

## THE IMPACT OF INVASIVE GRASSES ON THE POPULATION GROWTH OF *ANEMONE PATENS*, A LONG-LIVED NATIVE FORB

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**Abstract.** Negative impacts of invasive plants on natives have been well documented, but much less is known about whether invasive plants can cause population level declines. We used demographic models to investigate the effects of two invasive grasses on the demography and population growth of *Anemone patens*, a long-lived native perennial of North American grasslands. Demographic data of *A. patens* growing in patches characterized by *Bromus inermis*, *Poa pratensis*, or native grasses were used to parameterize integral projection models. Models based on both average conditions and those allowing for environmental stochasticity indicate that *A. patens* is slowly increasing in patches of native grass ( $\lambda = 1.02$ ) and declining in patches of invasive grasses, particularly those dominated by *B. inermis* ( $\lambda = 0.93$ ). Extinction probabilities indicate that *A. patens* should persist in native grass patches, but has a much higher probability of extinction in *Bromus* patches compared to *Poa* patches. While sensitivity analyses showed that survival had the biggest effect on population growth rates in all habitats, results of a Life Table Response Experiment (LTRE) revealed that slower individual growth rates in patches of invasive grasses contributed the most to the observed reduction in population growth. These results suggest that invasive grasses may cause slow declines in *A. patens*, despite short-term coexistence, and that controlling *B. inermis* only would not be sufficient to ensure *A. patens* persistence.

**Key words:** *Anemone patens*; *Bromus inermis*; demography; impact; integral projection model; invasive grasses; Life Table Response Experiment (LTRE); *Poa pratensis*; population growth; quasi-extinction probability; sensitivity; stochastic growth rate.

### INTRODUCTION

Exotic plants now dominate many landscapes, especially grasslands in western North America, where invasive grasses have replaced many native perennial grasses (Seabloom et al. 2003, Corbin and D'Antonio 2004). Traditionally, the decline of native abundance in highly invaded areas has been attributed to strong competition between natives and exotics. This competitive superiority of exotics may be driven by their ability to outcompete natives for light, soil resources, or through allelopathy (e.g., Huenneke and Thompson 1995, Callaway and Aschehoug 2000, Alvarez and Cushman 2002). More recently, this explanation for exotic dominance has been questioned. For example, MacDougall and Turkington (2005) proposed that disturbance, coupled with the superior colonizing ability of exotics, is a possible alternative mechanism for exotic dominance and the resulting declines in native abundance. Other studies have shown that even though natives can outcompete exotics, seed limitation prevents them from becoming more common in heavily invaded areas (Seabloom et al. 2003, Corbin and D'Antonio

2004). Distinguishing between these mechanisms centers on understanding the life stages of natives that are most greatly influenced by exotics, and then determining how those life stages contribute to the overall population growth of natives.

Addition and removal experiments have contributed to our current understanding of competition between natives and exotics (Levine et al. 2003), by measuring effects of exotics on native growth, biomass, or fecundity (e.g., Huenneke and Thompson 1995, Brooks 2000, Alvarez and Cushman 2002). These experiments indicate the strength of the competitive interaction between natives and exotics, but they do not reveal how competition affects long-term population persistence of natives. This is because effects on individual growth or fecundity during one growing season or generation may not translate to overall effects on population size (Goldberg and Barton 1992). To fully understand whether exotic plants are causing declines in native populations, we need to know how they affect native population growth and size over longer time spans than experiments typically provide.

Population modeling has been underused as an approach to understanding the impacts of exotics on native plants. Demographic models have been used to investigate the demography of exotic plants in recipient communities (Meyer and Schmid 1999, Parker 2000,

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Grigulis et al. 2001), and are frequently used in conservation biology to assess the population viability of rare plants (Menges 2000). However, their power to examine how populations change over multiple generations has not been fully used to assess the impacts of exotic plants on native population growth (but see Lesica and Shelly 1996, Thomson 2005). One advantage of using population models to quantify the impact of exotics on natives is that one can also determine which life history stages of natives are most impacted by exotics, suggesting the particular mechanism by which exotics gain dominance over natives.

Effects of invasive species on population dynamics of natives depend on both average population growth rates, and how these rates vary over time (Fagan et al. 2001, Inchausti and Halley 2003). Population models that do not separate environmental stochasticity from other sources of error can lead to incorrect conclusions (Clark 2003, Childs et al. 2004), yet relatively few studies of plant demography explicitly partition variation at different levels. Thus, a secondary goal of our paper is to serve as an example of how to separate different sources of variation in individual growth, survival, and fecundity, and translate these differences to population dynamics. First, we used mixed models to fit size-dependent functions to individual vital rates, while explicitly partitioning variance among years (environmental stochasticity), locations in space, fixed differences among individuals, and observation/sampling error. Random effects in mixed models have a long history of use in ecology, but have been used primarily to calculate significance tests (e.g., Sokal and Rohlf 1995, Gotelli and Ellison 2004). In contrast, we are interested in a random effect of variance among years as a key parameter for projecting population dynamics (e.g., Childs et al. 2004). Next, we used integral projection models (Easterling et al. 2000) to project population dynamics directly from fitted statistical models. Integral projection models are similar to size-based matrix models, but use continuous relationships between size and vital rates, rather than dividing plants into discrete size classes (e.g., Childs et al. 2003, Metcalf et al. 2003, Rose et al. 2005).

