recorded. In the laboratory, *I. longisepala* seeds were sifted from the soil and counted.

A single-factor analysis of variance (ANOVA) was used to compare mean seed densities (determined from direct seed counts) among sites with different burn histories ( $n = 3$ ); means were considered significantly different at  $P \leq 0.05$ . Tests for normality and homogeneity of variance indicated that data transformation was not necessary. A Pearson's correlation coefficient was computed to assess the relationship between mean seed density and the number of flowering plants at each site. Analyses were performed with SPSS 8.0 (SPSS 1998).

### Study 2. Spatial Distributions of Seeds and Germinants

In this study, we assessed the spatial distribution of emergent seedlings relative to extant plants following experimental burning in spring and fall at the Mission Creek site (Figure 1). Due to logistical constraints, this experiment could not be replicated at other locations. The site had not burned for several decades, and supported three distinct groups of two to four *I. longisepala* plants. Two adjacent rectangular plots (15 m x 75 m) were established between two

groups of plants (Figure 2). One plot was burned in October 1998 (fall burn) and one in May 1999 (spring burn). Seedling emergence was monitored between May and August 1999. We recorded seedling presence and distance to the nearest reproductive plant, and mapped areas of higher burn severity, where surface vegetation and the duff layer were consumed, exposing mineral soil.

### Study 3. Seed Production

In this study, we examined relationships between seed production and plant size and morphological traits, and documented annual variation in seed production within plants. On 10 June 1999 (prior to anthesis), 25 plants were selected at random from one population at Swakane Canyon (Figure 1). For each plant, we recorded number of stems, number of flowering stems, total plant height, crown diameter (broadest dimension), and total number of flowers (on 8 July 1999). We estimated seed production from a subsample of flowers on each plant. Ten fruits from each plant were collected prior to dehiscence on 17-18 August 1999 and the number of seeds per fruit was counted. The number of seeds per plant was estimated from the mean number of seeds per fruit and the total number of flowers per plant. The same measurements were taken on the same plants one year later (5 July 2000), and seed production was assessed on 14-15 August.

Multiple linear regression was used to model relationships between plant morphological traits (plant height, crown diameter, number of stems, and number of flowering stems) and seed production. Morphological and seed production data were assessed for departures from normality and for homogeneity of variance, and it was concluded that transformations were not necessary. Independent variables were entered stepwise into multiple regression models and were retained if significant ( $F$  test,  $P \leq 0.05$ ). Regression analyses were conducted with the linear regression procedures of SPSS 8.0 (SPSS 1998).

