

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Effects of community-level grassland management on the non-target rare annual *Agalinis auriculata*

Pati Vitt^{a,*}, Kayri Havens^a, Bruce E. Kendall^b, Tiffany M. Knight^c

^aDepartment of Plant Science and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA

^bDonald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106-5131, USA

^cDepartment of Biology, Washington University in St. Louis, One Brookings Drive, Box 1137, St. Louis, MO 63130, USA

ARTICLE INFO

Article history:

Received 4 August 2008

Received in revised form

2 December 2008

Accepted 6 December 2008

Available online 21 January 2009

Keywords:

Plant–herbivore interactions

Prescribed fire

Matrix projection models

Prairie restoration

Population viability analysis

Community-level management

Annual plant

ABSTRACT

The objective of grassland management is to maintain keystone species, as well as species diversity, to promote a particular community structure, or to preserve specific ecosystem processes. Studies of grassland management rarely ascertain the effects on rare plant species, although conservation plans for rare herbaceous plants often recommend habitat management as well as restoration activities. Indeed, conservation biology has evolved from a relatively species-specific discipline into one more focused on larger scale issues such as ecosystem function, community composition and habitat restoration. Few studies have tested whether species of concern are adequately managed with a community or ecosystem-level approach. In this study, we evaluate whether community-level management of white-tailed deer and woody brush improves the viability of the rare annual plant species, *Agalinis auriculata* (Earleaf false foxglove; Orobanchaceae). Reducing deer browse and removing brush each positively affect plant vital rates. Brush removal increases the proportion of plants that reach the largest size class. Reducing deer browse increases the fertility of plants, particularly those in the largest size class. We report on demographic matrix models created with data from five populations of *A. auriculata* studied across 4 years. We find that both management activities positively affect the non-target plant species and are, in fact, necessary for *A. auriculata* to persist. Conservation of *A. auriculata* at our study sites requires both reducing the density of white-tailed deer and brush removal. Our study demonstrates that management at the community and ecosystem levels can be compatible with conservation goals at the species and population levels.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Generally, the objective of grassland management is to maintain keystone species such as prairie dogs (Miller et al., 1994), to preserve or promote specific ecosystem processes such as biogeochemical cycling and carbon sequestration (Burke et al., 1997; Jones and Donnelly, 2004) and to promote a diverse assemblage of non-woody species such as herbs, grasses and forbs (Simberloff, 1998; Poiani et al., 2000). The

range of management activities usually involves the removal of invasive species (particularly woody brush), prescribed fire, deer control and propagule supplementation (Martin et al., 2005). Such habitat management and restoration activities are also recommended in conservation plans for rare herbaceous plants, making the critical assumption that they will increase the viability of individual species (Grumbine, 1994; Christensen et al., 1996; Simberloff, 1998). However, very few studies to date have explicitly monitored populations of

* Corresponding author: Tel.: +1 847 835 8268.

E-mail address: pvitt@chicagobotanic.org (P. Vitt).

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.12.009

rare herbaceous plant species to determine if ecosystem-level management is compatible with rare plant conservation. The few exceptions have focused mainly on prescribed fire (Gray et al., 2003; Kaye et al., 2001). However, brush control and control of deer browse are equally common management activities that might increase the vital rates of rare species (Thompson, 1992; McShea et al., 1997).

Encroachment by woody species is a common threat to grassland ecosystems, which may negatively affect population growth rates of herbaceous species. There has been a well-documented increase in density and cover of woody vegetation in grasslands worldwide for the past century or more (Archer, 1989; Van Auken, 2000). The suggested causes include changes in climate, increasing CO₂ levels, increases in grazing, the introduction of non-native woody species, and changes in historic fire regimes (e.g. Lett and Knapp, 2003; Van Auken, 2000; Archer, 1989). Such increases in woody vegetation have been associated with an increase in above-ground versus below-ground biomass, which has implications for net C storage in grasslands (Norris et al., 2001). Therefore, woody encroachment into grasslands may prove to be a significant issue if grasslands, and their soils, are to remain effective carbon sinks (ARS, 2007; Pepper et al., 2005). Woody encroachment has also been associated with decreases in grassland species abundance and diversity (Hobbs and Mooney, 1986; Briggs et al., 2002). As a result, we expect that woody encroachment will depress the vital rates of rare species and consequently their population growth rate and viability.

Control of woody encroachment by physical or mechanical removal is a primary management strategy for conservation and restoration of open habitats, such as prairies (Thompson, 1992). Not only does removal of brush slow the rate of conversion of prairie habitats into forests, it also reduces the prevalence and spread of invasive woody species. In our study region in the central plains of North America, European buckthorn (*Rhamnus cathartica*) is a commonly encountered woody invader that is actively controlled by mechanical removal. Graminoid responses to woody shrub removal are fairly well characterized and include responses to increased light, water and resources following woody removal (e.g., Scholes and Archer, 1997). While responses of herbaceous species are not as well known, brush removal should also increase light availability for herbaceous plants, and therefore may have immediate benefits to the vital rates of herbaceous plants. In the long term, however, brush removal may increase competition for light, nutrient and water resources as Graminoid species recover, and this may occur at the expense of populations of rare herbaceous species.

