

## Seed Production and Dispersal of Sulfur Cinquefoil in Northeast Oregon

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### Abstract

Sulfur cinquefoil (family Rosaceae) is an invasive, herbaceous perennial, native to Eurasia. It has wide ecological amplitude and has become established throughout North America in numerous habitat types. Sulfur cinquefoil reproduces only by seed (achenes), however, little is known about its regenerative strategy or reproductive biology. To improve understanding of the mechanisms of expansion for sulfur cinquefoil, we quantified seed production and measured seed dispersal at sites infested with sulfur cinquefoil in different habitats in northeast Oregon. Seed dispersal was measured by using sticky traps (30 × 100 cm, replaced every 2 weeks) radiating in 4 cardinal directions from individual source plants. Estimated seed production for 2 years (2001 and 2002) was nearly 4 times higher than previously reported (~6 000 seeds per plant; range = 2 620–15 150 seeds per plant). For most sites, seed production was similar in both years. However, site, year, and their interaction (site × year) had significant influence on flower and stem production. Seeds were dispersed from July through mid-October 2001, although almost 40% of the seeds were captured between mid-July and mid-August. Dispersal followed a classic decay function; approximately 83% of the seeds were captured within 60 cm of the source plants. Once sulfur cinquefoil reaches a site, it appears to spread and persist by releasing numerous seeds near the parent plants, thereby forming increasingly dense stands.

### Resumen

El "Sulfur cinquefoil" (familia de las Rosaceae) es una especie herbácea perenne, invasora, originaria de Eurasia. Tiene un rango ecológico amplio y se ha establecido a lo largo de Norteamérica en numerosos tipos de hábitat. El "Sulfur cinquefoil" se reproduce solo por semilla (aquenios); sin embargo, poco se sabe acerca de su estrategia regenerativa o biología reproductiva. Para mejorar el conocimiento de los mecanismos de expansión del "Sulfur cinquefoil" cuantificamos la producción de semilla y medimos el dispersión de semilla en sitios infestados con esta especie en diferentes hábitats del noreste de Oregon. La dispersión de semilla fue medida usando trampas con pegamento (30 × 100 cm, remplazadas cada dos semanas) alrededor de los cuatros puntos cardinales a partir de plantas individuales que eran la fuente de semilla. La producción estimada de semillas para dos años (2001 y 2002) fue casi cuatro veces mayor que la reportada previamente (= 6000 semillas por planta; rango = 2 620–15 150 semillas por planta). En la mayoría de los sitios la producción de semilla fue similar en ambos años. Pero, el sitio, el año y su interacción (sitio × año) tuvieron una influencia significativa en la producción de flores y tallos. Las semillas fueron dispersadas de julio a mediados de octubre, aunque casi el 40% de las semillas fueron capturadas entre mediados de julio y mediados de agosto. La dispersión siguió la clásica función de decaimiento, aproximadamente 8.3% de las semillas fueron capturadas dentro de 60 cm de las plantas fuente. Una vez que el "Sulfur cinquefoil" alcanza un sitio, parece que se disemina y persiste liberando numerosas semillas cerca de las plantas madre, formando así poblaciones densas en constante expansión.

**Key Words:** *Potentilla recta* L., invasive species, regenerative strategy

### INTRODUCTION

Sulfur cinquefoil (*Potentilla recta* L., Hitchcock and Cronquist 1973), a native of Eurasia, was introduced to North America prior to 1900 (Britton and Brown 1897). In the past 2 decades, this species has been recognized as having broad ecological amplitude in drier climates of northwestern North America, where it forms dense stands and is considered a threat to native plant communities (Rice 1991, 1999; Powell 1996). Sulfur cinquefoil has probably gone unnoticed in many parts of its range because this normative species is similar in appearance to native co-occurring congeners, particularly northwest cinque-

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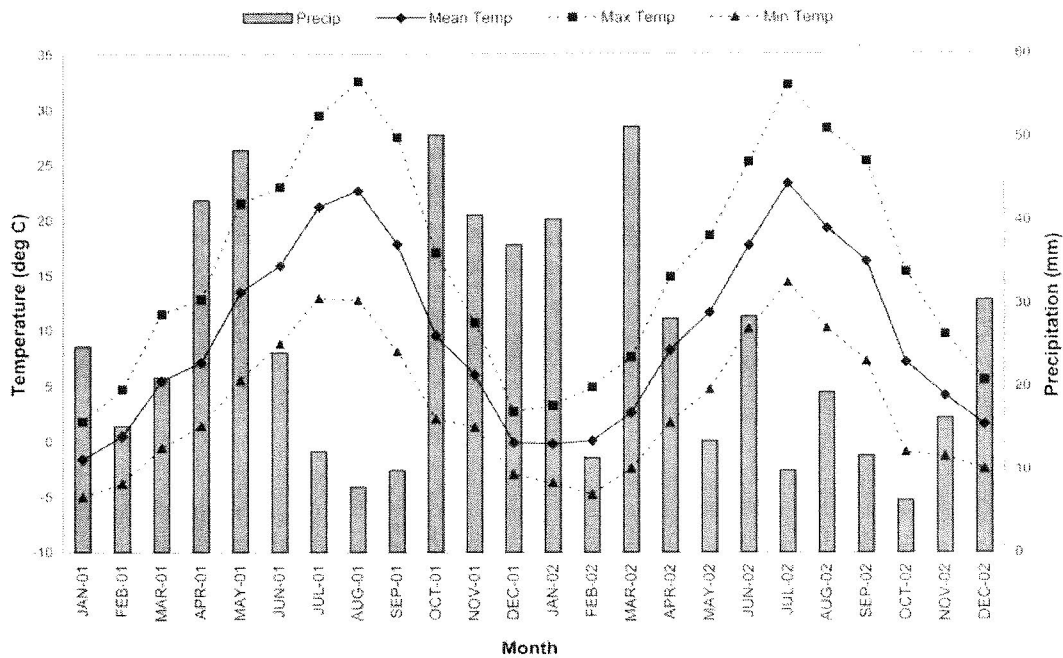