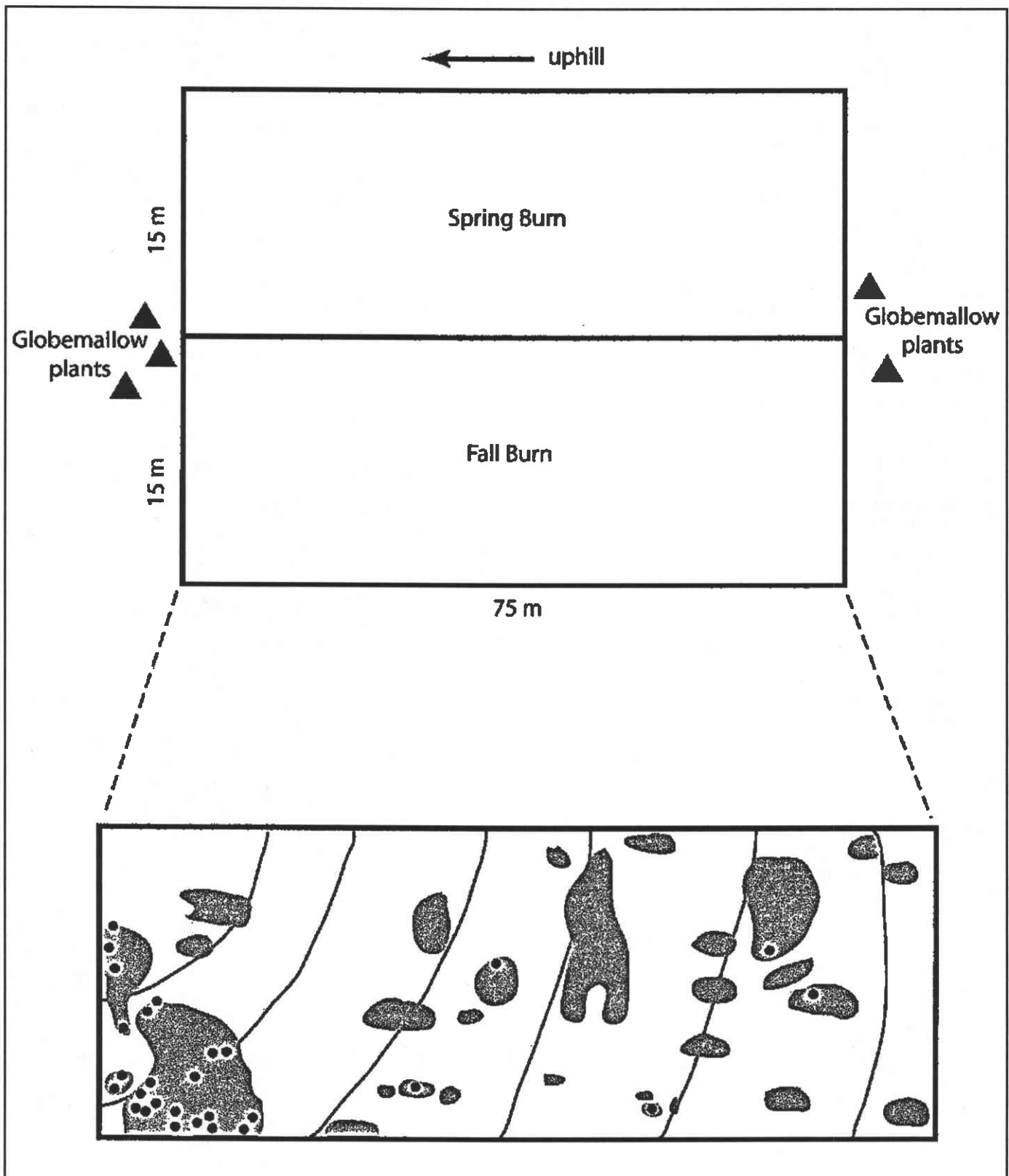


Figure 2. Schematic illustration of the plots burned in fall and spring to investigate the spatial distribution of germinants relative to reproductive plants and burn severity. The enlargement of the fall-burn plot illustrates locations of *Iliamna* germinants (dark circles) relative to flowering plants (dark triangles) and areas of higher severity burn (shaded regions). No germinants emerged in the spring-burn plots. The dark lines represent slope contours (3-m intervals).

#### Study 4. Germination Requirements

In this study, we attempted to isolate the germination requirements of *I. longisepala* by employing, in exploratory fashion, combinations of standard treatments known to stimulate germination in other species. Two types of experiments were performed with seeds collected in October 2000. First, sets of five seeds were subjected to various combinations: oven temperature (70-120°C), duration of heating (15-60 min), and prior stratification (8 days at 0°C vs. no stratification). Germination was then attempted on wet sand in Petri dishes in the greenhouse (16 h light, 8 h dark). Second, sets of 20 seeds were placed in soil in aluminum trays (24 cm x 34 cm x 8 cm) and subjected to combinations of treatments that contrasted: (1) burning of 150 g of dry *P. ponderosa* litter vs. no burning, (2) addition of ash (derived from separately burned litter samples) vs. no ash, and (3) depth of seed burial (0 vs. 3 cm). Trays were then placed in the greenhouse, watered periodically, and examined weekly for germinants until 20 March 2001.

Both sets of experiments yielded few germinants (see Results); thus, statistical tests were not conducted. Untreated samples of seed were then sent to the Oregon State University Seed Laboratory, Corvallis, to test for viability. These included 198 seeds extracted from April 1999 soil samples and 191 and 200 seeds extracted from fruits collected in October 2000 and September 2001.