In addition to an apparent increase in woody encroachment changing the structure and composition of grasslands, an unprecedented number of large ungulates such as red deer, elk, reindeer and eastern white tail deer are now rapidly altering native plant abundance, biodiversity and community composition worldwide (Russell et al., 2001; Augustine and DeCalesta, 2003; Schütz et al., 2003; Côté et al., 2004; Ims et al., 2007; Johnston et al., 2007), and even altering ecosystem function (Russell et al., 2001; Wardle et al., 2001). Moderate levels of grazing may promote plant diversity if ungulates suppress competitively dominant plants, allowing less competitive species to flourish (e.g., Schütz et al., 2003). However,

extremely high ungulate densities tend to decrease vegetation abundance and diversity. For example, throughout eastern North America there has been four-fold increase in the abundance of white-tailed deer (*Odocoileus virginianus*) over the past 50 years (McShea et al., 1997), and their browsing habits have largely led to decreases in forb abundance (Côté et al., 2004). Reducing deer density is a top priority for managers interested in preserving diversity of natural areas (McShea et al., 1997).

Several studies use matrix modeling to determine the effects of deer removal on the viability of long-lived perennial herbs (Rooney and Gross, 2003; Knight, 2004; McGraw and Furedi, 2005). All of these studies found that deer browse threatened the viability of the species because of their preferential herbivory of large, reproductive individuals. To date, no study has examined the effects of either brush encroachment or deer browse on the viability of annual species. The aim of our study is to quantify the viability of the rare annual plant species *Agalinis auriculata* (Michx.) (Orobanchaceae) in response to ecosystem-level management activities. We examined how deer control and brush removal affect the population structure and viability of this species and analyzed the demography of five populations of *A. auriculata* over 4 years to ask: what are the effects of deer browse and brush removal on its vital rates and population growth rate? By answering this question in the context of ecosystem-level management activities, we determined the separate and interactive importance of these factors on the viability of rare plant species.

2. Methods

2.1. Study organism and sites

A. auriculata (Earleaf false foxglove) is a hemi-parasitic annual plant that occurs in mesic black soil prairies, grass thickets, savannas and woodland borders throughout the tallgrass prairie biome of the Central United States, as well the Southeastern regions of the United States. There are 40–50 extant occurrences of this species, most with small populations of 25–250 individuals (Rawinski, 1990). The largest populations are found in relatively pristine natural communities (WIS, 2006), where either *Rudbeckia fulgida* or *Helianthus occidentalis* are present, as these are the only two species with which *A. auriculata* are known to form haustorial connections and grow to reproductive maturity (Cunningham and Parr, 1990).

Mature plants are covered with short, stiff hairs and may grow to 90 cm in height, usually as a single unbranched stem. Multiple-stemmed individuals, however, are thought to arise as a result of compensation for deer browse (Mulvaney et al., 2004), which may affect fecundity. *A. auriculata* has a short-lived seed bank; most seeds germinate within the first 3 years (Baskin et al., 1991) and no studies cite a longer lived soil seed bank. Seeds germinate in early spring, and plants flower in August and September (Swink and Wilhelm, 1994). *A. auriculata* outcrosses when pollinators are present but also readily self-pollinates; fruit set is 90% in the absence of pollinators (Mulvaney et al., 2004).

We included five populations from northeastern Illinois, USA in our study. Two sites, Paintbrush Prairie and

Gensburg-Markham Prairie, are small prairie remnants within the Indian Boundary Prairie, co-owned and managed by The Nature Conservancy, Northeastern Illinois University, and the Natural Land Institute. Paintbrush Prairie comprises 24.3 ha of wet mesic prairie. Gensburg-Markham Prairie is a 38.5 ha remnant that is best characterized by an old beach ridge that runs to the northwest through the prairie. Neither Paintbrush Prairie nor Gensburg-Markham Prairie contain high abundances of woody brush, and this is likely because these sites have a higher prescribed fire frequency than our other three study sites. The next two sites, Blodgett Road and Foxglove Prairie, are separate management units contained within the boundaries of the Midewin National Tallgrass Prairie, which is owned and managed by the US Forest Service. Blodgett Rd is 121 ha of wet mesic to mesic dolomite prairie whereas Foxglove Prairie is considerably smaller, at only 20 ha, and is a wet to mesic prairie. These two sites are separated from each other by approximately 6 km. Located on prairie remnants, both sites are being encroached upon by woody invasives. Our final site, West Branch Prairie, is the smallest site at only 0.84 ha of wet prairie. West Branch contains species that usually occur in either dry or moist conditions growing in close association and contains heavy growth of invasive shrubs, primarily *Cornus racemosa*.

Deer densities are reported to be high at all of our study sites, though no direct estimates of density are available. Deer control fencing has been established at the Midewin National Tallgrass Prairie, containing both the Blodgett Road and Foxglove prairies, but this appears to provide only nominal control given the level of deer browse observed at these sites. A deer control program was initiated at West Branch in 2004, when 27 animals were removed.

