

Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts

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Summary

1. Invasive species are one of the leading threats to biodiversity worldwide. Therefore, chemical herbicides are increasingly used to control invasive plants in natural and semi-natural areas. Little is known about the non-target impacts of these chemicals on native species.

2. We conducted an experiment to test the demographic effects of the herbicide picloram on a native dominant forb, arrowleaf balsamroot *Balsamorhiza sagittata*. As reported in earlier studies, picloram did not change leaf area of balsamroot in the short term (5 years). However, a single application of picloram dramatically reduced flowering and seed set, and these effects have persisted for at least 4 years after spraying.

3. Matrix population models based on these data suggest that arrowleaf balsamroot is slowly declining in the presence of weeds, rapidly declining in the presence of herbicide, but might experience a release period after the herbicide decays and before weeds invade.

4. Therefore, from the perspective of persistence of this native wildflower, herbicide use can be beneficial *or* detrimental, depending on how often a site is sprayed and how long the herbicide persists in the soil. In this system, spraying intervals of more than 10 years may be beneficial, but intervals of less than 5 years will be detrimental. In general, our results emphasize the importance of finding ways to combine herbicide use with other weed control techniques to maximize return intervals and minimize non-target impacts.

5. *Synthesis and applications.* Herbicide use in natural areas differs fundamentally from herbicide use in agricultural areas, because the non-target species are not directly under management control. Herbicides inevitably will impact non-target species due to limitations in selectivity. Herbicide persistence and reapplication intervals are key factors determining the demographic impacts of herbicides on native plants. Understanding how persistence and reapplication timing interact with native plant demography allows us to develop management prescriptions that minimize non-target effects in natural areas. To date, this interface of ecology and management has received little attention from practitioners or researchers.

Key-words: *Balsamorhiza sagittata*, *Centaurea maculosa*, decision analysis, grassland, matrix model, pesticide, picloram, population dynamics, sensitivity analysis, weed control

Introduction

Invasive plants are one of the leading threats to biological diversity in natural and managed areas (Mack *et al.* 2000). Because of their devastating ecological and economic impacts, significant resources are spent on their control and management (Duncan *et al.* 2004; Pimentel, Zuniga & Sheley 2005).

Unlike some environmental problems, once invasive plants become established, they often cannot be controlled by simply removing the initial mechanisms for invasion such as human-induced disturbance or by restoring natural processes such as fire. Instead, invasive plants must be controlled directly by using, either alone or in combination, herbicide treatments, manual removal, grazing, burning, biological control agents, or other methods capable of suppressing the target species in its invaded context (Petroff and Sheley 1999).

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Herbicide is an effective tool for quickly controlling numerous invasive weed species over local areas (Rice *et al.* 1997; Tyser *et al.* 1998; Sheley *et al.* 2000). However, methods for assessing the impacts of herbicide use come historically from agricultural (crop) systems, where the goal is usually to maximize yield of a single plant species (Smith *et al.* 2006). In agricultural settings, all plants except the crop plant are killed, and not much target specificity is required. In contrast, in natural areas, herbicides are used to target suppression of one or, occasionally, a few species of invasive plants, while attempting to maintain or restore the rest of the native community and/or other desirable species (Hobbs and Humphries 1995). Many commonly used chemicals are broadleaf herbicides that kill or suppress forbs to varying degrees depending on dose and species-specific sensitivity. Thus, these herbicides generally release grasses and the more herbicide-resistant forbs from suppression by the exotic weeds, but they may negatively impact many other forb species. They can potentially shift plant community composition away from forbs and toward grasses depending on application rates, timing, and reapplication (Marrs 1985; Rice *et al.* 1997; Pearson and Ortega 2009), as well as the life histories of the target weeds and non-target forbs. This is an important consideration given the preponderance of forbs in many wildland areas where weed treatments take place (Mueggler and Stewart 1980; Ortega and Pearson 2005; Pokorny *et al.* 2005). Herbicide is only an effective tool for restoration if the net gains from the herbicide suppressing the target weed outweigh its negative effects on non-target native species.

A small but growing number of studies have evaluated the non-target impacts of broadleaf herbicide application on native forbs (Marrs 1985, Rice *et al.* 1997, Rice and Toney 1998, Tyser *et al.* 1998, Sheley, Mangold & Anderson 2006). These are most often used to identify the compounds, timing and application rates that minimize reductions in biomass or cover of native species. This is important information that can greatly improve management programmes targeted at maintaining native forbs and natural areas' values. However, some commonly used broadleaf herbicides can substantially reduce fecundity for many years in relatively robust, long-lived forbs (Rice *et al.* 1997), suggesting that repeated herbicide applications may affect population dynamics of even long-lived species. To our knowledge, no studies have addressed the long-term demographic effects of herbicide applications on perennial species that make up a large component of many native plant communities.

Our research was inspired by the following observations of herbicide use in semi-arid grasslands and other natural areas of western Montana. First, native forbs appear to have declined in several areas with a history of herbicide use (E. Crone, D. Pearson, and M. Marler, personal observation; see also Sheley and Denny 2006), in spite of well-designed experiments to select chemicals, application rates and timing that minimize impacts on native communities (Rice *et al.* 1997; Rice and Toney 1998). Secondly, in many cases, whether or not herbicide directly affects leaf area or biomass of native species, it often alters other life-history traits, such as phenology or

individual reproductive effort (Rice *et al.* 1997; D. Pearson, personal observation). These changes could directly affect long-term population viability of native species, particularly if herbicide is used regularly (e.g. once every 5 to 10 years) to prevent reinvasion by weeds.