We used population models to analyze long-term demographic data of prairie crocus, *Anemone patens* L. (Ranunculaceae). Efforts to improve forage quality and provide erosion control in western North American grasslands since the early 1900s have often involved sowing seed of several nonnative pasture grasses, including *Bromus inermis* (smooth brome) and *Poa pratensis* (Kentucky bluegrass). At our study site in southwest Alberta (Canada), native prairie is dominated by native bunchgrasses such as *Festuca scabrella* (rough fescue), but the site has been invaded in the past 2–3 decades by both *B. inermis* and *P. pratensis*. Attempts to control *Bromus* with herbicide increased the abundance of *Poa* (Brown 1997). These species are functionally different from the native bunchgrasses in that they form

continuous stands in contrast to discrete clumps of natives (Grilz and Romo 1995, MacDougall and Turkington 2005). The goal of this study was to address the impacts of these invasive grasses on the demography and population dynamics of *A. patens*. This forb is long lived and stores resources underground, and so it is a good model for how other native species with similar life histories might respond to invasive grasses. Since the invasion is relatively recent, our study area provides the opportunity to examine if exotics limit native population growth.

We parameterized integral projection models using seven years of data from three different patch types in the same study area: native prairie, and *Poa* and *Bromus* patches. We used these models to address the following questions: first, do nonnative grasses negatively impact the population growth rate ( $\lambda$ ) of *A. patens*? Second, if  $\lambda$  is lower in patches of invasive grasses, which vital rates are most affected? Finally, how does temporal stochasticity affect  $\lambda$  in each patch type, and does the probability of extinction differ between patch types?

## METHODS

### *Field monitoring*

We used data from long-term demographic monitoring of *A. patens* from 1999 to 2005. In 1999, we established a 0.4-ha monitoring area in a grassland located at the Ann and Sandy Cross Conservation Area, ~40 km southwest of Calgary, Alberta, Canada. Patches of native bunchgrasses (primarily *Festuca scabrella* and *Danthonia spicata*, with some *Stipa* spp.) were interspersed with patches dominated by each of two invasive rhizomatous grasses, *Bromus inermis* and *Poa pratensis*. The invasive grasses appeared in Alberta ca. 1900, but were not present in our study area until the mid-1970s to 1980s (R. Rempel, *personal communication*). The distribution of the two invasive grasses did not appear to correspond to obvious abiotic gradients such as slope, elevation, or aspect. Native ungulates are present on the study area and both pellet piles and grazing have been observed in the plots (E. Crone, *personal observation*).

To quantify differences in plant communities and select sites for demographic monitoring, we divided the center of our site into 108 5 × 5 m squares (grid cells). We initially characterized grid cells as occupied by native grasses, *Poa*, or *Bromus*, based on which grass type was most conspicuous. To attain a relative measure of grass cover in each patch type, we counted the number of times pins on a 10-cm grid intercepted native (*F. scabrella* and *D. spicata*) and introduced (*B. inermis* and *P. pratensis*) grasses. This measure is comparable within but not among species, because it assesses the presence or absence of each grass species at the nodes of the grid, but does not accurately reflect differences in biomass. Due to the different morphologies of the grasses, clumped grasses (natives) had many fewer intercepts relative to their biomass than diffuse grasses (*P. pratensis*). Using these data, we selected five grid cells

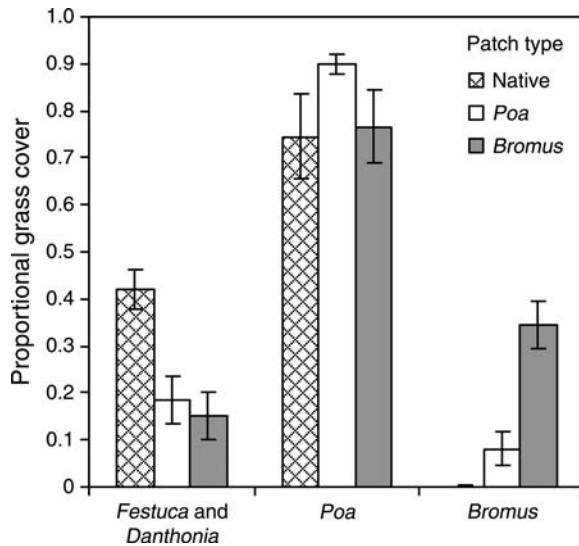


FIG. 1. Mean relative cover of *Bromus inermis*, *Poa pratensis*, and native bunchgrasses (primarily *Festuca scabrella* and *Danthonia scabrella*) in 2000 in each patch type used for long-term monitoring. Error bars indicate one standard error of the mean. Proportions sum to  $>1$ , due to overlap of grasses.

characterized by native grasses and five characterized by each of the invasive grasses. The chosen grid cells were interspersed across the site and each contained at least 10 *A. patens* individuals. We used the center  $1 \times 5$  m of each grid cell as a walking corridor and monitored all individual plants in the remaining  $20 \text{ m}^2$ .