2.2. Demographic data collection

Populations of *A. auriculata* were censused from 2001 to 2004 by highly trained citizen scientists and professional staff who participate in a Chicago, Illinois-based rare plant monitoring program (Plants of Concern: <http://www.plantsofconcern.org/>) that was initiated to determine effects of management on populations of non-target rare plant species, and to feedback results to managers and site stewards responsible for carrying out management practices. This citizen science program is similar in intent, scope and oversight as that being used by the Cornell Ornithological Laboratory, recently outlined and expanded by Cooper et al. (2007). The standardized data collection protocol used to collect demographic data was designed by the Plants of Concern staff and two of the authors of the current paper (P. Vitt and K. Havens). Data collection itself was conducted by a trained citizen scientist and a POC staff member, as well as the primary author of this paper.

Populations and individual plants were censused twice a year from 2001 to 2004. The first visit was conducted early in the season, when plants were visible but before much deer browse had occurred. During the first visit, all individuals in the population were censused. To obtain an accurate count, we first placed a permanent rebar stake in the densest portion of the population. We moved outward from the stake and placed a pin flag to denote the location of each plant. To en-

sure that even the smallest individuals were included, a “hands and knees” search was conducted. Plants were then counted by removing the pin flag to ensure that each plant was counted only once. For plants included in the ongoing demographic study, the pin flag was replaced with a numbered tag.

If population size was under 100 individuals, then all individuals in the population were included in the study. If the population size was greater than 100 individuals, then a subset of individuals was randomly chosen. Our demographic study included a sample of either 50 (all sites in 2001) or 100 (all sites for 2002 through 2004) individuals in each population. During the first visit, we counted the number of flowers (and flower buds), measured plant height, and documented whether there was evidence of deer browse for all individuals. During the second visit, we measured the height of each individual, counted the number of fruits produced by each individual, and documented deer browse. In some cases, deer browse resulted in the plants losing all of their above-ground biomass and not setting any fruit; fruit set was then regarded as zero. In other cases, browsed plants still had some remaining fruits, which were subsequently counted. To quantify the number of seeds per fruit, we collected one fruit from each of 30 randomly selected plants at each site in 2004, and counted the number of seeds in each fruit.

2.3. Matrix model

In our model, we classified reproductive plants into three size classes based on plant height early in the season: small (0–30 cm), medium (31–50 cm) and large (>50 cm). There were two- and five-fold differences in fruit production between plants in the small size class and those in the medium and large size classes, respectively. Seeds either germinate in the spring following their formation, or go dormant as part of the seed bank, subsequently emerging in years 2 and 3. Therefore, our model also incorporated two seed classes, corresponding to seeds after 1 and 2 years in the seed bank. In creating our model, we assumed that all seeds germinate by the end of their third year based upon the results found by Baskin et al. (1991) in a greenhouse study of seed germination in this species. The life-cycle graph of *A. auriculata* is shown in Fig. 1.

We describe the vital rates depicted in Fig. 1 in detail in Table 1. Based upon the results of Baskin et al. (1991), we set g , a and b to be constant values of 0.367, 0.5 and 1, respectively. For each population and year, we estimated the proportion of flowering individuals in each size class (p_s , p_m and p_l), as well as the average number of seeds per plant for each size class (f_s , f_m and f_l). We calculated this as the product of the number of fruits per individual and the mean number of seeds per fruit. Seedling survival, s , was calculated from the number of number of seedlings divided by the number of flowering plants in the population in the current year. We estimated the number of seedlings from the total fecundity of all flowering individuals in the past year and the germination probability of seeds (g). However, because of the 2-year seed bank (Baskin et al., 1991), we also considered the total fecundity of all flowering individuals in the past 2 years, and the probability of dormant seeds germinating (a and b).

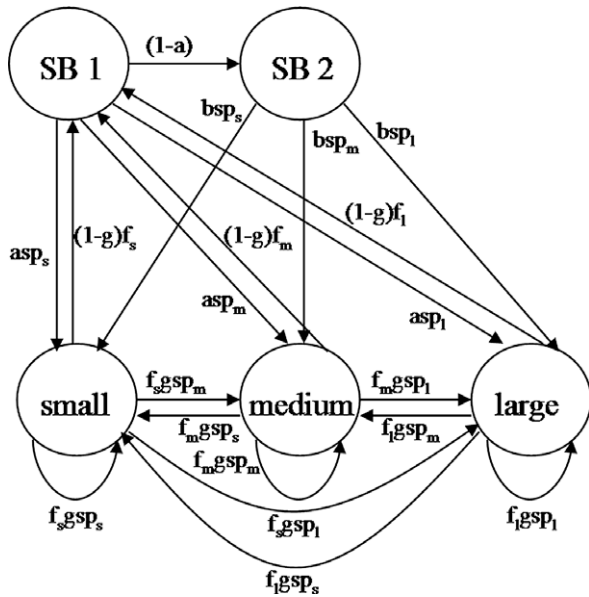


Fig. 1 – Life cycle of *Agalinis auriculata*.