#### RESULTS

##### Seed Bank Density

In the first greenhouse germination trial (untreated soils), only three seedlings emerged from the 450 samples. Following subsequent heating, however, emergence increased substantially (41 seedlings from 335 samples). Most germinants were from sites that burned in 1988 (Table 2). In contrast, germinants were absent or infrequent from sites that burned more recently (1994) or that had not burned for at least 50 years.

Estimates of seed density were considerably greater when soil samples were sifted. However, the frequency and density of seeds varied markedly within and among sites (Table 3). Densities in individual samples ranged from 0-78 (equivalent to 32,830 m<sup>-2</sup>) and mean densities at individual sites ranged from 0 to >8000 m<sup>-2</sup>. Despite large differences in mean seed density, we did not detect a significant effect of burn history due to high site-to-site variation ( $F = 1.93$ ,  $P = 0.225$ ) (Table 3). However, consistent with germination patterns from the second greenhouse emergence trial (Table 2), sites burned in 1988 had the highest frequency and density of seeds, and sites burned in 1994 had the lowest.

Plant densities at sites burned in 1988 and 1994 were 10 times greater than were densities at sites that had not burned recently (~1.1 vs. 0.1 m<sup>-2</sup>, respectively; Table 1). However, the relationship between density of seeds and flowering plants was not significant ( $n = 9$ ,  $R^2 = 0.068$ ,  $P = 0.497$ ).

##### Seed Bank Spatial Distribution

Twenty-nine seedlings appeared in the experimental plot burned in fall 1998 at Mission Creek. Of these, 72% were found within 10 m of reproductive plants and all were located in areas of high burn severity (Figure 2). No seedlings were observed in the plot burned in spring 1999 and no new plants were observed in 2001, two summers later.

##### Seed Production

In 1999, the mean number of seeds per fruit was 11.2 ( $n = 250$ , range of 0-42) and the mean number seeds per plant was 2450 ( $n = 25$ , range of 62-11,063). Crown diameter was the best predictor of seed production ( $R^2 = 0.696$ ,  $P = 0.002$ ; seeds per plant =  $-1249 + 52.3 \times \text{crown diameter [cm]}$ ) (Figure 3). In 2000, plants produced significantly fewer flowers, and no fruits or seeds were observed.

##### Germination Requirements

Heating/scarification trials and burning/ash

Table 2. Frequency and density of *I. longisepala* germinants from heated soil samples collected from sites with different histories of burning (see Table 1). Frequency is the proportion of flats (soil samples) with at least one germinant.

Burn history / Site	No. of soil samples <sup>a</sup>	Frequency (%)	Germinant density (no. m <sup>-2</sup> )		
			Mean	SE	Max.
Burned in 1994					
Mad River	40	0	0	0	0
Potato Creek	35	0	0	0	0
Tumwater Mtn.	30	3	14	14	421
Burned in 1988					
Burch Mtn.	34	21	87	30	421
Mills Canyon	28	0	0	0	0
Rattlesnake Spr.	56	50	226	34	1263
Not recently burned					
Deer Park Spr.	38	0	0	0	0
Red Hill	40	0	0	0	0
Mission Creek	34	9	37	21	421

<sup>a</sup> 335 samples were randomly selected from the original set of 450, thus sample sizes vary among sites (see Methods: Soil Seed Bank).

**Table 3. Frequency and density of *I. longisepala* seeds sifted from soil samples from sites with different histories of burning. Frequency is the proportion of samples with seeds.**