Patches classified as native, *Bromus*, or *Poa* differed in the relative grass cover of each species (Fig. 1). Each patch type had more of the grass that characterized it than the other patch types. For example, while *P. pratensis* was present in most grid cells, it was more abundant in patches identified as *Poa* than in either *Bromus* or native patches. Similarly, patches classified as native had more *F. scabrella* and *D. spicata* than the other patch types, and those classified as *Bromus* had more *B. inermis* than the other patch types. The cover of grasses in each grid cell has not changed significantly over the course of the study; each patch type remains visually distinct (E. Crone, *personal observation*). Hereafter, we refer to the grid cells in each category as native, *Bromus*, or *Poa* patches.

*A. patens* is one of the earliest plants to flower in spring. Flowers emerge in late April or early May, before grasses begin growing. In *Bromus* and *Poa* patches, *A. patens* flowers must push up through a layer of thatch formed by grass litter from the previous growing season. The layer of thatch in *Poa* patches tends to be finer and occur in tufts, in contrast to a continuous layer of coarse thatch in *Bromus* patches. Leaves of *A. patens* emerge in late May and early June, by which time the grasses have also begun growing, and persist through July; vegetative growth of both *A. patens* and the grasses occurs during this time. We permanently marked

individuals with aluminum tags and mapped their position within each grid cell; in each year, we relocated  $>99\%$  of tags from previous years. Each year, we counted the number of leaves and flowers on plants in late May (at peak flowering/fruitletting) and the number of leaves and flowers in early July (peak leaf mass). *A. patens* does not reproduce rhizomatously, but stems occasionally branch underground. We considered ramets to be from the same "individual" if they were within 2 cm of each other above ground.

#### Model structure

Integral projection models are similar to traditional demographic matrix models in that survival, growth, and fecundity are assumed to depend on individual plant size (Easterling et al. 2000). However, they incorporate continuous functions for size-based growth, survival, and fecundity. They also require less data to estimate, because size-based functions can typically be described using 2–4 parameters. Analyses developed for matrix models, such as sensitivity and elasticity, can also be used in integral projection models (Easterling et al. 2000, Childs et al. 2003).

An integral projection model describes the distribution of plants of size  $x$  at time  $t$ ,  $(n(x, t))$ , and predicts the proportion of individuals of size  $y$  in time  $t + 1$  by

$$\begin{aligned} n(y, t + 1) &= \int_{\Omega} [p(x, y) + f(x, y)]n(x, t)dx \\ &= \int_{\Omega} k(y, x)n(x, t)dx \end{aligned} \quad (1)$$

where  $k$  is a kernel that describes all of the possible transitions from plants of size  $x$  to plants of size  $y$ , integrated over all possible sizes ( $\Omega$ ). The kernel is composed of two functions that describe individual survival and growth ( $p$ ) and fecundity ( $f$ ), both of which depend on plant size.

More specifically, individual growth and the probability of survival are described as:  $p(x, y) = s(x)g(x, y)$ , where  $s(x)$  is the probability of a plant of size  $x$  surviving until the next year and  $g(x, y)$  is the probability of an individual of size  $x$  growing to size  $y$ . Fecundity is described as  $f(x, y) = f_n(x)c(f_n)f_d(x, y)$ , where  $f_n(x)$  is the number of flowers made by individuals of size  $x$ ,  $c(f_n)$  is the relationship between flowers produced in year  $t$  and recruits in year  $t + 1$ , and  $f_d(x, y)$  is the probability that a seedling of size  $y$  is produced by an individual of size  $x$ . Similar to other studies, we assumed there was no relationship between maternal plant size and seedling size (Childs et al. 2003, Rose et al. 2005).

#### Analysis of demographic rates

A small fraction of *A. patens* plants go dormant each year (i.e., they produce no aboveground leaves or flowers). Therefore, we analyzed survival using capture–recapture models (Alexander et al. 1997, Shefferson et al. 2001, Kéry and Gregg 2003), which statistically

TABLE 1. Model structures and functional forms for error distributions.