Figure 1. Climatic diagram for study areas in northeast Oregon, 2001 and 2002.

foil (*Potentilla gracilis* Dougl.) (Rice 1999; Mack 2000; Aitken and Parks 2004).

Sulfur cinquefoil has invaded a variety of habitats in North America and now occurs from British Columbia east to Newfoundland and Nova Scotia, south to Florida, and west to eastern Texas. In the western United States, the distribution of sulfur cinquefoil extends south to northern California and south in the Rocky Mountains to Wyoming. In the central and eastern United States, sulfur cinquefoil is considered to be primarily a minor agricultural weed (Werner and Soule 1976). In the western United States, sulfur cinquefoil frequently invades disturbed sites such as abandoned agricultural fields, meadows, pastures, and roadsides. However, relatively undisturbed bunchgrass communities, open-canopy ponderosa pine, drier Douglas-fir habitats, and seasonal wetland ecosystems are also susceptible to infestations by sulfur cinquefoil (Naylor et al. 2005). Over a period of 3 years, several sulfur cinquefoil colonies in Montana expanded to more than 400 contiguous hectares (Rice 1999). As yet, sulfur cinquefoil has not been reported to occur in the Great Basin, desert Southwest, southern Rockies, or the Rocky Mountain piedmont.

Limited information is available on the phenology, demography, and population ecology of sulfur cinquefoil in landscapes of the western United States. The species reproduces only by seed (achenes), has a single taproot, and may have several shallow, spreading branch roots but no rhizomes. Efforts to prevent the spread of sulfur cinquefoil and restore areas to native vegetation will benefit from an understanding of the mechanisms that allow sulfur cinquefoil to invade and persist. Our specific research objective was to characterize annual seed production and short-distance dispersal to better understand sulfur cinquefoil invasion ecology. Our broader

objective is to identify species characteristics and environmental factors that might confer an advantage to the expansion of sulfur cinquefoil in northeast Oregon.

## METHODS

### Study Sites

The study area is located in the Blue Mountain province of northeast Oregon, a transitional area with both continental and maritime climatic influences (Franklin and Dyrness 1988). During fall, spring, and winter, this semiarid region is affected by maritime weather systems flowing through the Columbia River Gorge (Bryce and Omernik 1997). Average annual precipitation (1965-2003) for La Grande, Oregon, the largest city near the study sites, was 430 mm (Western Regional Climate Center 2004). Most precipitation occurs as snow from October through May, with periodic thunderstorms in the drier months of summer and early fall (Fig. 1). From 1965 to 2003, average daily air temperature ranged from 3°C to 16°C, with an annual daily average of 9°C.

Vegetation is dominated by a mixture of conifers, including Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), grand-fir (*Abies grandis* [Dougl.] Forbes), ponderosa pine (*Pinus ponderosa* Dougl.), Engelmann spruce (*Picea engelmannii* Parry), western larch (*Larix occidentalis* Nutt.), and lodgepole pine (*Pinus contorta* Dougl.), with the overstory composition depending largely on elevation, aspect, and soils (Franklin and Dyrness 1988). Understory vegetation is composed of a mixture of low-growing shrubs, mostly snowberry (*Symphoricarpos* [Duhamel] spp.) and wild rose (*Rosa woodsii* Lindl. and *R. nutkana* Presl), and perennial native and nonnative forbs and graminoids (Franklin and Dyrness 1988). Soils in the

**Table 1.** Physical site attributes, landownership, disturbance types, location, and description for study sites of sulfur cinquefoil populations in northeast Oregon.

| Site             | Location                             | Ownership | Elevation<br>(m) | Aspect | Slope<br>(°) | Disturbance            | Description                             | Sulfur<br>cinquefoil<br>density<br>(plants/m <sup>2</sup> ) |
|------------------|--------------------------------------|-----------|------------------|--------|--------------|------------------------|-----------------------------------------|-------------------------------------------------------------|
| Morgan Lake West | Lat 45°17'48.1"N, long 118°08'00.6"W | City      | 1 285            | N      | 6            | Mechanical             | Forest opening near reservoir           | 3.3                                                         |
| Morgan Lake East | Lat 45°17'48.1"N, long 118°08'00.6"W | City      | 1 285            | N      | 6            | Mechanical             | Forest opening near reservoir           | 2.9                                                         |
| Rice             | Lat 45°17'13.8"N, long 118°06'18.0"W | Private   | 1 225            | W      | 15           | Mechanical             | Forest opening near power line          | 4.7                                                         |
| Red Bridge       | Lat 45°17'39.5"N, long 118°19'55.7"W | Private   | 970              | NW     | 3            | Mechanical             | Riparian area—some shading              | 3.6                                                         |
| Texaco           | Lat 45°18'46.6"N, long 118°05'14.9"W | Private   | 854              | NE     | 1            | Mechanical             | Vacant lot—city of La Grande,<br>Oregon | 2.7                                                         |
| Hamburger Hill   | Lat 45°31'40.0"N, long 117°55'27.2"W | Private   | 860              | E      | 6            | Grazed by<br>livestock | Forest opening                          | 3.8                                                         |
| Foothill East    | Lat 45°15'24.5"N, long 118°02'31.4"W | State     | 830              | E      | 6            | Cultivated             | Former agricultural field               | 3.4                                                         |
| Foothill West    | Lat 45°15'20.0"N, long 118°02'36.2"W | State     | 850              | E      | 9            | Grazed by<br>livestock | Forest opening                          | 1.3                                                         |

