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Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation

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Abstract

1. We studied the demographic viability of populations of a long-lived iteroparous prairie perennial, *Silene regia*, in relation to management regimes, population sizes, geographical region (Ohio and Indiana vs. Missouri and Arkansas), degree of isolation and amount of genetic variation. Demographic data were collected from 16 populations for up to 7 years.
2. This species has high survivorship, slow growth, frequent flowering and episodic seedling recruitment. Matrix projection methods were used to summarize population performance with and without recruitment. Median finite rates of increase by population varied from 0.57 to 1.82 and from 0.44 to 0.99, respectively.
3. Populations with the highest rates of increase had been burned. Six of eight populations, for which stochastic modelling predicted persistence for 1000 years, included fire in their management. None of the five populations with predicted 100-year extinction probabilities of 100% was managed for conservation or burned. An intermediate group of three populations with at least 10% probability of extinction between 100 and 1000 years was not managed, but was none the less kept open by mowing and herbicide application.
4. Analysis of composite elasticities showed that growth and fecundity terms were higher for growing (vs. declining) populations and that growth elasticity was higher in burned than unburned populations. Lack of burning shifts the elasticity spectrum from that typical of open habitat herbs (higher growth and fecundity elasticities) to values usually found for closed habitat herbs (higher survival elasticities).
5. In multivariate analyses predicting finite rates of increase (with and without recruitment), fire management and region were the strongest predictors, followed by genetic variation, population size, isolation and interactions of population size and fire, and region and fire. Populations with the highest rates of increase were burned, eastern, more genetically diverse, larger and less isolated. Discrimination of populations with different extinction risks (three classes) was related mainly to fire, genetic variation and region.
6. Most of these conclusions support conservation biology predictions that population viability will be highest in larger, less-isolated, more genetically diverse populations. However, management and geographic trends have overriding roles affecting demographic viability. Habitat fragmentation and genetic depletion have the potential to threaten residual prairie populations of *S. regia*, but lack of fire management appears to be the primary short-term threat.

Introduction

Population viability analysis (PVA) extrapolates from field-collected demographic data in order to understand the health and functioning of populations, and to model extinction probabilities for sample populations. By correlating habitat characteristics and management regimes with population survival estimates based on PVA, one can identify site management strategies that enhance the likelihood of long-term population survival (Menges 1991b; Boyce 1992). However, PVA has only recently been applied to rare plant species (Fiedler 1987; Menges 1990; Aplet *et al.* 1994; Nantel *et al.* 1996; Oostermeijer *et al.* 1996a, b).

Assessments of population viability have generally considered either demography or genetics (Pease *et al.* 1989; Boyce 1992; Nunney & Campbell 1993; Lacy & Lindenmayer 1995). Observed genetic variation is often used to decide which populations should receive top priority for preservation efforts (Lesica *et al.* 1988; Hickey *et al.* 1991; Purdy *et al.* 1994). Genetic variation is thought to be positively correlated with a population's ability to adapt to short-term environmental change, and populations with the highest levels of genetic variation are expected to suffer least from the negative effects of inbreeding depression or genetic drift (reviewed by Barrett & Kohn 1991 and Ellstrand & Elam 1993). However, the predicted negative genetic effects on rare species have sometimes been questioned. For most species, short-term, ecological impacts that directly influence survival and reproductions may pose the greatest extinction risk (Lande 1988; Menges 1991b; Schemske *et al.* 1994).

While genetic considerations have been used to formulate some general rules of thumb about viable population size (Franklin 1980; Lande 1995; Lynch *et al.* 1995), demographic analyses of individual species are more often used to assess short-term population health and suggest management alternatives (Menges 1990; McCarthy *et al.* 1995). Few studies have examined both genetic variation and demographically based PVA (Boyce 1992; Schemske *et al.* 1994). One exception combines environmental, demographic and genetic factors to evaluate extinction risk in *Banksia cuneata* (Burgman & Lamont 1992; Burgman *et al.* 1993). Another study of *Gentiana pneumonathe* combined genetic and demographic approaches (Oostermeijer *et al.* 1996a, b).

In this study, we consider the demographic population viability of a plant, *Silene regia*, that occurs in isolated fragments of North American prairies. Habitat fragmentation has great potential for affecting population viability of prairie plants. Populations reduced in size by habitat loss and fragmentation may lose genetic variation (Raijmann *et al.* 1994; Ouborg & Van Treuren 1995) and this may affect population viability (Menges 1991a; Widen 1993; Oostermeijer *et al.* 1994a). Also, small prairie fragments may suffer from edge effects due to invasion of woody plants and exotics. Periodic fire maintains tallgrass prairies and prevents woody plant encroachment (Vogl 1974; Bragg & Hulbert 1976; Axelrod 1985) and detrimental build-up of detritus (Knapp & Seastedt 1986) that can suppress herbs (Gehring & Bragg 1992).