Vital rate	Model	Sampling error	Stochasticity
Survival	$\phi$ ( size-independent)	beta	beta
Growth	$S_{t+1} = \exp(a_0)(S_t + 0.5)^{a_1} - 0.5$	normal	normal
Fecundity (flowering)	$F_{t+1} = \exp(b_0)(S_t + 0.5)^{b_1} - 0.5$	normal	$b_0$ normal, $b_1$ lognormal
Recruitment	$R_{t+1} = c_0 F_{t+1} = c_0 [\exp(b_0)(S_t + 0.5)^{b_1} - 0.5]$	normal	$b_0$ normal, $b_1$ lognormal
Size distribution for recruits	$\ln(S_R)$	normal	normal

Notes: Equations for survival ( $\phi$ ) and size ( $S_t$ ) form the survival and growth function  $p(x, y)$ , and equations for fecundity ( $F_t$ ), recruitment ( $R_t = c_0 F_t$ ), and offspring size ( $\ln[S_R]$ ) form the fecundity function  $f(x, y)$ .

separate temporary dormancy from death by simultaneously solving for maximum likelihood parameters for survival and transitions to the dormant state. We tested whether survival and detectability differed among years and grass patch types. We did not test for size-dependent survival, because survival was very high (see *Results*), giving us very little statistical power to evaluate differences among individual plants. Analyses were conducted using Program MARK (White and Burnham 1999).

We analyzed individual growth and fecundity using linear mixed models, in which size and flower production depended on size in the previous year (Table 1). We tested whether these rates depended on two fixed factors, plant size (number of leaves), and grass patch type (native, *Bromus*, or *Poa*), and three random factors, year, grid cell identity, and plant ID. The year term allowed us to explicitly model environmental stochasticity separately from estimation error. The grid cell and plant ID terms allowed us to account for background spatial heterogeneity not linked to grass type (grid cell) and repeated measures of individuals (plant ID).

We analyzed seedling recruitment using 5 × 5 m grid cells as replicates, and tested whether recruitment depended on the number of flowers in each plot in the previous year, the grass patch type, grid cell identity, and year. This is a reasonable estimation, because *A. patens* seeds are plumed to facilitate wind dispersal; dispersal distances for other plumed forbs include a median dispersal distance of ~1.7 m in *Senecio jacobaea* (McEvoy and Cox 1987), and an average distance of ~1.5 m in *Tragopogon dubius* (Greene and Johnson 1989). *A. patens* seeds germinate readily (Green and Curtis 1950), and do not form a persistent seed bank (Morrison 2002). We also analyzed size of recruits in the three different grass patches to test if size of new plants depended on the grass patch, grid cell identity, year, and the interactions. Again, year and grid cell were treated as random factors.

For each model, we tested statistical significance of random factors and all factors in survival models using likelihood ratio tests ( $\chi^2$  statistic). Fixed factors in mixed models were tested using Type III *F* tests. To obtain parameter estimates for demographic models, we reran models including only the statistically supported ( $P < 0.10$ ) variables or interactions (Table 2). All estimates of

size were log-transformed using natural logarithms ± 0.5. All analyses, except survival, were done with the “MIXED” procedure in SAS (SAS 9.0, SAS Institute 2002).

Model simulations and analyses

For the three types of grass patches, we used integral projection models (Eq. 1) to calculate  $\lambda$ , the population

TABLE 2. Statistical tests of possible factors to include in *A. patens* integral projection models.

Factors	$\chi^2$ or <i>F</i>	df	<i>P</i>
<b>Survival</b>			
Grass	22.0	12	<0.001
Year	16.5	15	0.005
Grass × detectability	14.4	12	0.004
Year × detectability	14.2	15	0.019
<b>Growth</b>			
Size	509.6	1, 4105	<0.001
Grass	0.8	2, 10	0.533
Size × grass	11.7	2, 4105	<0.001
Grid cell†	17.1	1	<0.001
Plant ID†	10.6	1	<0.001
Year†	0.9	1	0.192
Grass × year†	7.4	3	0.002
Size × year†	1.5	1	0.083
Size × grass × year†	0.1	3	0.960
<b>Flowering</b>			
Size	9.2	1, 5	0.029
Grass	0.3	2, 4100	0.768
Size × grass	3.2	2, 10	0.086
Grid cell†	16.3	1	<0.001
Plant ID†	32.2	1	<0.001
Year†	1.8	1	0.061
Grass × year†	0.0	3	1.000
Size × year†	8.6	1	<0.001
Size × grass × year†	4.6	3	0.027
<b>Recruitment</b>			
Flowers × grass	0.9	2, 70	0.406
Flowers × grid cell†	4.2	1	0.004
Flowers × year†	3.1	1	0.012
Flowers × year × grass†	0.1	3	0.992
<b>Recruit size</b>			
Grass	5.5	2, 434	0.004
Grid cell†	0.6	1	0.273
Year†	2.4	1	0.029
Grass × year†	0.0	3	1.000

Notes: Random factors (†) and all factors in survival models were tested using likelihood ratio tests ( $\chi^2$  statistic). Fixed factors in mixed models were tested using Type III *F* tests, with numerator and denominator degrees of freedom listed under df.