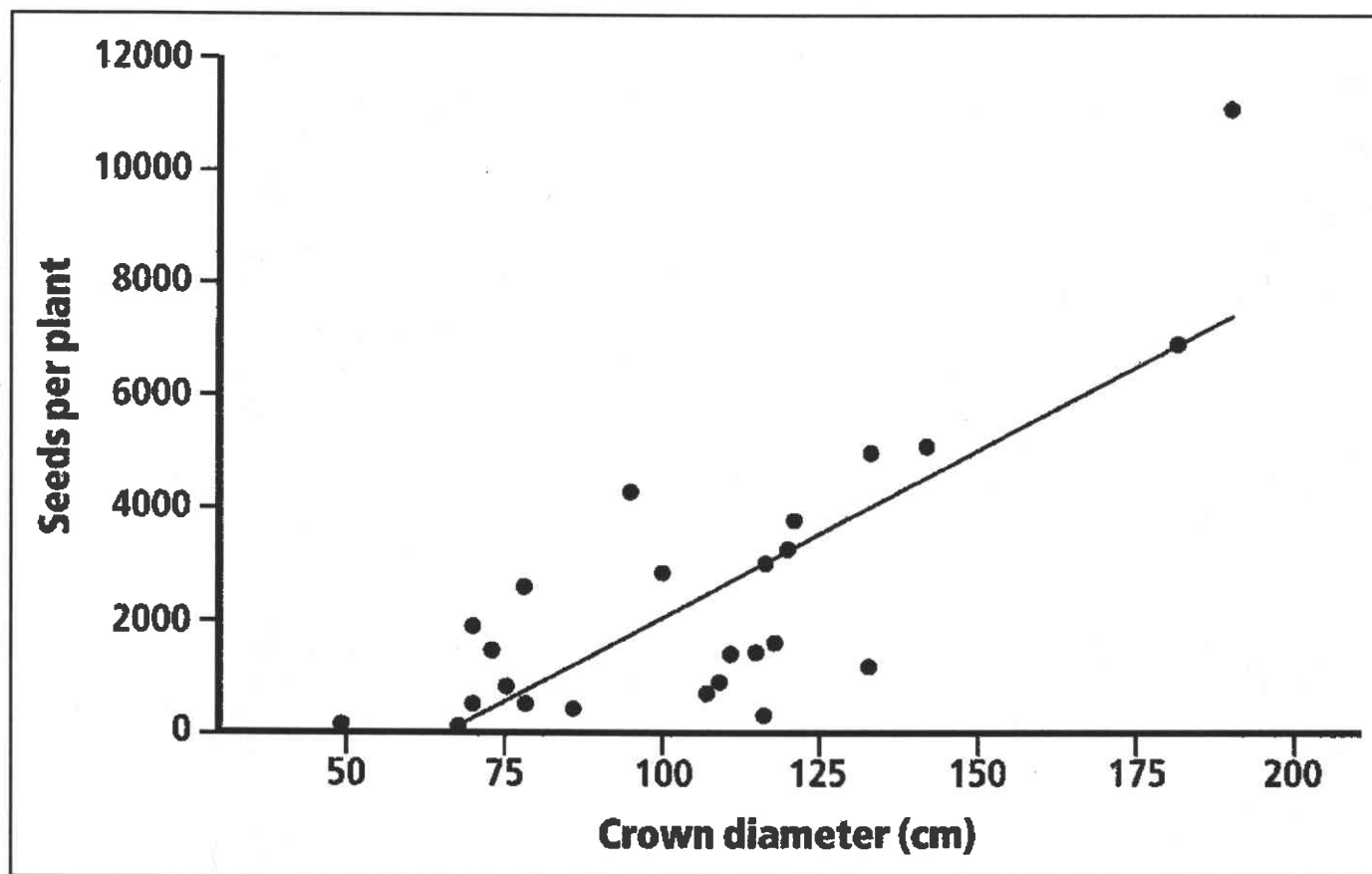
Burn history / Site	Frequency (%)	Seed density (no. m <sup>-2</sup> )		
		Mean	SE	Max.
Burned in 1994				
Mad River	40	421	236	5,893
Potato Creek	52	387	111	2,104
Tumwater Mtn.	0	0	0	0
Burned in 1988				
Burch Mtn.	92	2,441	523	10,102
Swakane Canyon	64	707	161	2,525
Rattlesnake Spr.	92	8,149	1,468	32,830
Not recently burned				
Deer Park Spr.	68	1,818	570	10,943
Red Hill	24	101	37	421
Mission Creek	60	968	233	2,946

addition/seed burial experiments yielded few germinants. In the first set of trials, four of 180 seeds germinated; in the second set, only one of 240 seeds germinated. X-ray and tetrazolium tests indicated that only 8% of the seeds collected from plants in 2000 (used for both sets of trials) were viable. In contrast, seeds collected from plants in 2001 showed 27% viability, and those extracted from soil samples in 1999 showed 91% viability.