North American prairies and savannas have been affected by habitat fragmentation for decades, yet we know of no studies on the effects of habitat fragmentation on prairie plants, nor any studies exploring their population viability. Prairies are among the most endangered ecosystems in North America (Klopatek *et al.* 1979; Noss & Peters 1995). Nine of the 16 North American vegetation types that have been reduced most in area are grasslands or prairies

(Klopatek *et al.* 1979). In the three physiognomic provinces in this study, the amount of original prairies are remaining ranges from less than 0.1% (Indiana, Ohio) (Menges 1988; Samson & Knopf 1994) to about 4% (southwestern Missouri) (Menges 1988). In the Darby Plain study area of Ohio, about 94% of the resettlement matrix of prairie, savanna and forest had been converted to agriculture and other human uses by 1988, with prairie conversion concentrated in the early 1900s as a result of widespread drainage (Simpson *et al.* 1994).

We report here on a 7-year study of 16 prairie populations of royal catchfly (*Silene regia* Sims; Caryophyllaceae; formerly a candidate species for federal protection under the Endangered Species Act; Federal Register 1980). We selected prairie populations across the east-west distribution of the species that varied widely in population size, degree of isolation and habitat management (burning and/or mowing). We used matrix projection models to formulate a demographically based PVA for each population and to project finite rates of increase and extinction probabilities. We then examined how population size, degree of isolation, geographic region, management regime and degree of genetic variation of the populations are related to demographic population viability.

Materials and Methods

Species and Sites

Silene regia, royal catchfly, is endemic to the mid-western and south-eastern USA (Fig. 1), being most abundant in unglaciated southern Missouri, where it is found in almost every county. Its range extends to the south-east and to the north-east, with scattered populations in Illinois, Indiana and Ohio (King 1981), mainly on deep soils in formerly glaciated areas. Royal catchfly grows in mesic and wet-mesic prairies, dry woods and glades, especially on calcareous soils (Fernald 1950; King 1981), and was undoubtedly once more common across its range.

The plants are tap-rooted, long-lived perennials with striking, red, hummingbird-pollinated flowers. Substantial fruit set in eastern populations requires hummingbird pollination (Menges 1995). Flowers are protandrous and self-compatible, but pollinations are primarily outcrossing or geitonogamous due to dichogamy (Menges 1995). The species does not spread clonally. Seeds are gravity dispersed, have no known dormancy, and do not accumulate in the soil (E. S. Menges, unpublished data). Seedling emergence is increased by soil disturbance and burning (Menges 1995).

We selected 16 *S. regia* populations in prairie areas of Ohio, Indiana, Missouri and Arkansas that varied in population size, vegetation and management (Table 1). Management regimes such as fire and mowing were applied annually before and during the study. Prairie remnants in Indiana and Ohio were generally very small (usually < 5 ha), managed by fire (or unmanaged), and isolated from each other by row-crop agriculture. In contrast, most Missouri sites were larger, less isolated from other prairies and other *S. regia* populations, and managed using various combinations of mowing, fire and grazing.

