Minimum Population Size for Reproduction in Willamette daisy

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PREFACE

This report is the result of a cooperative Challenge Cost Share project between the Institute for Applied Ecology (IAE) and a federal agency. IAE is a non-profit organization dedicated to natural resource conservation, research, and education. Our aim is to provide a service to public and private agencies and individuals by developing and communicating information on ecosystems, species, and effective management strategies and by conducting research, monitoring, and experiments. IAE offers educational opportunities through 3-4 month internships. Our current activities are concentrated on rare and endangered plants and invasive species.

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SUMMARY

- We located and visited 20 populations of Willamette daisy with a range of population sizes (<10 to >4000), representing the majority of remaining locations of this species.

- We counted all flowering individuals in all populations (or used current population sizes as determined by others), and collected mature flower heads from each population.

- We determined the percentage of viable seeds per flower head for each population by counting filled and empty ovules from approximately 30 flower heads from each location.

- Our results indicate that populations with 20 or fewer individuals generally fail to produce viable seeds. In populations larger than 20, filled ovule production ranged between two and 24 percent, with an overall average of 9.16% of ovules filled for plants sampled in all populations.

- Our results suggest that populations of Willamette daisy with fewer than 20 flowering individuals are unable to produce viable seed, and therefore will go extinct without intervention to increase population sizes or import pollen.

- In populations larger than 20, some filled seeds are being produced, indicating that recruitment by seed is possible. However, filled seed numbers were quite low, suggesting that all populations would benefit from management activities that boost seed production and potential recruitment.

- Sampling in 2006 supports the results from 2005: Populations of Willamette Daisy that fall below a population size threshold of 20 or fewer flowering individuals experience near-total reproduction failure

INTRODUCTION

Willamette daisy *(Erigeron decumbens* var. *decumbens)* is listed as an endangered species by the U.S. Fish and Wildlife Service and the Oregon Department of Agriculture (ONHIC 2004). The species is restricted to western Oregon prairies and grassland habitat remnants, and is currently known from fewer than 30 sites, all in the Willamette Valley. The highest density of existing populations is in the West Eugene area in Lane County, Oregon. Widespread loss of native Willamette Valley prairie habitat to agricultural and urban development is the primary threat to Willamette daisy. The species also faces additional threats of encroachment of prairie habitat by trees, shrubs, and invasive weeds, and possibly inbreeding depression arising from small population sizes (Clark et al. 1993). Limited information suggests that seed production in Willamette daisy may typically be quite low (Gisler 2004), with fewer than 20 percent of achenes filled in one small study (Clark et al. 1995).

Loss, fragmentation, and degradation of prairie habitat has led to continued declining population sizes for many of the known populations of Willamette daisy. Very small populations (≤ 5 individuals) have been documented to have zero seed production (Kaye, personal observation), indicating that as populations get very small, reproductive failure may occur. Although the breeding system of this species has not been studied, Willamette daisy attracts numerous insect species that are thought to act as pollinators, including butterflies, flies, and many types of bees (Gisler 2004). It is likely that this species only produces seed when out-crossed. Other members of the Asteraceae exhibit self-incompatibility (Allphin et al. 2002), and an out-crossing breeding system in Willamette daisy is consistent with the failure of very small populations to produce viable seeds.

Population size has been shown to be correlated with seed set in a number of other plant species (Menges 1991; Kéry et al. 2000). Reproductive failure in small populations of Willamette daisy is a serious concern for the conservation of this species, as at least half the known remaining populations contain fewer than 100 individuals. Current information suggests that populations that fall below some minimum size will no longer be viable. It is crucial that managers know if there is such a size threshold necessary to produce viable seed, so that populations that fall to or below this level can be managed appropriately to prevent local extinctions. The extent to which larger populations produce viable seeds also is not known.

There were two main objectives to this project. The first was to determine the minimum population size necessary for seed production and population maintenance in Willamette daisy. The second objective was to determine if conditions such as individual plant health or resource competition had an effect on seed production. We also assessed the overall seed production in a representative sample of remaining Willamette daisy populations. We located and visited 20 populations with a range of population sizes (<10 to >4000 individuals). For each population, we measured individual plant characteristics, determined the current population size, collected mature capitula (the flowering inflorescence of species in the Asteraceae family), and determined the ratios of filled to empty ovules. This allowed us to examine the relationship between population size and seed production in Willamette daisy.