growth rate (Easterling et al. 2000). Integral projection models generate an approximating matrix, from which typical matrix properties such as  $\lambda$  (the dominant eigenvalue) and sensitivities can be derived (Easterling et al. 2000, Caswell 2001, Morris and Doak 2002). The appropriate number of size categories in the approximating matrix is determined by choosing the smallest matrix size that generates the same value of  $\lambda$  as larger matrices. We incorporated estimation error in the calculations of  $\lambda$  using the distribution of statistics from 1000 stochastic matrices. These matrices were generated by sampling from beta, normal, or log-normal distributions defined by the mean and standard error for coefficients from generalized linear models (Table 1) of each vital rate (sampling error in the Appendix).

We calculated sensitivities of  $\lambda$  to vital rates in each grass patch type to evaluate if the importance of vital rates differed between types of grass patches. We obtained these estimates using manual perturbations of coefficients that differed among grass types. Sensitivity, then, is the ratio of the observed change in  $\lambda$  to the perturbation size. Perturbations of 0.01, 0.05, and 0.10 gave similar results, so we present results from perturbations of 0.05. As above, we calculated estimation error using the distribution of sensitivities from 1000 stochastic matrices, sampled from distributions defined by the mean and standard error (sampling error in the Appendix).

We used a Life Table Response Experiment (LTRE; Caswell 2001) to determine which vital rates best explained differences in  $\lambda$  between native, *Poa*, and *Bromus* grass patches. This approach decomposes differences in  $\lambda$  between treatments into contributions by each vital rate. By indicating which vital rate contributes most to differences in  $\lambda$ , this approach also allows for inference into the mechanisms of impact by the invasive grasses.

For the LTRE, we considered the two types of invasive grass patches (*Poa* and *Bromus*) as the treatments and the native grass patches as the control. We calculated contributions of each vital rate ( $i$ ) with parameter value ( $p_i$ ) as follows (Caswell 2001):

$$\Delta\lambda \approx \sum_{\text{all } p_i} \Delta p_i \left( \frac{\partial \lambda}{\partial p_i} \right) \Bigg|_{p_i \text{ native}} \quad (2)$$

where  $\Delta\lambda$  is the difference between  $\lambda$ 's and  $\Delta p_i$  is the difference in parameter values of a vital rate in each treatment (*Poa* or *Bromus* patch) and the control (native grass). Sensitivities for each vital rate were calculated from the model for native grass patches. Thus, the contribution of each vital rate is the difference between the vital rate in the invasive and native grass patches multiplied by the sensitivity of the vital rate in the native grass patches. Sensitivities used in LTRE analyses are typically calculated from a matrix that is halfway between the control and the treatment (Caswell 2001). Because our models were generated from nonlinear

functions for growth and flowering, coefficients chosen at the midpoint between the two values might have generated sensitivities that were not a fair comparison. Instead, we chose a simpler approach and used the sensitivities for native grass patches. The contributions of each vital rate summed to the differences in  $\lambda$  for both treatments (see *Results*), so this was an adequate approach for our system.

Finally, we incorporated yearly variation of vital rates into a stochastic model for each community type to estimate how year-to-year variation might change population persistence. If invasive grasses make vital rates more variable, they could have greater negative impacts on *A. patens* than those predicted by the deterministic model. Among-year variance was calculated from the random year effects in mixed models (year  $\times$  grass, and year  $\times$  grass  $\times$  size) and from annual values from capture–recapture models (environmental stochasticity in the Appendix). We calculated yearly values for each coefficient that described a time-dependent vital rate and used those to generate a correlation matrix. For each habitat in each year, coefficients were randomly chosen from this variance–covariance matrix for all vital rates and used in Eq. 1 to calculate a new population size. We ran 50-year simulations starting at the stable size distribution in each habitat, and calculated the geometric mean of  $\lambda$  at the end of 50 years. We included sampling error by calculating 1000 geometric means, where parameter values were sampled from a distribution defined by the mean and standard error (sampling error in the Appendix). We also calculated the probability of quasi-extinction for each simulation run using an inverse Gaussian distribution (Lande and Orzack 1988, Dennis et al. 1991, Morris and Doak 2002). Specifically, we calculated the probability that a population of 1000 plants in each grass patch type would drop below a quasi-extinction threshold of 100 plants in 50 years, based on the geometric mean  $\lambda$  and variance of log-transformed  $\lambda$  from that simulation run. We report the average extinction probability and the 95% confidence intervals over 1000 simulations in each patch type.