In this article, we present results from the first 5 years of an ongoing experiment in which we monitored non-target effects of the herbicide picloram (Tordon®) on a dominant perennial wildflower, arrowleaf balsamroot *Balsamorhiza sagittata* (Pursh). In the area surrounding our experimental site, picloram is used regularly to control invasion by spotted knapweed *Centaurea maculosa* (see Rice *et al.* 1997). These experiments were initiated with herbicide application in 2002, with plans to repeat herbicide application after knapweed reinvades. We anticipate that it will take at least 10 years to accurately estimate the population-dynamic consequences of herbicide application for arrowleaf balsamroot in this system (see Results). However, at this point, it is timely to explore the potential impacts of the most dramatic short-term (2002–2007) results for this species. Additionally, we use a demographic model to explore the possible long-term consequences of herbicide use for long-lived perennial wildflowers, such as balsamroot. This model provides broad rules of thumb for minimizing non-target impacts of herbicide on long-lived native forbs. Together, our data and analyses highlight issues relating to herbicide use in natural areas that have received little attention from the scientific or management communities to date.

Methods

STUDY SYSTEM

The native wildflower, arrowleaf balsamroot *Balsamorhiza sagittata* (Asteraceae) is a perennial herb with a large taproot and radiate, sunflower-like heads of yellow flowers. Plants are 20–80 cm tall, with basal leaves up to 30 cm long, and solitary (occasionally 2–3) flower heads on long, upright stalks (Lesica 2002). Flowering in our area occurs over about 3 weeks, beginning in late April or early May. Seeds require cold stratification for germination (Morrison 2002), but do not form a persistent seed bank, based on observation of seed addition plots (D. Pearson, unpublished data) and searching soil cores for seeds in May, between germination and seed set (A. Gundlach, unpublished data). Arrowleaf balsamroot grows in deep sandy soil in open areas, ranging from grasslands to sagebrush steppe to open Ponderosa pine *Pinus ponderosa* forests, sometimes forming spectacular stands (Taylor 1992). It is an ecologically important species because its relatively large, nutritious seeds are predated by a number of vertebrate and invertebrate species (Amsberry and Maron 2006).

Spotted knapweed *Centaurea maculosa* (= *Centaurea stoebe*) (Asteraceae) is one of the most widely established exotic plants in western North America (Sheley *et al.* 2000). A short-lived perennial herb of Eurasian origin, knapweed invades arid grasslands, prairies, and savannas, displacing diverse native plant communities through a variety of interactions (Tyser 1992; Marler, Zabinski & Callaway 1999; Ridenour and Callaway 2001; Bais *et al.* 2002). Unlike arrowleaf balsamroot and most other native forbs in our study area, knapweed grows and flowers in late summer. Flowering begins in late June, peaks in August, and continues through early September. Attempts to manage knapweed by releasing biological control

agents have proven problematic (e.g. Pearson, McKelvey & Ruggiero 2000), reinforcing interest in herbicide as a management tool.

Our experiment took place on Mount Jumbo, a city-owned natural area in Missoula, Montana. The plant community was a rough fescue *Festuca scabrella* and bluebunch wheatgrass *Pseudoroegneria spicata* prairie that was heavily infested with spotted knapweed. Other native wildflower species common at the site include but are not limited to spring chickweed *Cerastium arvense*, larkspur *Delphinium bicolor*, shooting star *Dodecatheon conjugens*, paintbrush *Castilleja hispida*, nine-leaved desert parsley *Lomatium triternatum*, western yarrow *Achillea millefolium* and prairie smoke *Geum triflorum*. This is a very common grassland community type in the intermountain regions of Montana and Idaho (Mueggler and Stewart 1980). Our specific study site had no known history of herbicide use. However, the City of Missoula uses a combination of herbicide and other methods (such as grazing and hand-pulling by community groups) to control noxious weeds in the Mount Jumbo natural area, as mandated by Montana's noxious weed law (Montana House Bill 395).

FIELD EXPERIMENT

We divided the hillside into four 20 × 20 m blocks. Two of the blocks were randomly selected to receive picloram application, and two were designated as non-sprayed experimental controls. We applied Tordon 22 k (active ingredient: 4-amino-3,5,6-trichloropicolinic acid, potassium salt 24.4%) at the manufacturer-recommended rate of 1.24 L ha⁻¹. We used a four-wheel all terrain vehicle (ATV) with a boomless sprayer to deliver the herbicide. Application was in early October 2002, when most native plants are dormant but knapweed is starting to 'green up' with autumn precipitation (M. Marler, personal observation). This timing is often recommended for conservation areas, because applying the herbicide after the growing season is expected to minimize impacts to native forbs (Rice and Toney 1998).

In June 2002 (prior to treatment), we established two 10 × 1 m permanent monitoring transects centred in each of the four blocks. We censused arrowleaf balsamroot plants in these transects using standard demographic methods (following Lesica 1987, except that we added tags at the base of each individual plant as well as mapping plants, to facilitate relocation in particularly dense areas). For each plant, we counted the number of leaves, and the number of inflorescences (i.e. flower heads). Most flowering stalks had just one inflorescence, and thus, we counted browsed flowering stalks as one inflorescence. Plants with single leaves (mostly seedlings) were noticeably smaller than plants with two or more leaves; therefore, we used the number of leaves from mature plants plus 0.25 × the number of leaves of seedlings as a measure of leaf density. (This choice was based on visual inspection but use of 0.10 or 0.50 did not change the conclusions; E. Crone, unpublished analyses.) Surveys of balsamroot plants were conducted yearly in late May or early June from 2002–2007. Differences among treatments were analysed with generalized linear mixed models, to account for repeated measures among years. We also used these data to create preliminary matrix models to explore possible management strategies.