## DISCUSSION

### Seed Bank Density and Spatial Distribution

Many studies have used the seedling emergence method to quantify the density and diversity of viable seeds in the soil (e.g., Strickler and Edgerton 1976, Brown 1992, Halpern et al. 1999). However, this method proved to be ineffective for *I. longisepala*.



**Figure 3. The relationship between seed production and crown diameter in *Iliamna*. Twenty-five plants were sampled on 8 July 1999 at the Swakane Canyon site (see Methods: Seed Production).**



Although heating soil samples broke the dormancy of some seeds, this method still underestimated an apparently large viable seed bank. Although the process is laborious, direct extraction of seeds followed by viability testing is the best method to estimate the density of viable seeds for this species.

Disturbance history appears to be important in the seed bank dynamics of *I. longisepala*. Although we did not detect a statistically significant effect of burn history on seed density, replication was low and site-to-site variation was high, as is often observed in soil seed banks (Halpern et al. 1999, Morgan 2001). However, mean trends for both frequency and density were consistent with a temporal pattern in which seed banks become depleted in recently burned sites due to mass germination and possible loss to lethal temperatures. Abundant germination of *I. longisepala* has been observed after wildfire (Kuhlmann and Harrod, unpubl. data), and similar observations have been made of its congeners, *I. rivularis* (Lyon 1971, Brown and DeByle 1989, Steele and Geier-Hayes 1989) and *I. corei* (Baskin and Baskin 1997). Although large declines in seed bank density can be attributed to the stimulatory effect of wildfire on germination, fire-induced mortality can also lead to depletion of the seed bank. For example, soil heating by fire in Mediterranean and chaparral ecosystems can deplete soil seed banks to a depth of 3 cm due to direct consumption and lethal temperatures (Ferandis et al. 1999, Odion and Davis 2000, Lei 2001). It is likely that for *I. longisepala*, depletion of the soil seed bank in recently burned sites reflects a combination of seed germination and mortality.

Density of seed in the soil may also reflect the density of reproductive plants, which can vary with disturbance history (generally declining with time since fire). Although the density of reproductive plants in our study was significantly higher on burned sites, seed bank density was not correlated with plant density. In contrast, Fuentes (2000) found a significant correlation between seed bank density and plant density at other locations in northeastern Washington, but no correlation between plant density and disturbance history.

However, others have observed significant relationships between soil seed bank density, plant density, and disturbance history. For example, seed density of *Adenostoma fasciculatum* Hook. & Arn. increased with time after fire occurred in mixed chaparral (Zammit and Zedler 1988). Seeds of an Australian grass, *Triodia basedowii* E. Pritz., were completely absent 3 y after a burn, but seed density returned to initial levels after 9 y (Westoby et al. 1988). For *I. longisepala*, greater replication of sites and burn histories may be necessary to fully understand the relationships among time since disturbance, plant density, and temporal patterns in the soil seed bank.

The results of both direct seed counts and field-burning studies indicate that the seed bank of *I. longisepala* is spatially heterogeneous. Spatial patterns of germination in the fall-burn plot suggest that seed densities are higher near reproductive plants and that long-distance (>10 m) dispersal is fairly limited. However, there also appears to be a strong effect of burn severity on the spatial distribution of germinants. Germination was most common in areas where severe fire consumed fine litter that had accumulated under *P. ponderosa* and *P. tridentata*, exposing mineral soil. Our observations suggest that differential heating of the soil during fall (but not spring) burns effectively determined the spatial pattern of seedling recruitment regardless of the distribution of seeds in the soil. Strong relationships between the spatial distributions of parent plants, the heterogeneous nature of fire, and the spatial pattern of seedling recruitment have been documented in many other systems in which fire is important (Davis et al. 1989, Rice 1993, Tyler 1995).

### Seed Production

Seed production in *I. longisepala* correlates well with plant size (crown diameter), but only when viable seed is produced, and this appears to vary annually. In 1999, an average-sized plant at the Swakane Canyon site yielded ~2500 seeds, but no seeds were formed on the same plants in 2000. We observed this failure at many other locations as well. Several factors may contribute to this temporal variability.