Table 1 – Vital rates of *Agalinis auriculata* used in model.

Parameter	Description
g	Probability of that a seed germinates without entering the seed bank
$1 - g$	Probability that a seed enters the seed bank
a	Probability that a seed germinates after spending 1 year in the seed bank
$1 - a$	Probability that a 1-year old seed remains in the seed bank
b	Probability that a seed germinates after spending 2 years in the seed bank
s	Probability that a seedling survives to reproduction
p_s	Probability that a reproductive individual is in the small stage class
p_m	Probability that a reproductive individual is in the medium stage class
p_l	Probability that a reproductive individual is in the large stage class
f_s	Average # seeds produced per small reproductive individual
f_m	Average # seeds produced per medium reproductive individual
f_l	Average # seeds produced per large reproductive individual

For example, if F_t is the number of seeds produced by all plants in a population in year t , then the number of seedlings in the population in 2004 is: $(F_{2003})g + (F_{2002})(1 - g)a + (F_{2001})(1 - g)(1 - a)b$. Because several years of data are necessary to calculate s , we have only one estimate of s per population.

Fecundity of flowering plants is reduced by deer when they consume vegetative and reproductive structures of *A. auriculata*. Further, deer may preferentially consume plants in larger size classes, which have the greatest fecundity. To examine the incidence of deer browse on flowering plants and the effects of deer browse on fruit production, we categorized plants in each population and year by whether or not deer consumption occurred. Pooling plants across years within each site allowed for an adequate sample size of plants in the consumed category. We used chi-square analyses to determine if the incidence of herbivory differed among size classes. We used ANOVA to determine if deer browse, size class, population and their interactions influenced the fruit production of plants in each site. Fruit production data were normally distributed, and thus data transformations were not necessary.

We incorporated browsing into the model by first constructing matrices for each population using only the individuals not consumed by deer (see also Knight, 2004; McGraw and Furedi, 2005 for a similar modeling method). Matrix elements for which we had multiple years of data were averaged across years, creating a single matrix for each population. We then incorporated effects of deer herbivory by altering fertility values for plants in each stage class. We examined intensities of deer herbivory ranging from 0% to 100% of plants consumed for each population. We did not have to incorporate a parameter to account for deer preference of larger stage classes, because deer do not preferentially consume large plants (see Section 3). This method only takes into account direct effects of deer herbivory (i.e., lower fertility due to deer consumption of plants). Deer may have indirect negative effects on plants through trampling and soil compaction. Thus, the projections of our models may represent an underestimate of the population-level effects of deer on *A. auriculata*.

All *A. auriculata* populations included in this study experienced some form of invasive brush encroachment (Table 2). Brush removal was conducted at Blodgett Road and Foxglove

Table 2 – List of woody species found near to *Agalinis auriculata* population at each site. (N) Indicates species native to the North American tallgrass prairie biome. (I) Indicates species that are invasive.

Associated woody species	Gensburg-Markham	Blodgett Road	Foxglove Prairie	Paintbrush Prairie	West Branch
<i>Cornus racemosa</i> (N)	–	–	–	x	x
<i>Eleaegnus umbellata</i> (I)	–	x	x	–	–
<i>Fraxinus pennsylvanica</i> var. <i>subintegerrima</i> (N)	–	x	x	–	–
<i>Lonicera x muendenienseis</i> (I)	–	–	–	–	x
<i>Rhamnus cathartica</i> (I)	–	–	x	x	–
<i>Rosa multiflora</i> (I)	–	–	–	–	x
<i>Salix glaucophylloides</i> (N)	x	–	–	–	–

Prairie in 2004 and at Blodgett Road in 2003. To examine effects of brush removal on plant size and fruit production, we categorized plants in each population and year by whether or not brush removal occurred. We used chi-square analysis to examine the effects of brush removal on the proportion of individuals in each size class. Further, we used ANOVA to determine if fruit production of unbrowsed individuals in each size class differed due to brush removal.

To examine effects of brush removal on the population growth rate of *A. auriculata*, we created two average matrices using the average values of p_s , p_m and p_l for plants in populations and years with brush removal and those in populations and years with no brush removal (we did not separately consider f_s , f_m and f_l because brush removal did not influence these vital rates [see Section 3]). A separate model that examined effects of brush removal on the growth rate of each population is not possible, since brush removal management only took place at two populations. To examine effects of both deer herbivory and brush removal, we incorporated herbivory into these matrices as above.

Matrix projections use the model: $N_{t+1}=AN_t$, where A is the matrix of stage specific vital rates. The population growth rate or λ is the dominant eigenvalue of A , and provides a critical threshold for population persistence. When $\lambda < 1$, the population declines towards extinction. When $\lambda > 1$, the population increases. For each population, we calculated 95% confidence intervals around λ using bootstrap resampling methods (Caswell, 2001) as follows: a bootstrap data set was created by sampling individuals, with replacement, from the original demographic data set until the sample size of each bootstrap data set was identical to the original data set. A total of 1000 bootstrap data sets were generated for each population and year using MATLAB (2000) and the data from each bootstrap data set were used to calculate the elements of a A . All bootstrap matrices for a given population and year had identical values for g , a and b because these values used data from the literature.