Picloram is widely used to kill knapweed, but we verified that knapweed was killed in sprayed plots by visually estimating per cent cover in 2003 and 2007. In 2003, we visually assigned each square metre in balsamroot transects to one of three density classes: no knapweed, 1–20% knapweed cover, and > 20% knapweed cover. In sprayed transects, 39/40 1-m² plots had no knapweed, and one plot had 1–20% knapweed cover. In the unsprayed transects, 8/40 plots had 1–20% knapweed cover, and 22/40 had > 20% knapweed cover.

We did not observe knapweed in the sprayed plots throughout this study (2003–2007). We confirmed this observation by counting knapweed densities in 2007; the two unsprayed plots had 18.8 ± 4.9 and 20.7 ± 3.7 knapweed plants m⁻² (> 20% cover) and the two sprayed plots had 1.7 ± 0.3 and 2 ± 0.7 knapweed plants m⁻² (< 5% cover; M. Ellis, unpublished data).

DEMOGRAPHIC MODELS

We used a matrix projection model (e.g. Caswell 2001; Morris and Doak 2002) to illustrate the consequences of different herbicide application frequencies on native perennial wildflowers such as arrowleaf balsamroot. We note at the outset that high among-year variability means that it will take several more years of monitoring to quantitatively estimate stochastic population growth rates for this species (c.f., Fieberg and Ellner 2001; Morris and Doak 2002; Tuljapurkar, Horvitz & Pascarella 2003). Nonetheless, analysis of the first 6 years of data with simple models illustrates general features of optimal herbicide use that can be used to guide management until more data are available.

Specifically, we constructed a matrix population model with five stage classes (Fig. 1): small vegetative plants (1–2 leaves; SV), medium vegetative plants (3–14 leaves; MV), large vegetative plants (≥ 15 leaves; LV), medium flowering plants (< 15 leaves; MF) and large flowering plants (≥ 15 leaves; LF). We chose a density-independent population model because intraspecific competition seems to be small relative to interspecific competition in these mixed species communities. Competition with native plants is implicit in our estimates of vital rates; competition with knapweed is explicitly modelled in our analyses (see below).

We chose stage class boundaries based on subjective relationships between plant size and vital rates in the field (biological classification *sensu* Kaye *et al.* 2001). We evaluated our classification numerically by shifting class boundaries by ±1, 2, and 5 leaves. These matrices had similar vital rates. We calculated transition rates by tabulating the proportion of individuals in each stage class that remained the same or moved to a different stage class in the next year. We identified newly recruited plants as plants that had not been marked the previous year; arrowleaf balsamroot does not appear to have prolonged dormancy (*sensu* Lesica and Steele 1994), and all apparent recruits had one or two leaves. We calculated *per capita* recruitment rates for medium and large flowering plants as the ratio of new recruits in 1 year over the number of inflorescences in the previous year, multiplied by the average number of inflorescences of medium and large flowering plants, respectively. This calculation implicitly includes seed predation, seed germination, and seedling survival, because it is the relationship between realized successful recruitment in year *t* + 1 and flowering in year *t*. Arrowleaf balsamroot does not appear to form a persistent seed bank in this area (see Study system, above); thus, we did not include a seed stage class. For these heuristic models, we created one transition matrix each for sprayed and unsprayed plots by tabulating all transitions (within treatments) over all years, then converting these to proportions (equivalent to a weighted average across years based on the number of plants in each class in each year).

Three sets of parameters are needed to simulate long-term effects of herbicide use: (i) vital rates in unsprayed plots with weeds (hereafter, the weed competition period), (ii) vital rates while herbicide is still in the soil (hereafter, the herbicide period), and (iii) vital rates during the years after the herbicide degrades but before weeds reinvade (hereafter, the release period). We measured rates during the weed competition and herbicide periods directly, but have not yet

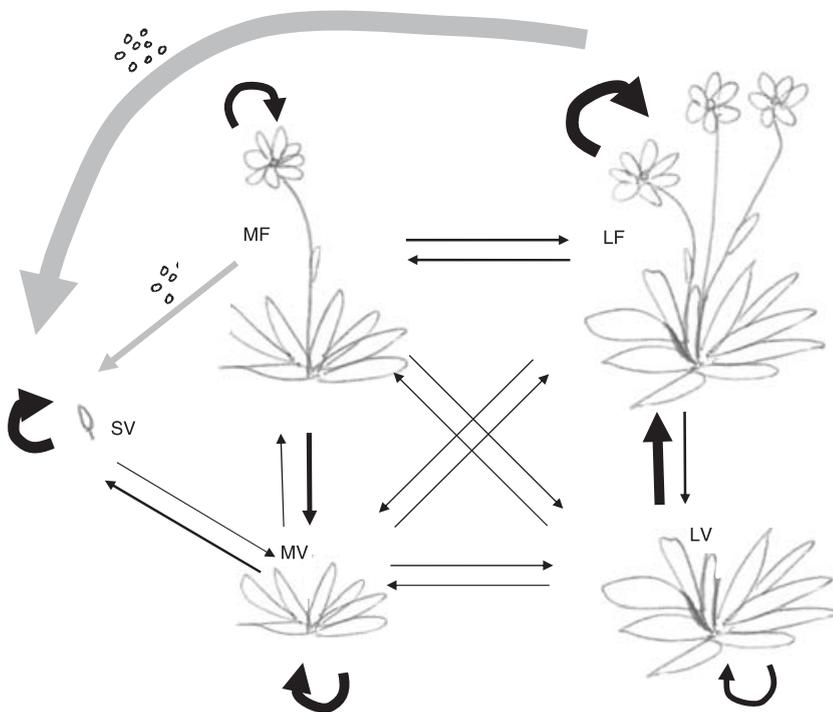


Fig. 1. Life cycle of arrowleaf balsamroot. Black arrows indicate transitions of individual plants, and grey arrows indicate fecundity. The width of arrows is proportional to the magnitude of the transition rate. See stage class abbreviations in Table 2.