First, annual variation in seed production can be attributed to patterns of temperature or rainfall that affect bud formation or survival or seed set (Keeley 1977, Coffin and Lauenroth 1992, Parsons and Whelchel 2000, Selas 2000). In our study area, timing of rainfall in 2000 may have contributed to poor seed production in *I. longisepala*. Although annual precipitation was lower than average in both 1999 and 2000, only in 1999 was August rainfall – at the time of fruit maturation – close to average (Figure 4). In 2000, insufficient rainfall in August may have induced fruit abortion (cf. Selas 2000). Annual variation in seed production might also be explained by effects of weather on the presence or activity of pollinators (Bergman et al. 1996, Parsons and Whelchel 2000). However, there is little evidence in the weather records for June, when plants are in flower, to invoke pollination limitation as an explanation for poor seed set. Regardless of its cause, temporal variation in seed production is likely to play an important role in the dynamics of a species that depends on periodic germination from the seed bank.

### Germination Requirements

Because of low viability of seed collected in 2000, we were unable to determine the temperature or heating requirements, or that ash is necessary to induce germination of *I. longisepala*. Nonetheless, greater viability of seeds collected in 2001 suggests that, similar to seed production, viability can vary in time. Further experimentation with seeds of known high viability is needed to confirm the physical and/or chemical factors that trigger germination. In previous experiments, Fuentes (2000) found that mechanical scarification and heating promoted germination of *I. longisepala*, although the significance of these results was limited by low treatment replication and total germination. The increased rate of germination in our second greenhouse emergence trial (after soils were heated) is consistent with this result.

Despite poor germination in laboratory and greenhouse trials, there is abundant evidence from the field to suggest that wildland fire or prescribed burning is