3. Results

Across all populations and years, 40% of *A. auriculata* were consumed by deer. The incidence of herbivory did not significantly differ among size classes (Chi square test: $\chi^2 = 4.7$, $P = 0.095$), so deer do not preferentially graze on the larger size classes. Fruit production differed among sites and size classes of plants, and between plants that were browsed and not browsed (Table 3, Fig. 2). The variation in fruit production

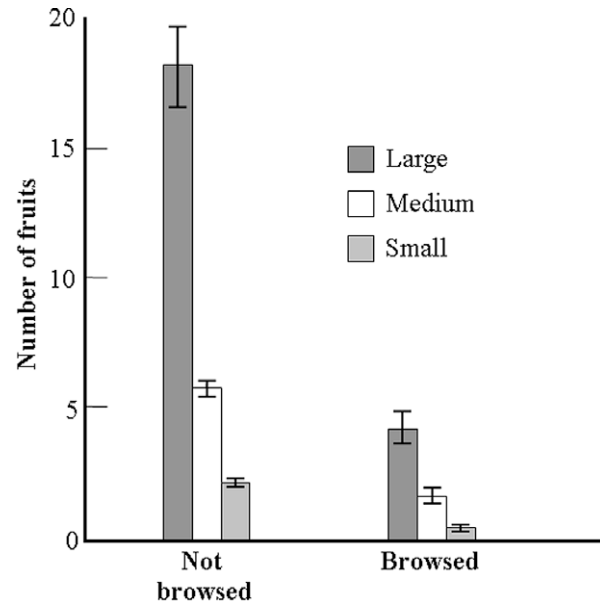


Fig. 2 – Effects of deer herbivory on size class-specific fruit number of *Agalinis auriculata*. Data pooled across all sites. Means and 1 standard error shown.

across sites is likely due to site differences in the proportion of plants in each stage class and/or in the incidence of browsing, as there was not a significant site by browsing or site by size class interaction (Table 3). There was a significant browsing by size interaction: plants in the large size class were most affected by herbivory (Table 3, Fig. 2). Although large individuals were not grazed preferentially, they did lose more fruits when they were grazed.

Brush removal increases the proportion of individuals in the large size class ($\chi^2 = 26.7$, $N = 384$, $P < 0.001$, Fig. 3). However, brush removal did not affect the size-specific fruit production of flowering individuals ($P = 0.35$).

Herbivory and brush removal both affect the viability of *A. auriculata* (Fig. 4). The amount of herbivory that can be sustained greatly differs across these sites; at Gensburg-Markham Prairie, the population can sustain less than 20% herbivory by deer, whereas the Blodgett population is projected to grow even when the incidence of herbivory is up to 80%. Paintbrush Prairie is projected to decline even in the absence of herbivory. Brush removal has significant effects on the population growth rate. In the absence of herbivory,

Table 3 – ANOVA results examining the roles of size class, deer browse and site on fruit number of *Agalinis auriculata*.

Source	Sum of squares	df	Mean square	F-ratio	P-value
Deer browse	6592.2	1	6592.2	80.437	<0.001
Size class	9803.5	2	4901.8	59.810	<0.001
Site	1014.1	4	235.5	3.093	0.015
Browse * size	3712.4	2	1856.2	22.649	<0.001
Browse * site	394.82	4	98.706	1.204	0.307
Size * site	1061.1	8	132.64	1.618	0.115
Browse * size * site	363.38	8	45.422	0.554	0.816
Error	82938.4	1012	81.955	–	–

these populations are expected to decline by 19% ($\lambda = 0.81$) each year when brush removal does not occur, whereas these populations are expected to grow by 22% ($\lambda = 1.22$) each year when brush removal occurs (Fig. 4). Average growth rates of these populations suggest that *A. auriculata* will not persist without frequent brush removal management as well as deer

management that ensures the browse level does not exceed 35% of the adult plants.

4. Discussion

As we strive to maintain both ecosystem functions and biodiversity in the face of anthropogenic habitat changes, it is both appropriate and necessary to step back and ask what level of diversity are we committed to maintaining, and if current management strategies support the maintenance of this level of diversity. Conservationists have long debated whether species, communities or landscapes are the most appropriate conservation targets (Hunter, 1991; Noss, 1996). In the United States, although most legal protection and recovery planning is done at the species level, single-species conservation has largely given way to the coarse filter approach of conserving communities, ecosystems and landscapes with the assumption that this management will also benefit rare species. However, imperiled species may not always predictably co-occur with community or ecosystem targets.