observed the release period (see Results). Y. Ortega and D. Pearson (unpublished data) conducted a weeding experiment to quantify the effects of knapweed on balsamroot size and recruitment at ecologically similar sites. They found that recruitment was 1.65 times higher in weeded than unweeded (knapweed-invaded) plots. They did not measure effects of weeding on survival of established plants. Therefore, we consider two hypotheses for vital rates during the release period: (i) identical to the weed competition period, but with 65% increase in recruitment; (ii) identical to the weed competition period, but with 65% increase in recruitment plus 5% increase in survival, up to maximum survival of 99.5%. In other words, we multiplied all transition rates except fecundity by 1.05, or the multiplier that would make these transitions sum to 0.995. (Note that this refers to survival in the broad sense of not dying, not longevity as opposed to growth, *sensu* Silvertown *et al.* 1993.)

We used these three matrices to calculate the effects of different herbicide application strategies, where strategy refers only to the number of years between spraying at a particular site, defined as the return interval, I . Note that I is the only control variable in this analysis, implicitly assuming a pre-determined appropriate spray strategy (dose and timing) which does not vary among the analyses (e.g. Rice *et al.* 1997). We also assumed that repeated application of herbicide has the same effect as the first application. This assumption is reasonable for a starting point in this general model, but is also one of the key hypotheses we will test in our ongoing experiments. Predicting the effects of herbicide application requires two other parameters about system dynamics. The first is how long the herbicide stays in the soil, which we will refer to as the persistence time, P . The second is how long it takes weeds to reinvade after the herbicide degrades, which we will refer to as the lag time, L . These parameters differ from the return interval, I , because they describe background features of the site to be managed, and are not directly under the control of managers. Therefore, we evaluated the effects of background variation in P and L on the optimal return interval, I .

Over one cycle of herbicide use, abundance changes as follows:

$$N_{t+1} = [M_H]^{T_H} [M_R]^{T_R} [M_W]^{T_W} \times N_t$$

where N_t is the population vector in year t , M_H , M_R , and M_W , refer to herbicide, release, and weed competition matrices, respectively, and T_H , T_R , and T_W refer to the number of years in each condition for a given management regime: $T_H = \min(P, I)$, $T_R = \max(0, \min(I - P, L))$, and $T_W = \max(I - P - L, 0)$. If this management cycle is applied repeatedly, the population will eventually change at an average annual rate, λ_{net} , equal to the I th root of the leading eigenvalue of the projection matrix, $M_{\text{net}} = [M_H]^{T_H} [M_R]^{T_R} [M_W]^{T_W}$ (c.f., Tuljapurkar *et al.* 2003, their equation 2, and note that, by definition, $T_H + T_R + T_W = I$). Therefore, we calculated the λ_{net} associated with different possible parameter values and strategies, as a simple measure of their relative merits. This measure includes temporal variation in environmental conditions due to management, but does not include environmental stochasticity.

Results

As expected, picloram applied in the autumn, and at recommended dosages, did not significantly affect the leaf density of arrowleaf balsamroot (Fig. 2, Table 1). However, picloram reduced arrowleaf balsamroot inflorescence production to 33% of the value in unsprayed plots, and densities of new recruits to 5% of that in unsprayed plots (Fig. 2, Table 1). This difference was most notable in 2004, a high-flowering year in unsprayed plots but in which almost no plants flowered in sprayed plots (Fig. 2). At the individual level, sprayed plots had significantly more medium and large vegetative plants, and fewer large flowering plants (Table 1). The density of medium flowering plants did not differ among treatments.