study area are variable, but most are derived from volcanic materials including volcanic debris and ash, andesite, basalts, rhyolites, and tuffs (Bryce and Omernik 1997).

The 8 study sites represented different disturbance histories and occurred over a range of elevations, aspects, and slopes (Table 1). The study sites were extensively infested with sulfur cinquefoil and ranged in size from approximately 1 to 5 ha. Each site was located within 500 m of a road, was influenced by human-related disturbances, and was open to grazing by native wildlife. The study sites were classified as "moderate integrity dry-forest rangeland" (Quigley et al. 1996), a common rangeland community type that extends across northeast Oregon. The sites were probably heavily grazed in the late 1800s and early 1900s and have recovered over time as a result of decreased grazing pressure (Skovlin and Thomas 1995). Current land management disturbances were categorized as 1) mechanical soil disturbance, 2) cultivated, and 3) grazed by livestock (Table 1). Mechanical soil disturbance other than cultivation involved disturbance to the soil and vegetation by mechanized equipment associated with the building and maintenance of railroads, roads, developed recreation sites, and power lines. Maintenance activities in these areas required chronic vehicle traffic and included soil deposition and removal. Cultivation disturbance refers to agricultural tilling; the cultivated site (Foothill East) was plowed in the past and had been fallow for 7 years at the time of this study. Grazed sites have been continually grazed by wildlife, primarily elk and deer, and grazed by domestic livestock at different intensities for the past 70-100 years. Currently, these 2 sites receive moderate midseason grazing by cattle; during the years of this study (2001-2002), the sites maintained a "fair" rangeland condition.

### Seed Production

To estimate seed (actually fruits, achenes) production, we collected sulfur cinquefoil plants in 2001 (24 July-24 August) and 2002 (23 July-30 July) just following peak flowering. At each site, entire plants (25-35 per site) representing the full range of plant size classes of reproductive plants (no rosettes)

were collected at random, including all aboveground material and primary and secondary taproots. The single criterion for collection was that the plant had produced current-year flowers. Plants were carefully dug from the soil with trowels and shovel and were individually placed in plastic bags for transport. In the laboratory, the following attributes were recorded for each plant: number of stems, number of flowers per stem, and number of previous year's stems. The number of flowers per stem and the number of stems per plant were counted for 30-32 plants per site in 2001 and for 25 plants per site in 2002. In both years, we randomly selected 5 plants per site, then 5 flowers per plant, and counted the number of seeds per flower. To obtain an estimate of seed weight, we counted out batches ( $n = 10$  seeds) of ripe seeds from 12-15 plants per site, weighed each batch, and divided by 10.

### Seed Dispersal

We measured dispersal of seeds from individual sulfur cinquefoil plants at all 8 sites (1 plant per site) from 25 July through 15 October 2001. Seed dispersal traps at Rice and Foothill West were repeatedly disturbed or destroyed by native ungulates, and results from these sites were not included in the analysis. At each site, random selection of a "source plant" was conducted using a combination of randomly generated numbers for distance and direction to locate potential candidate plants within the sulfur cinquefoil stand. We selected the first candidate plant that appeared to be of average height and stem number and that had not obviously released any seeds at the time of trap installation as the source plant for that site. We removed all sulfur cinquefoil plants within 5 m of the selected source plant. The following information was collected for each source plant: number of stems, number of flowers per stem, total number of flowers, and plant height. At each site, we also recorded elevation, aspect, and type of disturbance (Table 1).

Seed dispersal was measured by using sticky traps that are most commonly used for entomology research (Intercept Varroa Mite Traps™, IPM Technologies Inc, Portland, OR). These traps are constructed of durable sheets of poster board with a sticky layer of Tanglefoot™ on 1 side (Fig. 2). Traps were



**Figure 2.** Method for trapping seeds, showing sticky traps ( $1.0 \times 0.3$  m) radiating from central dispersal plant.

placed in 4 cardinal directions (north, south, east, and west) around each individual source plant. A  $30 \times 30$ -cm center trap was placed directly around the base of the selected dispersal plant and oriented north. Four wings, each composed of  $230 \times 50$ -cm sticky sheets attached on the end, were connected to the center trap. The length of each wing was about 100 cm from the edge of the center trap and 110 cm from the base of the dispersal plant itself (Fig. 2). The traps occupied approximately 32 % of the circular area (radius = 110 cm) surrounding each source plant. The traps were collected and replaced biweekly for 10 weeks. Following collection, traps were brought back to the lab and overlain with a  $30 \times 50$ -cm transparent piece of acetate marked in 2-cm increments. For each direction, seeds captured on the sticky traps were counted in 2-cm intervals from the central source plant. Traps were removed from the field in mid-October, when plants were beginning to senesce and fall rains reduced the adhesive properties of the traps.