Grassland conservation often includes ecosystem-level treatments, such as prescribed fire, deer control and woody brush removal. Many types of grasslands also contain plant species of conservation concern. In the current study, we examined effects of community-level management activities on population growth rates of a non-target rare plant species. Our results indicate that certain community-level manage-

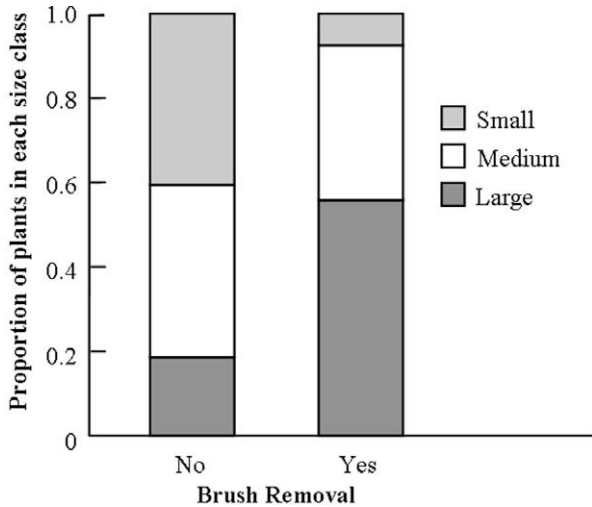


Fig. 3 – Effects of brush removal on proportion of flowering *Agalinis auriculata* in each size class.

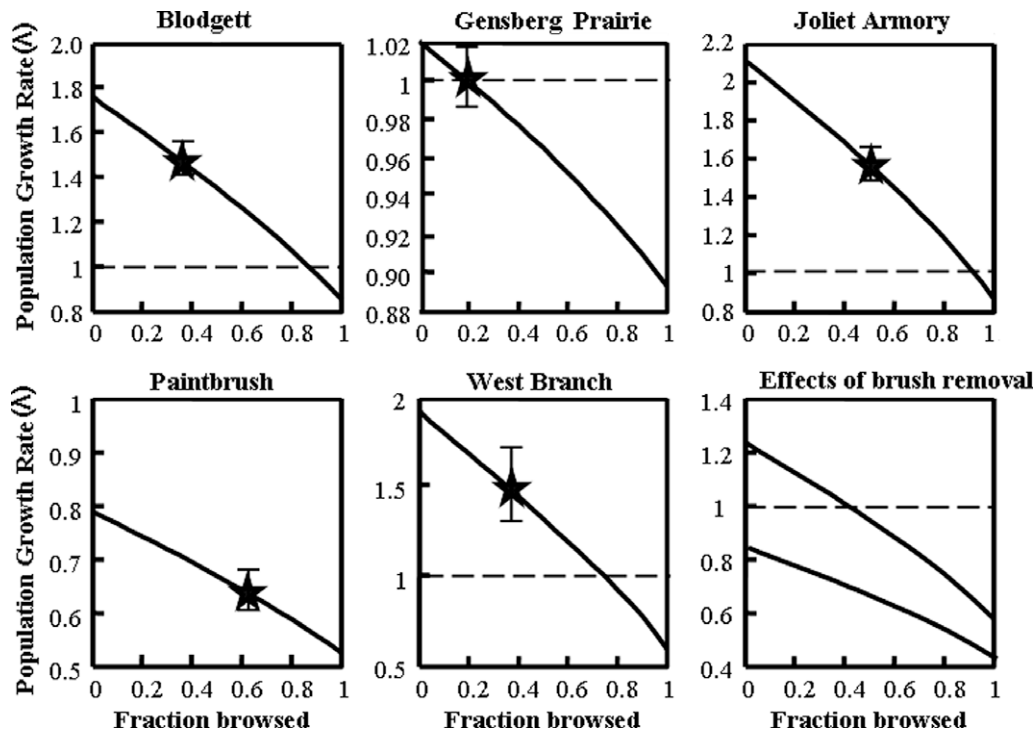


Fig. 4 – For each population, population growth rate as a function of the fraction of adult plants browsed is shown with a solid curve. Star indicates actual value for each population (and 95% confidence intervals), averaged across all years. Dotted line is the critical threshold ($\lambda = 1$) for viability. Areas on the curve above this dotted line indicate levels of herbivory that will allow the population to increase in the future. Areas on the curve below this dotted line indicate levels of herbivory that will result in the population decreasing towards extinction. Bottom right panel shows effects deer herbivory on population growth rate with and without brush removal using average vital rates of four populations (all except West Branch). Top curve indicates results for parameters incorporating brush removal whereas the lower curve indicates no management for brush.

ment activities are favorable to the non-target rare species, *A. auriculata*, and, indeed, a multifaceted management strategy is necessary to produce positive population trajectories in this species.

Rare species management often calls for strategies that increase reproduction and recruitment (Schemske et al., 1994). In annuals and monocarpic perennials seed output and seedling recruitment often drive population growth, in contrast with long-lived iteroparous species where population growth is driven by survival of individuals in the largest size class, rather than annual fertility rates (Silvertown et al., 1996). As our study species is an annual plant, we expect population growth in *A. auriculata* to be highly dependent upon seed output, as well as upon management inputs that increase seed production.