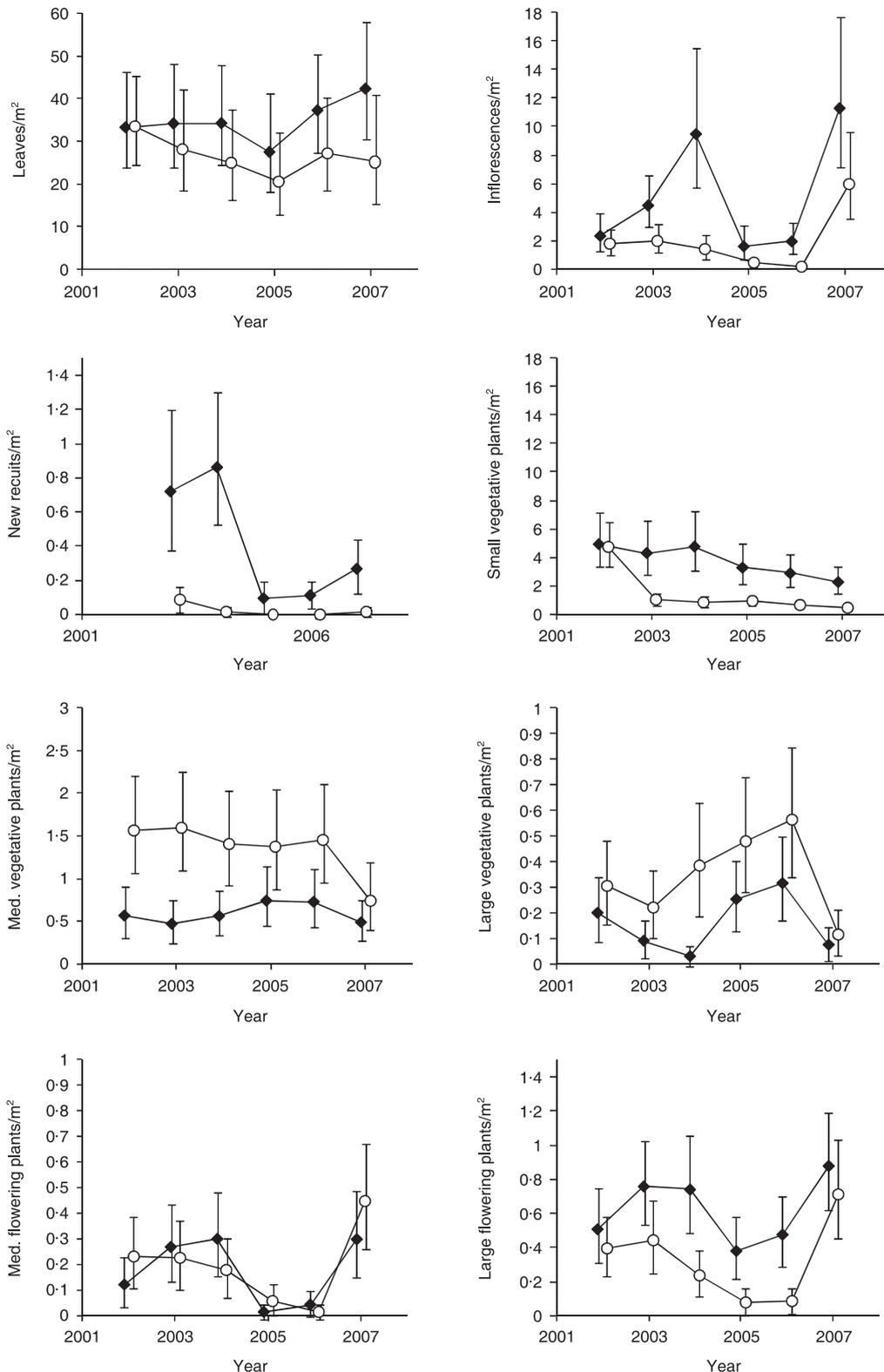


Fig. 2. Effects of picloram on densities of leaves, inflorescences, and individual plants by stage class in sprayed (O) and unsprayed (●) plots. The solid line separates counts before and after picloram application. New recruits could not be distinguished from small vegetative plants in 2002 (see Methods), and thus, they are pooled in the ‘SV’ stage class for matrix models.

Few new recruits were observed in sprayed plots, and small vegetative plants were less abundant in sprayed plots.

Overall, transition rates differed between sprayed and unsprayed plots [chi-square (χ^2) test comparing two sets of

rates to one set for each stage class: $\chi^2 = 157.8$, d.f. = 20, $P < 0.001$]. This overall significant difference reflects differences between treatments for all stage classes except medium flowering plants. ($\chi^2 = 1.0$, d.f. = 4, $P = 0.91$ for medium

Table 1. Analysis of effects of picloram on leaf and inflorescence density, and counts of individuals by stage class (see Fig. 2). All data are counts m⁻². Stage class abbreviations are as indicated in Table 2

	Before spraying, 2002				After spraying, 2003–2007					
	Treatment		<i>Block*</i>		Treatment		<i>Block</i>		<i>Year</i>	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Plot-level totals										
Leaves		0.74	113.7	<0.01		0.40	1369.8	<0.01	27.8	<0.01
Inflorescences		0.29	60.0	<0.01		<0.01	563.2	<0.01	1326.8	<0.01
Number of individual plants, by stage class†										
Recruits					17.0	<0.01	99.7	<0.01	12.7	<0.01
SV	0.0	0.97	150.4	<0.01	6.7	0.01	89.0	<0.01	662.8	<0.01
MV	3.8	0.05	13.6	<0.01	3.6	0.06	4.5	0.03	117.6	<0.01
LV	0.9	0.34	2.0	0.16	5.8	0.02	25.0	<0.01	10.1	<0.01
MF	1.1	0.29	10.6	<0.01	0.0	0.89	54.8	<0.01	14.6	<0.01
LF	0.9	0.34	0.0	0.96	4.5	0.03	27.3	<0.01	8.1	<0.01

*Random effects are listed in italics.

†As in Figure 2, recruits and small vegetative plants are shown separately although they were combined in matrix models (see Methods).

flowering plants; $\chi^2 > 15$, d.f. = 3–5 (depending on possible transitions), $P < 0.01$ for all other classes; see Appendix S1, Supporting Information.)

In unsprayed ('weed competition') plots, we estimated the following transition model:

$$\begin{bmatrix} N_{SV,t} \\ N_{MV,t} \\ N_{LV,t} \\ N_{MF,t} \\ N_{LF,t} \end{bmatrix} = \begin{bmatrix} 0.73 & 0.13 & 0 & 0.41 & 1.23 \\ 0.03 & 0.58 & 0.03 & 0.43 & 0.04 \\ 0 & 0.03 & 0.31 & 0.06 & 0.13 \\ 0 & 0.16 & 0.05 & 0.39 & 0.02 \\ 0 & 0.05 & 0.59 & 0.12 & 0.76 \end{bmatrix} \times \begin{bmatrix} N_{SV,t+1} \\ N_{MV,t+1} \\ N_{LV,t+1} \\ N_{MF,t+1} \\ N_{LF,t+1} \end{bmatrix} \quad \text{eqn 1}$$

(See parameter definitions, Table 2). The asymptotic rate of increase for this matrix, λ_w , is 0.99, suggesting a stable-to-slowly-declining population in the absence of weed management.