## RESULTS

All prairie crocus vital rates were significantly different in native vs. invasive grass patches, except the relationship between number of flowers and number of recruits (Table 2, Fig. 2). Survival was highest in the native grass patches, followed by *Poa* and *Bromus*. The same pattern was true for growth as well as fecundity, where both size in the next year and number of flowers was higher in native grass patches than in the invasive grass patches (Fig. 2B, C). In contrast, mean recruit size was highest in *Bromus* patches (3.8 leaves), followed by *Poa* (3.4 leaves) and then native grass patches (2.8 leaves; Table 2, Fig. 2C). The relationship between flower production and recruitment did not differ among grass patch types, although it did differ among grid cells

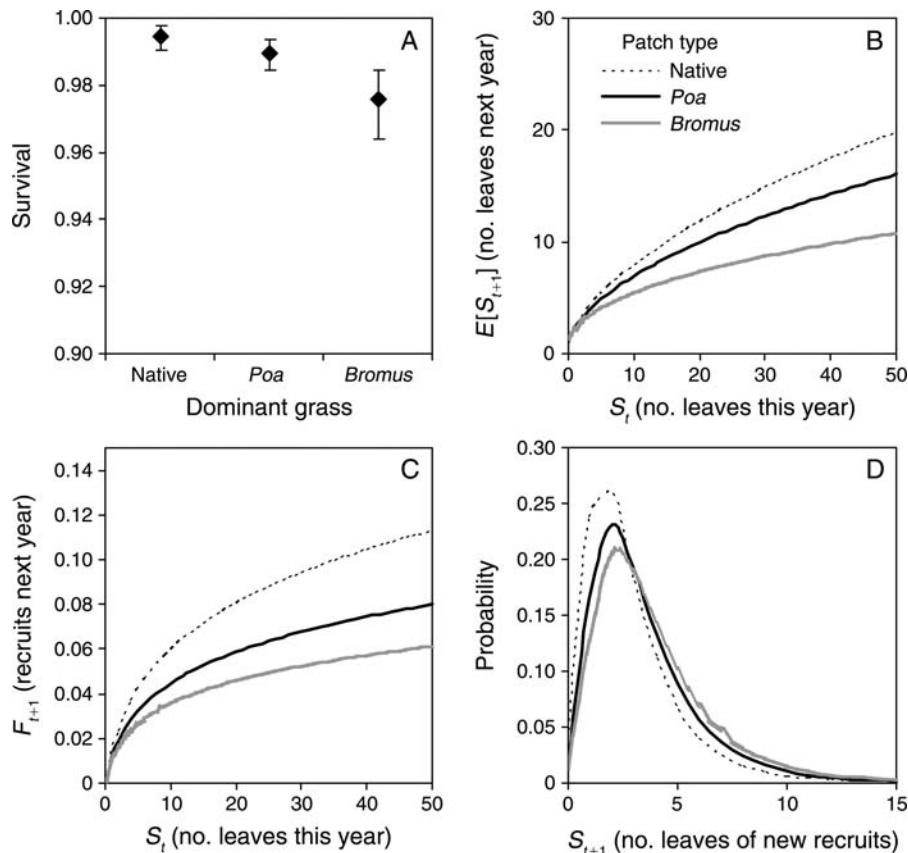


FIG. 2. Grass-patch-specific vital rates for *A. patens*: (A) mean survival (error bars indicate 95% confidence limits); (B) predicted individual growth; (C) predicted recruitment; (D) size distribution of new recruits. As defined in Table 1,  $S_t$  refers to plant size in year  $t$ ,  $R_{t+1}$  refers to the number of recruits produced by a plant in year  $t + 1$ , and  $E[S_{t+1}]$  is standard mathematical notation for the expected size of a plant in year  $t + 1$ .

and years (Table 2). On average, each flower produced 0.178 recruits (Appendix).

Population growth ( $\lambda$ ) in an average year was depressed by the invasive grasses (*Poa* and *Bromus* patches) compared to the native grasses (Fig. 3). Moreover,  $\lambda$  was only estimated to be  $>1$ , indicating population persistence, in the native grass patches. In contrast, 95% confidence intervals for  $\lambda$  in *Bromus* patches do not overlap 1, indicating eventual population extinction. The two invasive grasses do not have equally negative effects on *A. patens*; 95% confidence limits for  $\lambda$  in *Poa* vs. native patches overlapped considerably, suggesting that some *Poa* patches are more benign for *A. patens* than are *Bromus* patches.

Survival had the highest sensitivity in all habitats, while sensitivity for offspring size was very close to zero (Fig. 4A). The relative importance of vital rates differed among habitat patches, with survival being somewhat less important and growth more important in *Bromus* patches. Results of the deterministic LTRE indicate that the reduction in individual growth of *A. patens* contributed the most to reductions in deterministic  $\lambda$  in invaded grass patches (Fig. 4B). Using sensitivities