### Data Analysis

The mean number of seeds produced per plant was calculated as the product of (mean number of seeds per flower)  $\times$  (mean number of flowers per stem)  $\times$  (mean number of stems per plant) = estimated number of seeds produced per plant. Annual flower and seed production was estimated by averaging data from the 6 sulfur cinquefoil populations in 2001 and 2002. We assumed independence among the number of seeds per flower, number of flowers per stem, and number of stems per plant and calculated means and standard errors for site estimates of annual flower and seed production (Ramsey and Schafer 1997). For the 5 populations with data from both 2001 and 2002, between-year variation in number of seeds per flower, number of flowers per stem, and number of stems per plant was tested for each site by using unpaired Student's *t* tests. The influence of site and year on seed, flower, and stem production was examined using nested analysis of variance (PROC Mixed), with plant nested within year (2001, 2002) as the basic sampling unit. Statistical analyses on seed production data were performed in SAS (SAS 2001).

To evaluate seed dispersal, the number of seeds captured was averaged for each sampling period ( $n = 24$ , 6 plants by 4 directions) and direction ( $n = 6$  plants) and plotted against distance at 2-cm intervals. The influence of source plant, direction, sampling period, and distance on the number of seeds captured was evaluated by using a series of generalized

additive models, assuming both normal and Poisson distributions of the data (Hastie and Tibshirani 1990). In addition, the influence of interactions among source plant, direction, sampling period, and distance were tested assuming both normal and Poisson distributions. Statistical analyses on dispersal data were performed in S-PLUS (S-PLUS 2000).

## RESULTS

### Seed Production

The estimated number of sulfur cinquefoil seeds produced per plant (all sites combined) was about 6000 and was similar in 2001 and 2002 (Table 2). Between years, the average number of seeds per flower was similar at 4 out of 5 sites, the average number of flowers per stem was similar at 3 out of 5 sites, and the average number of stems per plant was similar at 4 out of 5 sites (Table 2).

Site conditions had a significant effect on the number of flowers per stem and the number of stems per plant (Table 3) but not the number of seeds per flower. For individual plants, the number of flowers per stem differed significantly, although the number of seeds per flower and the number of stems were similar. The highest seed production occurred at Foothill East, the formerly cultivated site (Table 2), where few other plant species were present, and sulfur cinquefoil formed a near monoculture. Average seed (achene) weight was  $0.19 \text{ mg} + 0.04$  standard deviation (SD;  $n = 2640$  from 5 different sites), and seeds ranged from 1.5 to 2.5 mm in length.

### Seed Dispersal

The pattern of seed dispersal followed a decay function in which the number of captured seeds declined with distance from the source plant (Harper 1977; van der Valk 1992), and seeds were most abundant near the base of the source plants (Figs. 3A, 3B, and 4A). Although the dispersal curve is distinct, considerable variation is obvious, particularly for distances from 10 to 40 cm, reflecting the influence of wind and sampling period. The model that explained the most variance in the pattern of captured seeds (i.e., resulted in the smallest residual deviance) was a generalized additive model that assumed a Poisson distribution of the data and included the following variables: source plant + sampling period + direction +  $\ln$  (distance), where  $\ln$  (distance) was a loess smoothed function of dispersal distance. The residual deviance was an order of magnitude smaller when assuming a Poisson distribution, thus resulting in a closer fit to the data. Adding interactions among the factors did not significantly improve the model. More than half the seeds were captured within 30 cm of the source plants, and approximately 83%, of sulfur cinquefoil seeds were dispersed within 60 cm of the source plant (Fig. 3B).

Direction of the seed trap had a detectable influence on the number of captured seeds (Fig. 3A). Although wind speed and wind direction vary considerably throughout the study area, prevailing winds usually come from the south (Western Regional Climate Center 2004), as reflected in the seed dispersal patterns. Approximately 52% of the captured seeds were dispersed in the combined north and west directions, and the fewest number of seeds, approximately 18%, was dispersed in the southerly direction. The timing of seed maturation and

**Table 2.** Mean number ( $\pm 1$  SD) of seeds (achenes) per flower, flowers per stem, and stems per plant for sulfur cinquefoil in Union County, Oregon, 2001 and 2002. Within each site, different letters denote a significant difference between annual means (Student's *t* tests;  $Pr > |t| < 0.01$ ).