METHODS

In the spring of 2005, we obtained information on all known locations of Willamette daisy from the US Fish and Wildlife Service, Eugene district BLM staff, area botanists and land managers familiar with Willamette daisy populations. We gathered information on land ownership, current conditions, recent counts or estimates of population sizes, and maps and descriptions of both existing and extinct populations. From this information, we developed a list of potential populations and sites to include in this study.

Sampling procedures and results from 2005 are described in Wise and Kaye (2006). In June and July 2006, we visited sites of known or suspected Willamette daisy populations (Table 1). At each site, we located plants, determined their flowering stage, and flagged plants for later seed collection. For each flagged individual, we measured its widest diameter and the diameter perpendicular to the widest diameter to determine crown cover. We also recorded the plant's height, number of flowers, and ground cover within one square meter for each flagged individual. Depending on site, population size and monitoring history, we determined whether plant counts were necessary and feasible. Sites with large Willamette daisy populations (Oxbow West, Vinci, Fisher Butte, Willow Creek and Holley) are currently being monitored. At these sites, we used a randomization method to locate and flag 30 to 40 individuals for later seed collection, but we did not attempt to count all individuals. Several smaller populations are also being monitored or have recently been counted; Greenhill Ash Grove, Balboa, Kingston Prairie East, two Basket Butte sites and Allen and Allen Farm. At these sites, we flagged most or all of the Willamette daisy plants we located for later seed collection. The remaining populations were fairly small (fewer than 100 individuals) and had not recently been counted; these included the three Bald Hill sites, one Baskett Butte site, Mill Creek, East Coyote, Lanel substation, Bailey Hill and Sublimity grasslands. At these sites, surveys were done to locate and count all plants during the flowering season and flag 30-40 individuals for later seed collection. In populations smaller than 40, all plants were flagged (figure 1).

At several sites, decisions had to be made about population delineations. For example, Willamette daisy occurs at three locations at Baskett Slough National Wildlife Refuge. Two of these, identified on the Refuge as Area 3 and Area 4, are on different aspects of a butte, separated by approximately 150 meters. The small population in Area 10 is approximately 2 km away. These sites were considered separate populations because we believed pollen and seed flow between them is unlikely. Similar reasoning was used to delineate sites at Bald Hill. In one case, (Speedway in Lane County) plants were dispersed over a large area in such a way that it was not possible to confidently assign a population size to any single group of plants at the site. It was therefore excluded from this study.

Figure 1. A flagged Willamette daisy at the Sublimity site in 2005.

We returned to each population at least once (often several times) in order to collect flower heads with mature seeds. We relocated flagged plants, and then collected 1 or 2 flower heads that had finished flowering and had mature seeds still attached from each plant. We placed each individual flower head in a separately labeled coin envelope. Because seeds of this species remain on the head for only a short time after they reach maturity, collecting seeds required getting to each site shortly after most flowers had withered and seeds had matured, but before seeds fell or were blown off the flower heads. Seed collection was conducted throughout July of 2005 and 2006.

To determine the number of filled seeds, seeds from each population were examined under a dissecting microscope. For each population, one capitulum from 30 different individuals was examined. For populations where capitula were not collected from 30 individuals, we examined 30 capitula from all flowering individuals in the population. For each sampled capitulum, we determined the numbers of filled and empty ovules (figure 2), which allowed us to calculate the percentage of ovules successfully converted to seeds (proportion seed set) along with total seed set per capitulum. In populations with fewer than 30 individuals, average seed set per individual was calculated based on all capitula sampled for each plant. The contribution of populations size and other population and community variables to the proportion seed set was analyzed by regression analysis with NCSS.

Table 1. Populations of Willamette Daisy included in this study along with population sizes, land ownership, and County.

Population Name	No. of Flowering plants (2005-06)		Landowner	County
Bald Hill North Prairie	3	7	City of Corvallis	Benton
Mill Creek	7	14	ODOT	Polk
Bald Hill South	10	13	City of Corvallis	Benton
Bald Hill North Trail	12	12	Private	Benton
Baskett Butte Area 4	20	75	USFWS	Polk
Baskett Butte Area 10	27	43	USFWS	Polk
East Coyote	36	36	USACE	Lane
Baskett Butte Area 3	52	141	USFWS	Polk
Kingston Prairie East	52	100	TNC	Linn
Sublimity Grassland	58	55	Private	Marion
Bailey Hill	*	78	TNC	Lane
Balboa	80	83	BLM	Lane
Greenhill Ash Grove	86	86	BLM	Lane
Lanel Substation	89	89	Railroad	Lane
Allen and Allen Farm	131	135	Private	Benton
Vinci	526	528	BLM	Lane
Willow Creek	597	846	TNC	Lane
Holley	*	551	Private	Linn
Oxbow West	1480	3092	BLM	Lane
Fisher Butte	4631	4631	USACE	Lane

***** These populations were added to study in 2006.

Figure 3. Filled and empty ovules of Willamette daisy from Sublimity grassland (2005).