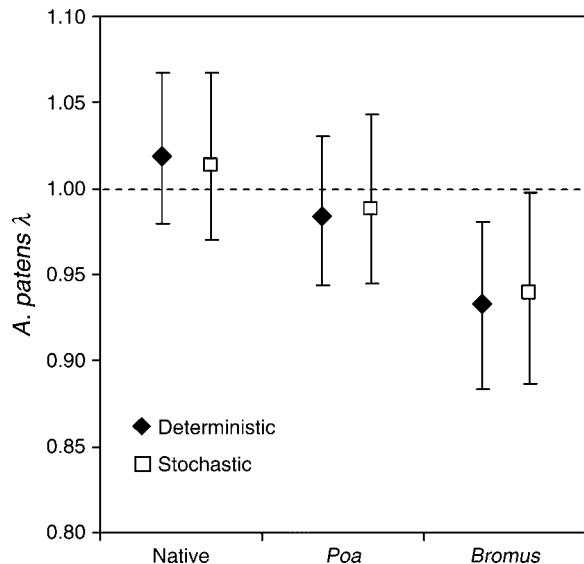


FIG. 3. Projected population growth rate ( $\lambda$ ) for *A. patens* in each type of grass patch. Error bars indicate 95% confidence limits calculated by resampling parameters from error distributions defined in Table 1, and therefore they represent sampling error, not environmental stochasticity.

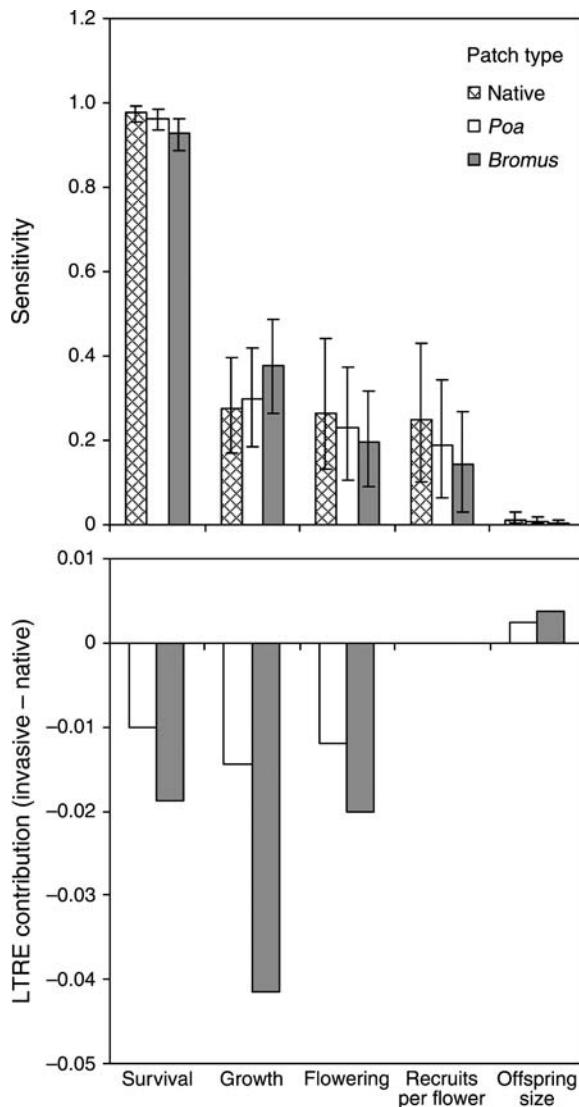


FIG. 4. (A) Sensitivity of deterministic  $\lambda$  to manual perturbations of each vital rate. Error bars indicate 95% confidence limits and represent sampling error. (B) Life Table Response Experiment (LTRE) contribution of each vital rate to  $\Delta\lambda$  (invasive grass - native).

from the model for native grass patches was an adequate approximation, because the LTRE contributions summed to the differences in  $\lambda$  between invasive and native grass patches for both *Poa* and *Bromus*. Slower individual growth rates particularly depressed  $\lambda$  in *Bromus* patches. In *Poa* patches, lower growth, flowering, and survival contributed almost equally to lower  $\lambda$  than in native grass patches. The slightly larger size of recruits in invasive grass patches (Fig. 2D) made a small positive contribution to differences in  $\lambda$  (Fig. 4B).

Stochastic population growth rates did not differ substantially from those estimated from mean values (Fig. 3). Over a 50-year time period, extinction risk was much higher in invasive grass patches. *A. patens* growing

in native grass patches has an almost zero probability (0.0001, 95% CI = 0.00, 0.0013) of quasi-extinction in 50 years. Extinction would be likely in *Bromus* grass patches (probability = 0.69, 95% CI = 0.0036, 1) and possible in *Poa* patches (probability = 0.07, 95% CI = 0, 0.96).

#### DISCUSSION

We found that both vital rates and population growth rate of *A. patens* were greatly reduced when growing among invasive grasses, particularly *B. inermis*, compared to native grasses. In fact,  $\lambda$  was positive only in patches of native grass, suggesting that long-term persistence of *A. patens* in habitats dominated by invasive grasses is unlikely. While sensitivity analyses showed that survival had the biggest effect on population growth rates in all habitats, the LTRE results revealed that slower growth rates in patches of invasive grasses contributed the most to reduced population growth.