Sprayed plots had similar vital rates, except that flowering and recruitment were much lower:

$$\begin{bmatrix} N_{SV,t} \\ N_{MV,t} \\ N_{LV,t} \\ N_{MF,t} \\ N_{LF,t} \end{bmatrix} = \begin{bmatrix} 0.41 & 0.08 & 0 & 0.05 & 0.14 \\ 0.10 & 0.72 & 0.08 & 0.50 & 0.02 \\ 0 & 0.02 & 0.54 & 0.06 & 0.40 \\ 0 & 0.09 & 0.02 & 0.29 & 0.04 \\ 0 & 0.02 & 0.32 & 0.12 & 0.51 \end{bmatrix} \times \begin{bmatrix} N_{SV,t+1} \\ N_{MV,t+1} \\ N_{LV,t+1} \\ N_{MF,t+1} \\ N_{LF,t+1} \end{bmatrix} \quad \text{eqn 2}$$

The asymptotic rate of increase for this herbicide period matrix, λ_H , is 0.94, suggesting faster declines in the continuous presence of herbicide than in the presence of knapweed. To simulate the recovery period, we increased recruitment in the weed competition model by 65% (see Methods):

$$\begin{bmatrix} N_{SV,t} \\ N_{MV,t} \\ N_{LV,t} \\ N_{MF,t} \\ N_{LF,t} \end{bmatrix} = \begin{bmatrix} 0.73 & 0.13 & 0 & 0.68 & 2.03 \\ 0.03 & 0.58 & 0.03 & 0.43 & 0.04 \\ 0 & 0.03 & 0.31 & 0.06 & 0.13 \\ 0.00 & 0.16 & 0.05 & 0.39 & 0.02 \\ 0 & 0.05 & 0.59 & 0.12 & 0.76 \end{bmatrix} \times \begin{bmatrix} N_{SV,t+1} \\ N_{MV,t+1} \\ N_{LV,t+1} \\ N_{MF,t+1} \\ N_{LF,t+1} \end{bmatrix} \quad \text{eqn 3a}$$

The asymptotic rate for this release period matrix, $\lambda_{R,1}$, is 1.01. If we add a 5% increase in survival, up to a maximum of 0.995 per stage class (see Methods), this model becomes:

$$\begin{bmatrix} N_{SV,t} \\ N_{MV,t} \\ N_{LV,t} \\ N_{MF,t} \\ N_{LF,t} \end{bmatrix} = \begin{bmatrix} 0.76 & 0.14 & 0 & 0.68 & 2.03 \\ 0.03 & 0.61 & 0.04 & 0.43 & 0.04 \\ 0 & 0.03 & 0.31 & 0.06 & 0.13 \\ 0 & 0.16 & 0.05 & 0.39 & 0.02 \\ 0 & 0.05 & 0.59 & 0.12 & 0.80 \end{bmatrix} \times \begin{bmatrix} N_{SV,t+1} \\ N_{MV,t+1} \\ N_{LV,t+1} \\ N_{MF,t+1} \\ N_{LF,t+1} \end{bmatrix} \quad \text{eqn 3b}$$

with $\lambda_{R,2} = 1.04$. These matrices suggest that balsamroot populations could plausibly grow during the period between picloram degradation and knapweed reinvasion.

We used these matrices to predict the long-term consequences of different herbicide return intervals. Based on these models, using herbicide can be beneficial or detrimental for balsamroot, depending on how often it is used (Fig. 3). For lower persistence times, λ_{net} is highest when herbicide is sprayed every $P + L$ years, that is the number of years that herbicide persists in the soil plus the number of years it takes knapweed to reinvade. If the herbicide persists for a long time in the soil, then all spraying intervals lead to lower population growth rates (λ_{net}). The switch from potentially-good to always-bad occurs when λ_{net} for $[M_H]^P [M_R]^L$ is less than λ_w . The relationship between λ_{net} and return interval is a much steeper slope below the optimum than above it. In other words, it is better to spray too seldom than too often, at least from the perspective of arrowleaf balsamroot. This result occurs as long as the direct effects of the herbicide are worse than the effects of competition with weeds.

Discussion

To effectively use herbicides and other management tools for natural areas, we need to understand all of their potential implications. Other studies have reported impacts of herbicide

Table 2. Summary of parameters and variables used in population models

Parameter	Definition
N_t	Total no. of arrowleaf balsamroot plants in year t , summed across stage classes
$N_{SV,t}$	No. of plants with 1–2 leaves in year t , small vegetative plants + new recruits
$N_{MV,t}$	No. of plants with 3–14 leaves in year t , medium vegetative plants
$N_{LV,t}$	No. of plants with ≥ 15 leaves in year t , large vegetative plants
$N_{MF,t}$	No. of plants with 3–14 leaves and ≥ 1 inflorescence in year t , medium flowering plants
$N_{LF,t}$	No. of plants with ≥ 15 leaves and ≥ 1 inflorescence in year t , large flowering plants
M_W	Projection matrix for ‘weed competition’ period, with weeds and no herbicide
M_H	Projection matrix for ‘herbicide’ period, i.e., while herbicide persists in the soil
M_R	Projection matrix for ‘release’ period, after herbicide degrades and before weeds reinvade
λ_W	Long-term population growth rate of ‘weed competition’ matrix
λ_H	Long-term population growth rate of ‘herbicide’ matrix
λ_R	Long-term population growth rate of ‘release’ matrix
M_{net}	Projection matrix for change in abundance over one complete cycle of herbicide spraying, recovery, and weed reinvasion
λ_{net}	Realized average annual rate of change over repeated cycles of herbicide spraying, recovery, and weed reinvasion, i.e., the I th root of the leading eigenvalue of M_{net}
I	Return interval, total number of years between herbicide application
P	Persistence time, number of years herbicide persists in soil after application
L	Lag time, number of years between herbicide degradation and weed reinvasion
T_H	Length of ‘herbicide’ period, for a given return interval
T_R	Length of ‘release’ period, for a given return interval
T_W	Length of ‘weed competition’ period, for a given return interval
SV	Stage class for plants with 1–2 leaves in year t , small vegetative plants
MV	Stage class for plants with 3–14 leaves in year t , medium vegetative plants
LV	Stage class for plants with ≥ 15 leaves in year t , large vegetative plants
MF	Stage class for plants with 3–14 leaves and ≥ 1 inflorescence in year t , medium flowering plants
LF	Stage class for plants with ≥ 15 leaves and ≥ 1 inflorescence in year t , large flowering plants