RESULTS

Seed production in Willamette daisy was low in all populations, ranging between zero and 24% filled seeds in 2005 and between 0.10 and 38.75% in 2006 (Table 2 & Figure 3). In very small populations, those with 20 or fewer flowering plants, seed production rates were between zero and 1.5% in 2005 and 0.10 and 2.14% in 2006. In populations with more than 20 individuals, seed production varied from about 2% filled seed (Balboa) to 23.5% filled seed (Sublimity grassland) in 2005 and from 1.32% filled seed (Baskett Butte Area 4) to 38.75% filled seed (Fisher Butte). Population size (number of flowering individuals) explained about 19% of the variation in seed set among populations ($p = 0.07$, Figure 3) in 2005 and 52% of seed set variation among populations in 2006 ($p= 0.0023$, Figure 4).

Table 2. Percent filled seed and population sizes for 20 Willamette daisy populations sampled.

	2005		2006	
Site	**Population Size**	**% Filled Seed**	**Population Size**	**% Filled Seed**
Bald Hill North Prairie	3	0.00	7	2.14
Mill Creek	7	0.33	14	0.10
Bald Hill South	10	1.22	13	0.67
Bald Hill North Trail	12	1.28	12	1.11
Baskett Butte Area 4	20	0.08	75	1.32
Baskett Butte Area 10	27	9.74	43	13.19
East Coyote	36	5.14	†	1.47
Baskett Butte Area 3	52	7.13	141	11.19
Kingston Prairie East	52	9.46	100	19.25
Sublimity Grasslands	58	23.55	55	35.86
Bailey Hill	*	*	78	5.01
Balboa	80	1.82	†	8.90
Greenhill Ash Grove	86	5.57	†	14.96
Lanel Substation	89	10.47	89	6.41
Allen and Allen Farm	131	20.23	135	10.34
Vinci	526	9.87	†	10.16
Holley	*	*	551	7.99
Willow Creek	597	9.51	846	19.61
Oxbow West	1480	4.85	3092	20.79
Fisher Butte	4631	11.40	†	38.75

***** Populations added to study in 2006.

†Population size estimates were not available in 2006; 2005 estimates were used in analyses.