In *A. auriculata*, deer browse has a large effect on seed production. In some sites and years, deer consumed 90% of individuals. At the West Branch population, deer control was exercised in 2004. Levels of deer herbivory were on average 38.1% before 2004, and only 4.2% in 2005, suggesting that the reduction in deer densities immediately resulted in lower browsed incidence on *A. auriculata*. Overall, there was no difference in herbivory among plants in different size classes. However, the negative effects of deer browse on fruit production in large individuals was particularly acute; when deer did browse a large plant, they greatly reduced its total fruit production. While reducing the incidence of deer browse had strong positive effects on the population growth rate of *A. auriculata*, deer control alone will not be enough to ensure stable or growing populations.

A second management strategy, removal of woody species, both native and exotic, changed the size structure of populations, by increasing the proportion of large individuals. Individuals may achieve greater size as a result of decreased competition, both for soil resources such as water and nutrients, and for light. A similar finding has been reported for other grassland species such as *Gentianella campestris* (Lennartsson and Oostermeijer, 2001), where rosette size was negatively correlated with the density of surrounding vegetation. In addition, survivorship of seedlings and rosettes of *Gentiana pneumonanthe* and *Gentianella amarella* were negatively affected by chalk grassland height and cover (Kelly, 1989). We found that short-term effects of brush removal include increases in population growth rate of *A. auriculata* as the proportion of large individuals, with much greater seed production, increased significantly with brush removal. However, as with deer control, brush removal alone, will not be sufficient to maintain stable or growing populations. While brush removal increased the number of plants in larger size classes, without concurrent deer control, these large plants produced few seeds.

We do have concerns about the use of brush removal management: (1) *A. auriculata*, as an annual plant, can immediately benefit from brush removal, but this may be counteracted by competition with other species that also respond positively and (2) we are mindful that the immediate increase in population growth rate in *A. auriculata* may be short-lived. Anecdotal evidence given by land managers suggests that populations of *A. auriculata* respond positively to brush removal for a period of two to three years, only to be

out-competed by the Graminoid components of the community as they also respond, albeit more slowly, to the decreased competition that brush removal affords. (Steve Handel, personal communication). This is affirms that grasslands are best managed as habitat mosaics, allowing multiple communities to co-exist at the landscape scale.

Our study highlights the use of demographic data and population modeling to test how management at large scales influences rare species. In our example, the many goals of management (e.g. maintenance of grassland structure, elimination of invasive species, decrease of grazing pressures), all interact to support a threatened species, potentially increasing the biodiversity of the system.

Acknowledgements

The authors wish to thank the following staff at the Chicago Botanic Garden for collecting data in the field: Elaine Kneller, Yasko Matsuoka, Rebecca Mann, Lailah Reich and Andrew Bishop. Mary Stupen collected fruits and counted the seeds for all populations in the study. Staff members at the Chicago Botanic Garden, as well as land managers at the various study sites were also instrumental in site selection, data collection and undertaking the management activities reported upon. These include Scott Kobal, Jason Zylka, Andrea Tietmeyer Kramer and Lara Jefferson. Several highly trained volunteers monitored these populations as part of the Plants of Concern program, coordinated by the Chicago Botanic Garden. The following volunteers collected data: Chris Mulvaney, Stuart Goldman, David Hodge, Don Nelson, Espie Nelson, Gail Pyndus, Gary Horn, Steve Bubulka, Deb Petro, Melissa Mulvaney, Frank Keller and Wayne Lampa. Susanne Masi is the Coordinator for the Plants of Concern program and her contribution to program management, including coordinating data collection and data management, was fundamental to the successful analysis reported herein. Michael E. Pereira commented on an earlier draft of this manuscript. The Plants of Concern program is funded by Chicago Wilderness, Illinois Department of Natural Resources, USDA Forest Service Midwestern National Tallgrass Prairie and the National Fish and Wildlife Foundation.

REFERENCES

- Archer, S., 1989. Have Southern Texas savannas been converted to woodlands in recent history? *The American Naturalist* 134, 545–561.
- ARS 2007. United States Department of Agriculture, Agricultural Research Service. <http://www.ars.usda.gov/research/programs/programs.htm?np_code=204&docid=308> (accessed 15.01.08).
- Augustine, D.J., DeCalesta, D., 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecoscience* 10, 472–486.
- Baskin, J.M., Baskin, C.C., Parr, P.D., Cunningham, M., 1991. Seed germination ecology of the rare hemiparasite *Tomanthera auriculata* (Scrophulariaceae). *Castanea* 56, 51–58.
- Briggs, J.M., Knapp, A.K., Brock, B.L., 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and