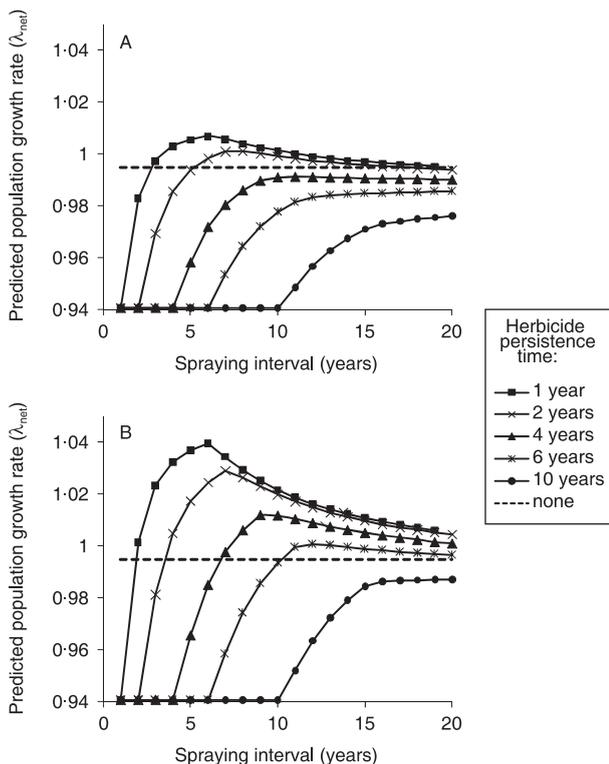


Fig. 3. Predicted population growth rate vs. spraying return interval and persistence time in soil. ‘None’ refers to no herbicide use. (A) 65% increase in fecundity during the release period; (B) 5% increase in survival and 65% increase in fecundity during the release period.

application for invasive plant control on native plant biomass and percentage cover (Marrs 1985; Tyser *et al.* 1998; Rice *et al.* 1997; Rice and Toney 1998; Sheley *et al.* 2006); these studies indicate that some herbicides can affect non-target forbs as much as target weeds, whereas other herbicides kill target species but are non-lethal, or less lethal, to native forbs. As far as we are aware, our study is the first to investigate long-term demographic consequences. We found that non-target effects of herbicide on growth and survival of native plants that seem negligible over a few years have the potential to cause population declines over longer time periods.

Our short-term results are consistent with most previous work in this system. We found that there was no difference in the leaf density between sprayed and unsprayed plots throughout the study, which is consistent with no significant change in leaf area (Rice *et al.* 1997; Rice and Toney 1998). Rice *et al.* (1997) and Rice and Toney (1998) concluded that native plant species and communities, respectively, recover rapidly after a low rate of picloram application, but they only examined percentage cover and biomass or crude indices of species richness (presence or absence in large plots). Y. Ortega and D. Pearson (unpublished data) also showed that herbicide killed balsamroot seedlings and suppressed flowering and seed production for at least 3 years post-treatment, suggesting the potential for herbicides to have important long-term demographic impacts on perennial native forbs. They also noted that picloram did little to release arrowleaf balsamroot from spotted knapweed impacts 3 years after treatment,

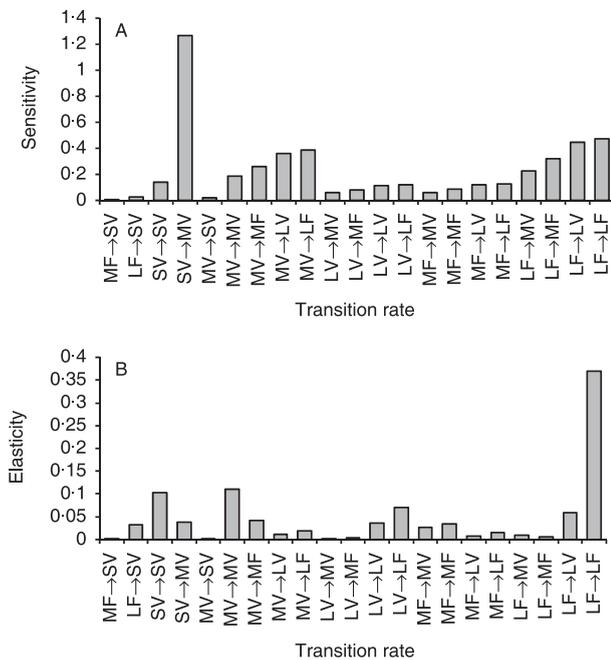


Fig. 4. Sensitivity and elasticity analyses, based on the transition matrix for unsprayed plots, M_w , calculated using the standard analytical formula (Caswell 2001; Morris & Doak 2002). See abbreviations for stage classes in Table 2.

consistent with the persistent effects of picloram we report in this study. Our results, however, emphasize the importance of using population models to interpret short-term impacts in a long-term context.