| Site             | No. seeds per flower <sup>1</sup> |            | No. flowers per stem <sup>2</sup> |           | No. stems per plant <sup>2</sup> |             | Estimated no. seeds per plant |        |
|------------------|-----------------------------------|------------|-----------------------------------|-----------|----------------------------------|-------------|-------------------------------|--------|
|                  | Mean ± 1 SD                       |            | Mean ± 1 SD                       |           | Mean ± 1 SD                      |             |                               |        |
|                  | 2001                              | 2002       | 2001                              | 2002      | 2001                             | 2002        | 2001                          | 2002   |
| Morgan Lake West | NA <sup>3</sup>                   | 105 ± 78   | 22 ± 13 a                         | 16 ± 9 b  | 2.3 ± 0.9 a                      | 2.1 ± 0.8 a | NA                            | 3 530  |
| Morgan Lake East | 93 ± 44 a                         | 96 ± 71 a  | NA                                | 13 ± 7    | NA                               | 2.1 ± 1.0   | NA                            | 2 620  |
| Rice             | 108 ± 28 a                        | 108 ± 65 a | 18 ± 8 a                          | 16 ± 9 a  | 2.8 ± 1.0 a                      | 2.7 ± 1.7 a | 5 440                         | 4 665  |
| Red Bridge       | 142 ± 31 a                        | 84 ± 76 b  | 25 ± 14 a                         | 19 ± 8 b  | 2.5 ± 1.9 a                      | 3.1 ± 1.7 a | 8 875                         | 4 950  |
| Hamburger Hill   | 99 ± 23 a                         | 84 ± 49 a  | 14 ± 6 a                          | 18 ± 11 a | 2.0 ± 0.9 a                      | 2.4 ± 1.8 a | 2 770                         | 3 630  |
| Foothill East    | 93 ± 41 a                         | 101 ± 55 a | 34 ± 20 a                         | 30 ± 17 a | 2.8 ± 2.1 a                      | 5.0 ± 1.9 b | 8 850                         | 15 150 |
| Foothill West    | 59 ± 34                           | NA         | 27 ± 16 a                         | NA        | 2.5 ± 1.2 a                      | NA          | 3 980                         | NA     |
| All Sites        | 99 ± 42 a                         | 97 ± 66 a  | 24 ± 16 a                         | 20 ± 13 a | 2.5 ± 1.4 a                      | 3.1 ± 1.9 b | 5 940                         | 6 015  |

<sup>1</sup>*n* = 25 flowers; 5 flowers per plant, 5 plants per site.

<sup>2</sup>*n* = 30–32 plants per site in 2001; *n* = 25 plants per site in 2002.

<sup>3</sup>NA indicates data not available.

release is reflected in the number of seeds captured during each of the 5 sampling periods over the summer in 2001 (Fig. 4). Approximately one-third of the seeds were captured from late July through 16 August 2001, the first sampling period. Sulfur cinquefoil plants continued to release seeds through summer 2001, with the lowest number of seeds captured in the last 2 weeks of September (Fig. 4B). During the first 2 weeks of October, there appears to be an increase in the number of seeds captured, possibly due to windy and rainy conditions. By using the descriptive data collected for each source plant, we estimated the potential number of seeds that each plant would likely produce in the 2001 season and calculated the approximate proportion of seeds captured on the traps. Mean percentage of seeds captured was 17%  $\pm$  0.04% SD (range 12%–22%, *n* = 6). Stem and flower numbers of each source plant were within the range of the plants used to estimate seed production (Table 2).

## DISCUSSION

### Seed Production

Our estimates of seed production for sulfur cinquefoil in north-east Oregon are nearly 4-fold higher than previously reported for a single population of sulfur cinquefoil growing in southern Michigan (Werner and Soule 1976). In the Michigan study, the average number of seeds per flower was lower (mean  $\pm$  SD, 61  $\pm$  28), the number of flowers per stem was comparable (25  $\pm$  11), and the number of stems per plant was lower (1.1  $\pm$  0.4). Because of more flowering stems and a higher number of seeds per flower, our estimates of seed production far exceeded theirs (6 000 vs. 1 650 seeds per plant). We were unable to rigorously test the relationship between plant density and seed production; however, plant density did not appear to influence stem or flower numbers. At a northwestern Montana grassland site, sulfur cinquefoil plants produced an average of 123 seeds per flower (3-year average; P. Lesica, unpublished data, 2002), which is within the range of our estimate for both years. Higher seed production in populations of the western United States may be due to more favorable growing conditions or marked differences in regional genotypes (Barrett 2000). Because we

calculated seed number on the basis of characteristics of plants collected in July and August, we likely underestimated the total annual seed production.

Many invasive plant species produce considerably more than 5 000 to 6 000 seeds per plant annually (Blossey and Notzold 1995). Sulfur cinquefoil plants, however, may flower and produce seeds in the first growing season, and we assume they continue to produce seeds throughout their lifetime. Plants have been reported to live from 20 to 30 years in Michigan (Rice 1991) and 10 years in Oregon (Perkins et al. 2006). Average age of sulfur cinquefoil plants in infested areas in northeast Oregon is 3 to 4 years (3.5  $\pm$  0.10.10 SE years; Perkins et al. 2006), so an "average" plant may produce over 19 000 seeds in its life span. Sulfur cinquefoil seeds have high viability and germinability (Baskin and Baskin 1990); if even a fraction of the seeds germinate and establish successfully on