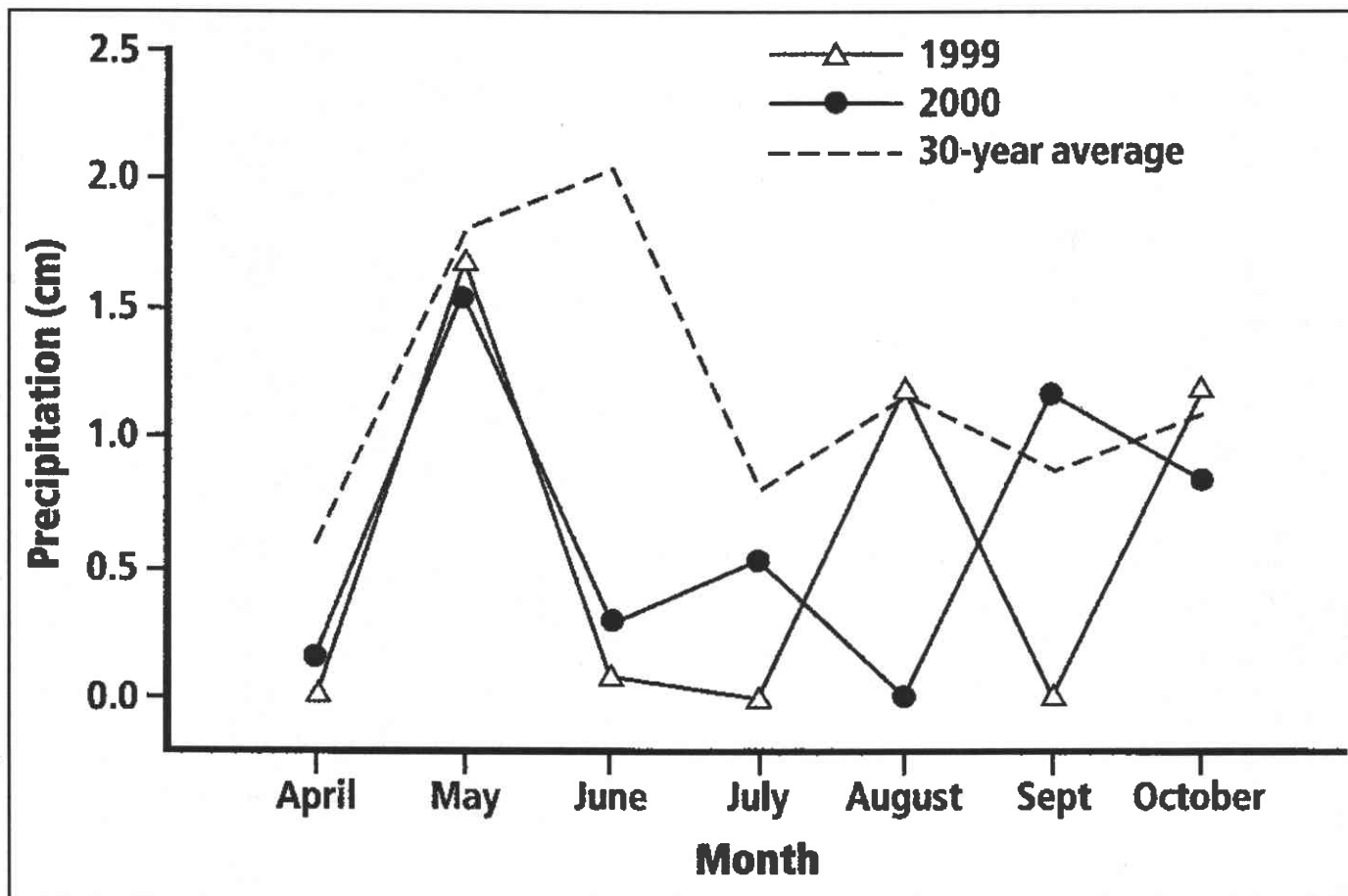


Figure 4. Monthly precipitation from the Entiat remote automated weather station during 1999 and 2000 compared to the 30-yr average.

sufficient to break seed dormancy in *I. longisepala*. Localized germination in areas of high fire severity in this study, and abundant germination after fall (but not spring) burning in a companion study (Harrod 2003), strongly suggest that fire, and its seasonal timing, are important for successful recruitment of seedlings. Field studies of several congeners support this conclusion: heat from fire was the primary factor to break seed dormancy in *I. corei* (Baskin and Baskin 1997), spring burning induced germination in *I. remota* (Schwegman 1990), and hot broadcast burning and intense wildland fire led to abundant germination of *I. rivularis* (Steele and Geier-Hayes 1989).

#### Implications for Management and Conservation

For plants with a persistent seed bank, the density and dynamics of seeds in the soil

are determined by rates of input and loss (Harper 1977, Simpson et al. 1989). For *I. longisepala*, seed input derives from local sources (although production and viability can vary), and loss, at least historically, occurred through mass germination or mortality from lethal fire temperatures. Thus, under a regime of frequent fire, we would expect seed density to show an oscillating, but asymmetrical pattern of gradual increase followed by abrupt decline after fire. Density of reproductive plants would mirror this pattern with a slight lag as fire induced abundant recruitment of seedlings (with some short-term mortality). Plants achieve reproductive status within 1-3 y; thereafter mortality occurs very gradually. Fire exclusion in eastern Cascade forests is likely to have changed this dynamic, reducing the frequency of recruitment and subsequent seed production and increasing the cumulative mortality of seed in the soil through time-dependent processes

(granivory, decay, exposure, or transport). Because mature plants are capable of resprouting after prescribed fire (Harrod 2003), strategies to maintain or enhance existing populations should focus on the dynamics of the seed bank. Our field observations suggest that periodic fire will stimulate seedling emergence from a well-developed seed bank, and that germination and subsequent survival will be more likely after fall burning. However, our estimates of seed bank densities in recently burned sites suggest that burning at intervals <10 y will deplete seed reserves. At the other extreme, if burning is too infrequent, populations may be lost as reproductive plants, seed inputs, and buried viable seeds gradually decline.

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*Richy Harrod is the fire ecologist for the Okanogan-Wenatchee National Forests where he is engaged in restoration planning and research. He previously served as plant ecologist for the Leavenworth Ranger District, Wenatchee National Forest. His primary interests are in fire effects, biological diversity, rare plant biology and conservation, and noxious weed management.*

*Charles Halpern is a Research Professor in the College of Forest Resources at the University of Washington. His research explores the successional dynamics of forests and meadows of the Pacific Northwest, and considers the roles of disturbance, climate change, species' life histories, and biotic interactions in shaping plant community patterns.*

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