Our demographic approach to analysing the effects of herbicide application differs from prospective approaches such as sensitivity and elasticity analysis that evaluate management strategies before they are implemented (see reviews by Heppell, Pfister & de Kroon 2000; Menges 2000; Morris and Doak 2002). Most often, these approaches combine demographic models for unmanaged populations (e.g. M_w) with qualitative estimates of the direction in which vital rates are likely to be affected by management. For comparison with these studies, we calculated matrix element sensitivities and elasticities using M_w , the matrix from unsprayed plots (Fig. 4). Recruitment rates had low sensitivities, and transitions to flowering had only slightly higher sensitivities than transitions to similar-sized vegetative plants (e.g. compare the sensitivity of LF→LF to LF→LV). Elasticities indicated a greater importance of recruitment; flowering by large plants (LF→LF) had the largest elasticity, and elasticity was also relatively high for successful recruitment from these plants (LF→SV; Fig. 4B). Both results are consistent with patterns in most long-lived perennial plants (Silvertown *et al.* 1993; Franco and Silvertown 2004); survival of mature plants is more important than fecundity *per se*. These methods could be used to conclude incorrectly that management that negatively affects fecundity, but not survival, would not severely impact population dynamics, or that the effects are ambiguous. In reality, both analyses compare the impacts of small changes in vital rates, whereas herbicide application led to large

changes in flowering and recruitment rates and subsequent large changes in population growth rates. If they are feasible, short-term experiments, such as ours, that quantify the magnitude of expected changes in vital rates, greatly improve our ability to predict long-term consequences of management (see also Lesica and Shelly 1996; Lesica 1999; Baxter *et al.* 2006; Lubben *et al.* 2008).

In many ways, herbicide management is analogous to the impacts of natural disturbances, such as hurricanes (Horvitz, Tuljapurkar & Pascarella 2005), floods (Menges 1990) and fires (Schultz and Crone 1998; Menges and Quintana-Ascencio 2003). These disturbances have a negative short-term impact, but typically improve conditions for surviving or recolonizing plants, and are often necessary for long-term persistence. In the same way, the net effect of herbicide use is only positive if the short-term negative effects are followed by a period when herbicide is no longer persistent in the soil, but competition by weeds and other native species is reduced. Relatively high flowering in 2007 in sprayed plots indicates that the effects of herbicide are starting to dissipate (Fig. 2). The analogy between our study and these other studies of responses of perennial plants to other disturbances suggests that the general pattern illustrated by our models is likely to extend to changes in abundance of other forbs in response to herbicide management. However, if there is no release period, or if it does not last long enough to make up for the negative impacts of herbicide, herbicide will only accelerate the decline of balsamroot populations. Similarly, use of broad-leaved herbicides may stimulate growth of grasses, which could in principle have larger negative impacts than competition with knapweed. Most studies of herbicide use in natural areas – including ours – assume that this release period will eventually occur, but we are not aware of any that have documented dynamics at these long time-scales.

Throughout this study, we have referred to effects of herbicide on balsamroot as if they reflected continuous effects of persistent soil residues. This assumption reflects our observation that balsamroot flowering may recover faster in areas with more well-drained soils (E. Crone, conversations with local landowners who use Tordon). However, long-lived perennial plants such as balsamroot have the capability to store and reallocate resources over time; reproductive effort in 1 year often reflects environmental conditions over three or more previous years (Primack and Stacy 1998; Ehrlén and van Groenendael 2001; Crone and Lesica 2006). Therefore, persistent effects of herbicide application probably reflect some combination of direct effects of picloram residues in the soil and indirect effects mediated by changes in resource stores in response to stress in previous years. Disentangling these effects is beyond the scope of this study because we did not measure picloram residues in soil or stored resources of individual plants. However, investigation into the physiological mechanisms of herbicide effects on fecundity could help extrapolate results among sites, and would be a valuable avenue of future research.

Our hope is that this case study will raise awareness of the potential long-term non-target effects of herbicide in natural

areas, and the importance of explicitly evaluating return intervals among years, as well as dose and timing within years. Herbicide use may be a necessary component of natural areas management, especially for areas like our study site, where funds are limited and weed control is legally mandated (Montana House Bill 395). However, even in this context, our models indicate the importance of minimizing non-target impacts of herbicide and 'stretching' the lag period before weed reinvasion as long as possible. At a minimum, the optimal herbicide application interval is $P + L$, the length of time the herbicide persists in the soil plus the number of years between herbicide degradation and weed reinvasion (see Results). As defined in our models, 'weed reinvasion' occurs when the competitive effects of weeds become substantial, not when weed seedlings first appear. Depending on the target weed and the site conditions, hand weeding and grazing may be feasible to prevent weed reinvasion, even if they are not feasible ways to control the initial infestation. Secondly, spot application instead of broadcast spraying could minimize non-target impacts as well as prevent reinvasion. Thirdly, if broadcast application is the only option, the optimal return interval from a site perspective occurs after target weed species becomes dense enough to have competitive impacts on native plant community.

In conclusion, we reiterate that herbicide management of natural areas differs fundamentally from use in agricultural areas, because the dynamics of non-target species in natural and semi-natural areas are rarely under direct management control. This example is only the beginning of a very broad and largely unexplored research area in environmental management. We encourage future research to evaluate herbicide management options in the context of population and community dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Transition frequencies among life stages in sprayed and unsprayed plots

Table S2. χ^2 test of homogeneity of transition frequencies (pooled across years) between sprayed and unsprayed plots. Across all stage classes, $\chi^2 = 157.8$, $df = 20$, $P < 0.001$

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