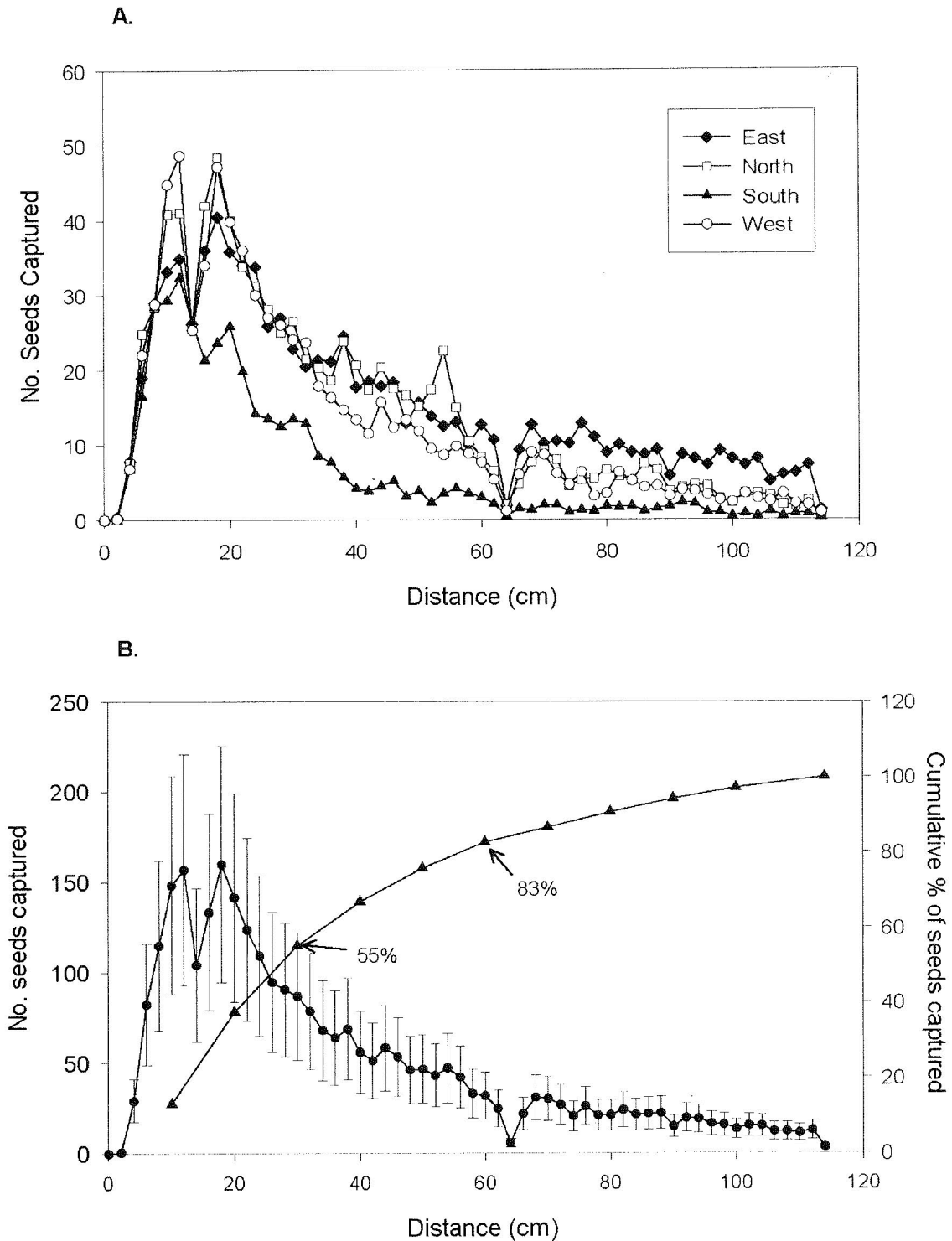
**Table 3.** Results of nested analysis of variance (ANOVA) for effects of site, year, and site  $\times$  year interaction on the number of seeds per flower, the number of flowers per stem, and the number of stems per plant. For each ANOVA, plant (factor) was nested within year (2001, 2002).

| Source                                  | df     | F     | Pr > F  |
|-----------------------------------------|--------|-------|---------|
| Number of seeds per flower <sup>1</sup> |        |       |         |
| Site                                    | 4, 240 | 1.59  | 0.1771  |
| Year                                    | 1, 240 | 3.46  | 0.0640  |
| Site $\times$ year                      | 4, 240 | 3.43  | 0.0094  |
| Number of flowers per stem <sup>2</sup> |        |       |         |
| Site                                    | 4, 734 | 41.25 | <0.0001 |
| Year                                    | 1, 734 | 7.56  | 0.0061  |
| Site $\times$ year                      | 1, 734 | 3.57  | 0.0068  |
| Number of stems per plant <sup>3</sup>  |        |       |         |
| Site                                    | 3, 214 | 9.48  | <0.0001 |
| Year                                    | 1, 214 | 19.74 | <0.0001 |
| Site $\times$ year                      | 3, 214 | 3.17  | 0.0252  |