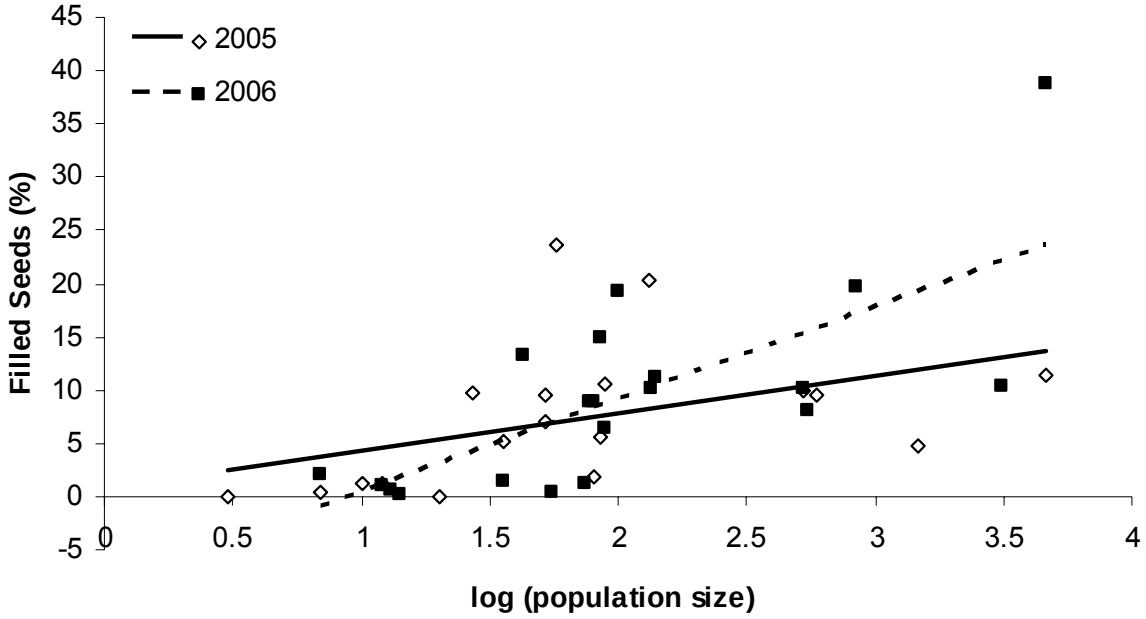

Figure 4. The relationship between the percent of filled seeds and the log of population size in twenty population of Willamette daisy in 2005 and 2006. 2005, y = 3.5085 log (population size) + 0.8578, R^2 = 0.1895. 2006, y=8.8184 log (population size) - 8.2952, R^2 = 0.5215.

A multiple regression analysis using population size, crown size, plant height, and cover of grasses, forbs, shrubs, and bare ground as explanatory variables found that only population size affected the % seed set in Willamette daisy in 2006 ($P_{\text{population size}}$ = 0.087; all others, P > 0.12).

DISCUSSION

Our results indicate that populations of Willamette daisy with 20 or fewer flowering individuals experience near-total reproductive failure. The percent of filled seeds in the five populations sampled in 2005 that had 20 or fewer flowering individuals was between zero and 1.5%. In 2006, the percent of filled seeds in the four populations with fewer than 20 flowering individuals was between 0.10 and 2.14%.

These results suggest that there is a population size threshold below which seed production effectively stops. The most likely explanation for this result is self-incompatibility in Willamette daisy. Under this mechanism, pollen from an individual plant or a close relative is incapable of successfully fertilizing ovules in that individual, and only out-crossed pollen from a compatible mating type will result in successful seed production. Self-incompatibility is found in approximately 60% of flowering plant species (Hiscock and Tabah 2003), and has been documented in many members of the Asteraceae (DeMauro 1993, Allphin et al. 2002). In the very small populations of Willamette daisy that were sampled, a small number of filled seeds were produced in only one or two individuals, suggesting that a compatible mating type exists in the population for only 1 or 2 individuals.

In populations above 20, seed production was generally low, but highly variable among populations. Fore example, in 2006, fewer than 1.5% of ovules were filled in seeds sampled from Basket Butte Area 4 (N=75) while more than 38% of seeds sampled from Fisher Butte (N>4631) were filled. Many factors may be contributing to seed viability variation among populations when population sizes are above 20 individuals. Although we did not find any significant effects of plant size variables (crown size and height) or course community measurements (percent cover of grasses, forbs, shrubs, and bare ground), there are a number of other factors that may affect reproduction in Willamette daisy that we have not measured. Variation in habitat quality (disturbance, competition, soil biota and fertility, etc.), moisture availability, pollinator service, extent of inbreeding, and genetic drift can impact seed set. Willamette daisy plants exhibit huge variation in size and flower number both among and within populations (Wise, personal observation), and this variation may be a reflection of genetic or environmental factors, or more likely a combination of the two. Inbreeding depression – lower fitness among inbred individuals – is well documented for both out-crossing and selfing plant species (McKay et al. 2005). The present study does not assess the potential impact of inbreeding on Willamette daisy fitness. However, in any species with populations that are small and in decline, inbreeding depression is a potentially serious threat that should be examined.

We also found that there was variation in the percent of filled seeds within sites between years. It was suspected that the unusually cool and wet May and June of 2005 limited pollinator activity (Wise and Kaye 2006). There was also a large amount of vole activity in 2005, which likely damaged some plants. However, there was an increase in the percent of filled seeds in only 13 of the 20 populations. It is still unclear what may drive this year-to-year variation in fitness in Willamette daisy.

MANAGEMENT RECOMMENDATIONS

We sampled a large proportion of the remaining known populations of this species. Four of the 20 populations appear to be below the size threshold required to produce viable seeds. Twelve additional populations had fewer than 100 flowering individuals in 2006. Reproductive failure is a serious concern in this species, and should be addressed. We recommend the following actions:

1. Augmentation of the four smallest populations (N ≤ 20) with plants grown from seed and cross-pollination of mature plants with pollen from nearby Willamette daisy populations.
2. Careful monitoring of all populations below 100, because those below 20 individuals are in danger of rapid decline and local extinction, and those with size ranges between 20 and 100 individuals are at risk of declining to a point where reproductive failure will start to occur..
3. Additional studies to determine management activities to reverse the decline in Willamette daisy numbers to prevent further loss of seed viability.

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