As is typical for long-lived perennials, the most important vital rates were the least variable (Pfister 1998). Survival had by far the highest sensitivity to  $\lambda$  (Fig. 4A), and since very few plants died during the study, it exhibited very little variation (Fig. 2A). The rank order of the sensitivities for each vital rate was identical in all habitats, but the relative magnitudes of each rate differed among habitats. In general,  $\lambda$  for plants growing among invasive grasses appeared to have increased sensitivity to individual growth and decreased sensitivity to flowering, compared to uninvaded habitats. This means that there could be selection for higher resource allocation to growth and decreased allocation to flowering in the presence of invasive grasses.

Translating the effects of lower vital rates in invasive grass patches to effects on population growth rates is an important step, because differences in vital rates may cause only negligible differences in population growth, which is what ultimately matters for population persistence. Both the deterministic and stochastic models predict that *A. patens* will not persist in *Bromus* patches ( $\lambda < 1$ ) and is likely to decline in *Poa* patches, where the confidence interval of  $\lambda$  overlaps 1 (Fig. 3). Results from calculations of quasi-extinction probabilities confirm this pattern. *A. patens* has a three times higher probability of going extinct when growing in *Bromus* patches compared to *Poa* patches. Wide confidence limits around these rates reflect the fact that extinction risk is highly sensitive to changes in  $\lambda$  for values just below 1 (see error bars in Fig. 3). As is expected for a nonthreatened species, our models indicate that *A. patens* populations in native grass patches are slightly increasing and are likely to persist. While there are currently no differences in *A. patens* abundance between different grass patches, we predict *A. patens* will persist only in the native patches.

The differences in  $\lambda$  indicate that invasive grasses are having a negative impact on *A. patens* at the population

level, but differences in  $\lambda$  alone offer little insight into the mechanism causing declines. While a comparison of vital rates between the different grass patches shows that survival, growth, and fecundity all decreased in *Poa* and *Bromus* patches compared to native grass patches (Fig. 2), it is the results of the LTRE that suggest a mechanism. This analysis shows that decreased growth rates in the invasive grass patches are contributing the most to decreases in overall  $\lambda$  (Fig. 4B), and suggests that the invasive grasses are limiting growth of *A. patens* individuals. This pattern is more pronounced for *Bromus* than for *Poa* patches. The response of *A. patens* to exotic grasses that we found is similar to experimental studies of competition, which demonstrate that exotics can decrease growth of natives at the individual level (Huenneke and Thompson 1995, Moen and Meurk 2001). Our results suggest that short-term negative effects of exotics on natives can be large enough to lead to long-term population declines. For long-lived organisms, an experiment may capture a very small fraction of its life span, but demographic population models allow us to translate differences in vital rates over small time scales to predict population persistence over the long term.

One of the biggest differences between patches characterized by native vs. invasive grasses in our system is the presence of a thick layer of thatch in invasive grass patches. This layer of dead grass from the previous year is especially prominent in *Bromus* patches. In other grassland systems, thatch or a litter layer can play a key role in affecting seedling emergence (Bergelson 1990, Facelli and Pickett 1991). Thomson (2005) showed that thatch of invasive annual grasses contributed strongly to very low seedling emergence of a federally listed endangered plant, *Oenothera deltoides*, and that thatch accumulation along with soil disturbance more strongly influenced the decline in population size than direct resource competition. While we observed no significant differences in recruitment of *A. patens* between invasive and native grass patches, seedlings were larger in patches of invasive grass, but we observed fewer of them (Fig. 2D; E. E. Crone, unpublished data). It is likely that many seeds germinated in *Bromus* and *Poa* patches, but died before they were visible above the thatch. As Chapin et al. (1996) and Vitousek (1990) suggest, functional differences, such as the presence of thatch in patches with invasive grasses, should lead to predictable impacts of invaders on native residents. In our study, since seedling size and even recruitment had very low sensitivity to  $\lambda$ , the thatch layer is only important to  $\lambda$  in its effects on individual growth, survival, and flowering.

Our study has important implications for restoration in this system, where attempts to control *Bromus* in the past have increased *Poa* density (Brown 1997). Although *A. patens* is declining most quickly in *Bromus* patches, suggesting that controlling *Bromus* would be beneficial, it is also declining in *Poa* patches. Thus, while controlling only *Bromus* might reduce extinction risk in the short term, it will not completely reverse declines in *A. patens*.

Nevertheless, for *A. patens*, although invasive grasses are predicted to lead to population decline, it is a slow decline, allowing time to develop effective control methods. Our results suggest that other wildflowers with similar life histories, that is, long-lived perennials with a large underground storage capacity, could experience similar declines due to the spread of invasive grasses.

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#### APPENDIX

Coefficients and error distributions for each vital rate used in the integral projection model (*Ecological Archives* E087-193-A1).