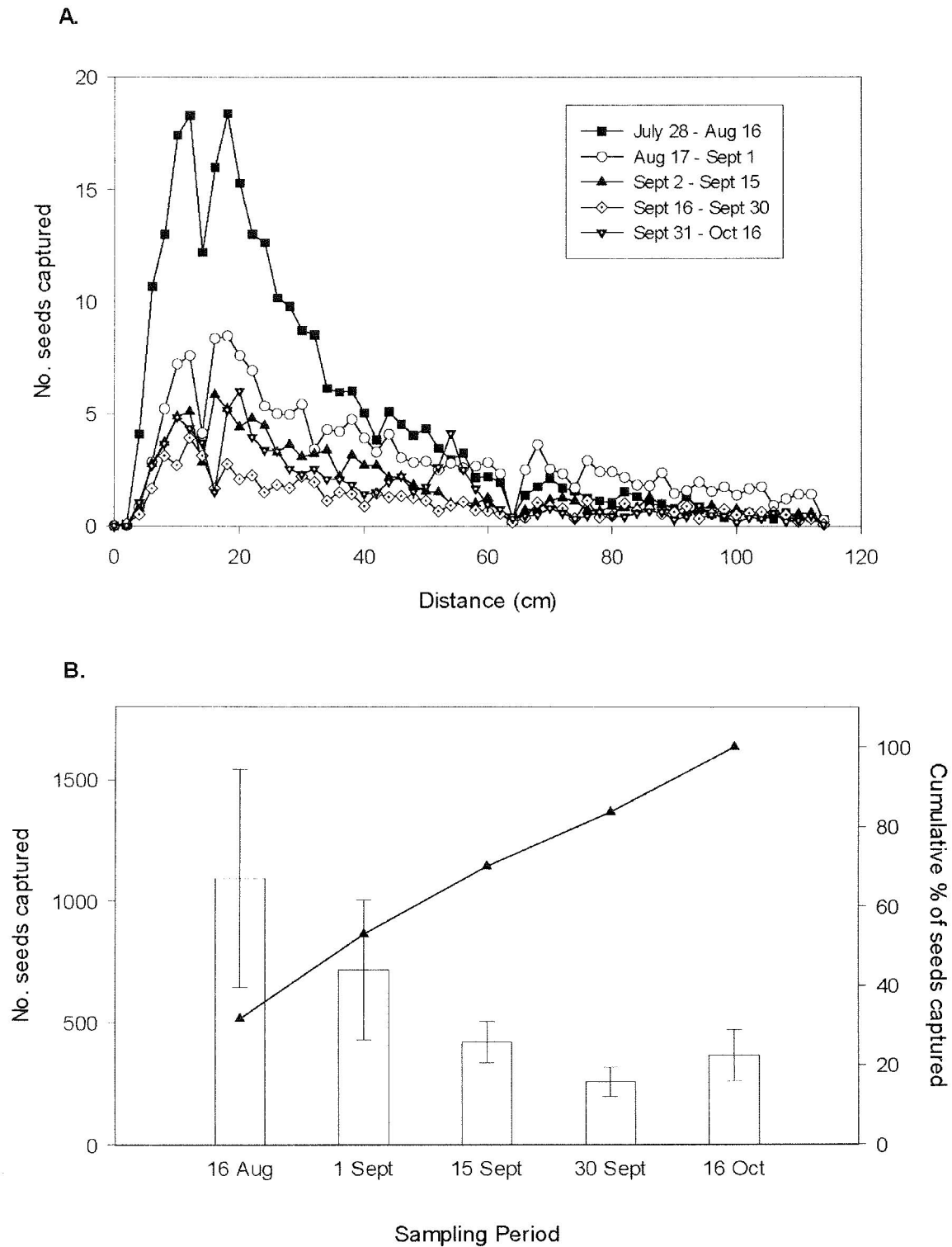
<sup>1</sup>Number of seeds per flower counted for 5 flowers per plant, 5 plants per site, 5 sites, 2001 and 2002.

<sup>2</sup>Number of flowers per stem counted for 25–32 plants per site, 5 sites, 2001 and 2002.

<sup>3</sup>Number of stems per plant counted for 25–32 plants per site, 4 sites, 2001 and 2002.



**Figure 3.** Mean number of sulfur cinquefoil seeds dispersed in the north, south, east, and west directions ( $n = 6$  plants) from late July to mid-October 2001 in northeast Oregon (**A**); mean total number of seeds ( $\pm 1$  SD) captured and cumulative percentage of seeds captured against distance from source plant (**B**).



**Figure 4.** Mean number of sulfur cinquefoil seeds ( $n = 6$  sites) captured (**A**) and cumulative percentage of seeds captured (**B**) during each sampling period in northeast Oregon (2001).

an annual basis, a local area may become dominated by sulfur cinquefoil within several years. In addition, Baskin and Baskin (1990) reported that percent germination of sulfur cinquefoil seeds did not decrease with more than 2 years of burial. Although Rice (1991) noted that sulfur cinquefoil seeds remain viable in the soil for up to 4 years, it is likely that viable seeds persist for considerably longer, and we speculate that sulfur cinquefoil may potentially dominate the seed bank in infested areas. Additional studies are needed to quantify sulfur cinquefoil seed longevity and propagule supply in the seed bank (Powell 1996).

Although little is known about the environmental requirements and competitive ability of sulfur cinquefoil, our results suggest that site conditions, including presence of native vegetation, influence reproductive capacity. In a northeast Montana grassland, the proportion of sulfur cinquefoil plants that produced seeds ranged from 3%, to 86% was highly variable, and increased during years with higher precipitation. Further, plants produced more seeds per flower in the 2 wettest years, and the lowest number of seeds per flower occurred on the most xeric plot (P. Lesica, unpublished data, 2002). In northeast Oregon, average maximum temperature for the growing season (March–September) is 21.5°C, average minimum temperature is 5.8°C, and average annual precipitation is 250 mm (Western Regional Climate Center 2004). In our 2 study years, total precipitation from March through September was 16.5 cm, considerably below the long-term average (Fig. 1). It is possible that seed production would exceed our estimates in wetter years.

### Seed Dispersal

Use of seed traps allowed us to characterize the pattern of local seed rain for sulfur cinquefoil. While recognizing our relatively small sample size ( $n = 6$ ), the standard decay function (dispersal curve, Fig. 3) occurred for each plant and likely represents the general pattern of short-distance dispersal for sulfur cinquefoil seeds. These results are consistent with previous observations that sulfur cinquefoil seeds are distributed by falling passively to the ground (Werner and Soule 1976). Sulfur cinquefoil seeds are relatively heavy and have no distinctive structures for wind or animal dispersal. The seed rain pattern (Fig. 3) suggests that once a population of sulfur cinquefoil is established in an area, it could potentially increase its range as an advancing front, expanding outward from source plants through short-distance dispersal (Grime 1979). Although sulfur cinquefoil seeds tend to fall near the source plant, wind direction does affect the fate of seeds. The influence of wind may explain why only 17% of the seeds were captured in approximately 32% of the circular area (radius = 110 cm) surrounding the source plants. Wind direction is a local phenomenon and differs from site to site; however, it may be an important consideration in efforts to control expansion of sulfur cinquefoil populations.