- fire-grazing interactions. *The American Midland Naturalist* 147, 287–294.
- Burke, I.C., Lauenroth, W.K., Milchunas, D.G., 1997. Biogeochemistry of managed grasslands in the Central Grasslands of the US. In: Paul, E., Paustian, K. (Eds.), *Organic matter in US agroecosystems*. Lewis Publishers, pp. 85–102.
- Caswell, H., 2001. *Matrix population models: construction analysis and interpretation*, second ed. Sinauer Associates, Sunderland, MA. 722pp.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6, 665–691.
- Cooper, C.B., Dickinson, J., Phillips, T., Bonney, R., 2007. Citizen science as a tool for conservation in residential ecosystems. *Ecology and Society* 12, 11 (<<http://www.ecologyandsociety.org/vol12/iss2/art11/>>).
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* 35, 113–147.
- Cunningham, M., Parr, P.D., 1990. Successful culture of the rare annual hemiparasite *Tomanthera auriculata* (Michx.) Raf. (Scrophulariaceae). *Castanea* 55, 266–271.
- Gray, J.B., Wentworth, T.R., Brownie, C., 2003. Extinction, colonization, and persistence of rare vascular flora in the longleaf pine-wiregrass ecosystem: responses to fire frequency and population size. *Natural Areas Journal* 23, 210–219.
- Grumbine, R.E., 1994. What is ecosystem management? *Conservation Biology* 8, 27–38.
- Hobbs, R.J., Mooney, H.A., 1986. Community changes following shrub invasion of grassland. *Oecologia* 70, 508–512.
- Hunter Jr., M.L., 1991. Coping with ignorance: the coarse filter strategy for maintaining biodiversity. In: Kohm, K.A. (Ed.), *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future*. Island Press, Washington, DC, USA, pp. 266–281.
- Ims, R.A., Yoccoz, N.G., Bråthen, K.A., Fauchald, P., Tveraa, T., Hausner, V., 2007. Can reindeer overabundance cause a trophic cascade? *Ecosystems* 10, 607–622.
- Johnston, D.B., Cooper, D.J., Hobbs, N.T., 2007. Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture. *Oecologia* 154, 467–478.
- Jones, M.B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO₂. *New Phytologist* 164, 423–439.
- Kaye, T.N., Pendergrass, K., Findley, K., Kauffman, J.B., 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications* 11, 1366–1380.
- Kelly, D., 1989. Demography of short-lived plants in chalk grassland. I. Life-cycle variation in annuals and strict biennials. *Journal of Ecology* 77, 747–769.
- Knight, T.M., 2004. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecological Applications* 14, 915–928.
- Lennartsson, T., Oostermeijer, J.G.B., 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *Journal of Ecology* 89, 451–463.
- Lett, M.S., Knapp, A.K., 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. *Journal of Vegetation Science* 14, 487–496.
- Martin, L.M., Moloney, K.A., Wilsey, B.J., 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* 42, 327–336.
- McGraw, J.B., Furedi, M.A., 2005. Deer browsing and population viability of a forest understory plant. *Science* 307, 920–922.
- McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), 1997. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC, USA.
- Miller, B., Ceballos, G., Reading, R., 1994. The Prairie Dog and Biotic Diversity. *Conservation Biology* 8, 677–681.
- Mulvaney, C.R., Molano-Flores, B., Whitman, D.W., 2004. The reproductive biology of *Agalinis auriculata* (Michx.) Raf. (Orobanchaceae), a threatened North American prairie inhabitant. *International Journal of Plant Sciences* 165, 605–614.
- Norris, M.D., Blair, J.M., Johnson, L.C., McKane, R.B., 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. *Canadian Journal of Forest Resources* 31, 1940–1946.
- Noss, R.F., 1996. Ecosystems as conservation targets. *Trends in Ecology and Evolution* 11, 351.
- Pepper, D.A., Del Grosso, S.J., McMurtrie, R.E., Parton, W.J., 2005. Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO₂], temperature and nitrogen input. *Global Biogeochemical Cycles* 19, GB1004.
- Poiani, K.A., Richter, B.D., Anderson, M.G., Richter, H.E., 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *Bioscience* 50, 133–146.
- Rawinski, T.J., 1990. Final status survey report: the distribution and abundance of eared false foxglove (*Tomanthera auriculata*). Unpublished report submitted to the US Fish and Wildlife Service, Region 5. Newton Corner, MD, USA.
- Rooney, T.P., Gross, K., 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. *Plant Ecology* 168, 267–277.
- Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146, 1–26.
- Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M., Bishop, J.G., 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75, 584–606.
- Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28, 517–544.
- Schütz, M., Risch, A.C., Leuzinger, E., Krüsi, B.O., Achermann, G., 2003. Impact of herbivory by red deer (*Cervus elaphus* L.) on patterns and processes in subalpine grasslands in the Swiss National Park. *Forest Ecology and Management* 181, 177–188.
- Silvertown, J., Franco, M., Menges, E., 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* 10, 591–597.
- Simberloff, D., 1998. Flagships, umbrellas and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83, 247–257.
- Swink, F., Wilhelm, G., 1994. *Plants of the Chicago Region*, fourth ed. Indiana Academy of Science, Indianapolis, IN, USA.
- Thompson, J.R., 1992. *Prairies, Forests and Wetlands: The Restoration of Natural Landscape Communities in Iowa*. University of Iowa Press, Iowa City, IA, USA.
- Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31, 197–215.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., Ghani, A., 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* 71, 587–614.
- WIS, 2006. Wisconsin vascular plants-on species, including maps and photos. Wisconsin State Herbarium, University of Wisconsin, Madison (WIS). <<http://www.botany.wisc.edu/wisflora/>> (accessed 15.01.08).