Some seeds may have been released prior to installation of the seed traps; the selected source plants, however, appeared to be just setting seeds at the initiation of seed capture. Our observations of sulfur cinquefoil phenology in northeast Oregon over 3 years indicate that flowers begin to bloom in mid- to late June, seeds ripen and set in July, and the first seeds

are released in late July (C Parks, unpublished data, 2001–2003). Sulfur cinquefoil plants continue to produce and release seeds through September in northern Oregon.

## IMPLICATIONS FOR MANAGEMENT, RESTORATION, AND FUTURE RESEARCH

Our results suggest that seed production and short-distance dispersal may contribute substantially to the local expansion of sulfur cinquefoil populations. We speculate that when sulfur cinquefoil reaches a site, it persists and expands by producing many viable seeds, saturating the seed bank over time, and eventually outcompetes other species. Belker (1965) described an "ideal weed" as an adaptable perennial that is tolerant of a wide range of physical conditions, grows quickly, flowers early, is self-compatible, produces many seeds that disperse widely, reproduces vegetatively, and is a good competitor. Although sulfur cinquefoil does not reproduce vegetatively, it appears to have many of these traits and has become a problematic weed throughout much of the western United States (Endress and Parks 2004). Control of seed production and dispersal to prevent annual seed set would likely assist in managing expansion of sulfur cinquefoil populations. Restoration and management practices such as prescribed fire and herbicide application, which reduce the seed bank or promote seedling germination when environmental conditions are unfavorable for seedling growth, have potential as control methods if executed at the correct time and under specified conditions (Lesica and Martin 2003).

Whereas our results provide insight into how sulfur cinquefoil expands locally, new populations apparently establish via long-distance dispersal. Probable vectors include animals, people, and vehicles. Animals, particularly wild and domestic ungulates, may transport seeds in fur and hooves. Because many areas are grazed by livestock and native populations of deer and elk, it is important to address the role of these animals as vectors of seed dispersal and to design grazing management strategies that improve the ability of grazed native plants to compete with sulfur cinquefoil (Safford and Harrison 2001; Endress and Parks 2004). Dispersal by seed-eating birds may also occur. It is also likely that people hiking, horseback riding, and driving all-terrain vehicles inadvertently disperse numerous seeds. Because abundant seeds reside in the soil surface are infested sites, careful cleaning of soil from equipment and shoes before leaving the area may prevent new infestations. Each of our study sites was located near a road, and it is likely that the road network in the study area has served as a dispersal corridor and contributed to the increased spread of sulfur cinquefoil through both dispersal and increased disturbance (Formann and Alexander 1998; Gelbard and Belnap 2003; Ritters and Wickham 2003). Increased awareness of the identity of sulfur cinquefoil on both private and public lands may assist in early detection and may reduce further expansion (Aitken and Parks 2004).

The great majority of plant invasions occur in habitats that have been disturbed either naturally or by humans (Rejmanek 1989; Hobbs and Huenneke 1992; Hobbs 2000). In northeast Oregon, our sulfur cinquefoil study sites represented a range of

disturbance from a severely disturbed cultivated field (Foothill East) to variously disturbed forest openings (Table 1). The formerly cultivated site supported a dense stand of sulfur cinquefoil and had the highest seed production in both 2001 and 2002 (Table 2). Although infested sites are visibly disturbed, scattered sulfur cinquefoil plants have also been observed in relatively undisturbed native forest (Endress and Parks 2004). Little is known about the ecological requirements, tolerances, and competitive ability of sulfur cinquefoil; however, it appears to be capable of establishing in a wide variety of habitats. For example, the importance of soil condition on sulfur cinquefoil establishment and spread is unknown, though its wide distribution across North America suggests that it can tolerate a range of soil conditions, and it has been found to colonize areas with sandy, gravelly, rocky, and clay soils (Werner and Soule 1976; Rice 1991).

Studies are needed to determine ecological tolerances and to quantitatively demonstrate the competitive influence of sulfur cinquefoil. Observations suggest that sulfur cinquefoil displaces native grasses and forbs in grasslands and forest openings (Lesica and Martin 2003; Endress and Parks 2004). Because of its high tannin content, sulfur cinquefoil is unpalatable to most wildlife and livestock and tends to crowd out desirable forages (Rice 1999). In areas where sulfur cinquefoil grows with spotted knapweed, cattle prefer knapweed to cinquefoil (Rice 1999). It remains unclear which native species are directly at risk or which plant communities are most affected by the occurrence and expansion of sulfur cinquefoil. The co-occurrence of sulfur cinquefoil with similar native *Potentilla* species in many parts of the western United States provides an ideal situation to compare growth performance and examine competitive ability of congeners (Daehler 2003). Since the expansion of exotic plants continues to be a substantial management challenge in Oregon (Quigley et al. 1996), integrated strategies are needed to effectively control sulfur cinquefoil while promoting invasion-resistant native plant communities.

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