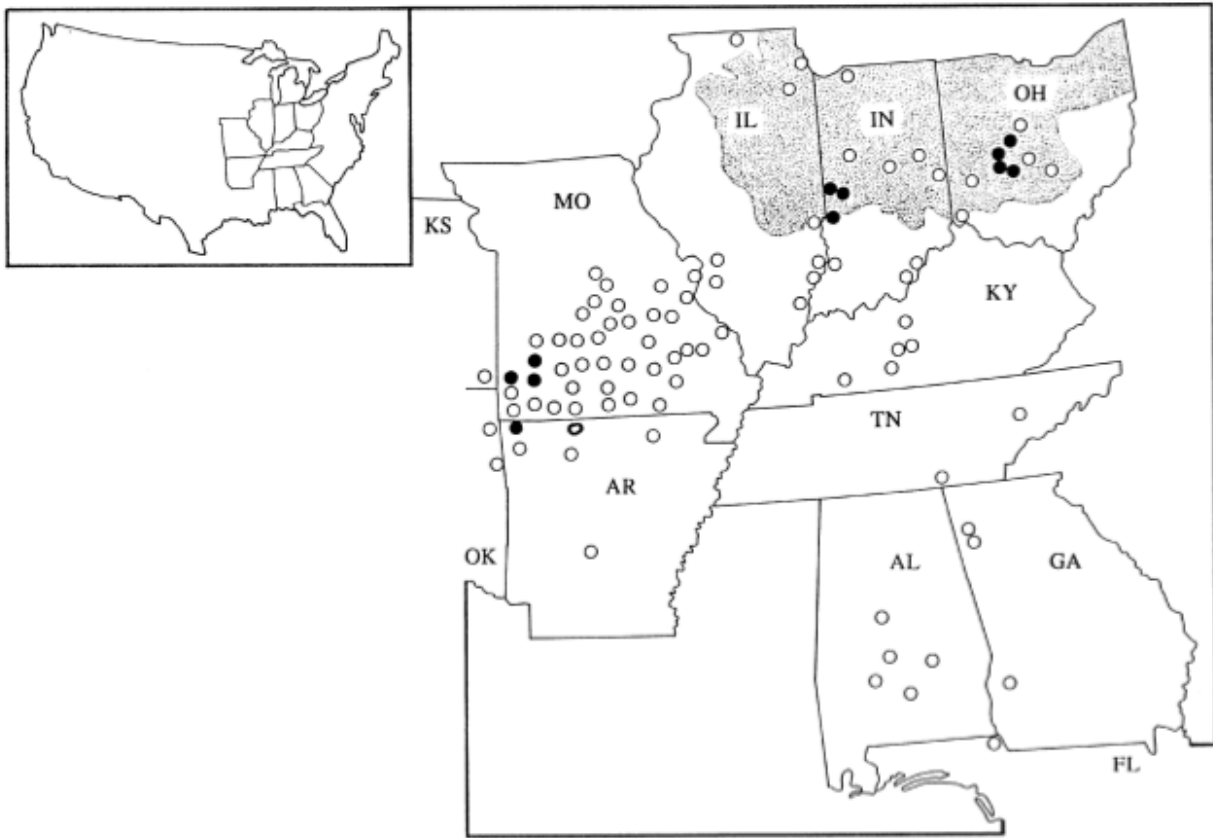


Fig. 1 Counties known to once have supported royal catchfly (*S. regia*) (indicated by open circles), counties with study populations (closed circles), and the continental ice sheet of late Wisconsinian time (shaded) (from Dolan 1994).

Field Methods

Demography

During annual census trips at peak flowering, we mapped and marked all *S. regia* non-seedlings within defined areas (macroplots or belt transects) at each site. Data were gathered from 1985 to 1992, although not for all years at all sites (Table 1). We counted or measured numbers of stems, height and, for each stem, base diameter, flowering status and number of flowering whorls. We also noted stem breakage and vine presence.

Due to the rarity of seedlings and the difficulty of spotting them in dense prairie and thicket vegetation, we initiated special seedling searches in narrow 10 m x 10 cm (1 m²) quadrats in 1987 for five populations and in 1990 for all other populations. These areas were searched intensively and all seedlings were marked and monitored annually for survival and size.

Table 1 Names and locations for populations of *S. regia* used in this demographic study

Population	County, state	Number of plants sampled*	Population size†	Site	Management	Years with demographic data
Milford	Union, OH	362	418	RRP	F	7
Bigelow	Madison, OH	454	376	CP	F	7
Paint Creek	Madison, OH	98	149	RRP,OV	O	5
Florence	Madison, OH	140	500	RRP,OV	O	5
Selma	Clark, OH	74	45	RRP,OV	O	4
Smith	Vermillion, IN	152	895	CP	F	7
Stone Bluff	Fountain, IN	120	64	RP	O	6
Wabash	Warren, IN	128	165	RP	O	3
Ruppert	Fountain, IN	51	58	CP	O	3
Niawathe	Dade, MO	212	178	LP	F,M	2
Cox	Lawrence, MO	112	1302	LP	F,M	2
New Marionville	Lawrence, MO	120	200	RRP	O	2
Rescue	Lawrence, MO	120	191	RP	O	3
Rescue A	Lawrence, MO	133	150	RP	O	3
Kendricktown	Jasper, MO	109	77	RRP,OV	O	3
Baker	Boone, AR	119	166	LP	F,M	3

* Over period of study. Not all plants necessarily alive at one time.

† As of 1992 except for Florence, estimated in 1990.

Site: RRP, railroad prairie; CP, cemetery prairie; RP, roadside prairie; LP, large prairie; OV, overgrown.

Management: F, fire; M, mowing/haying; O, other (sporadic herbicides, mowing, or none).

Environmental Measurements, Population Sizes and Isolation

We recorded environmental data at the location of each plant: percentage vegetation cover (six classes), litter depth and substrate class (undisturbed, disturbed, gravel, moss). Population sizes were determined by direct counts at the time of peak flowering in 1992. We determined the distribution of neighboring populations by direct observations (as feasible) and by distribution records for *S. regia*, which are relatively complete in the four states covered by this study. Study populations were characterized as isolated if no other *S. regia* populations were known to occur within 2.5 km. This cut-off divided populations into two similar-sized groups of isolated and not isolated populations. Long-distance movements of *S. regia* pollinators have not been quantified.

Analytical Methods

Defining Demographic Parameters and Stages

We summarized stem-level data such as height, base diameter, and number of flowering whorls at the plant level. Survival variables were summarized for each plant. We categorized plants absent in one year, but found again later, as dormant (as in Mehrhoff 1989), although their absence could also be due to herbivory, human error, etc. Dormant category plants comprised less than 5% of all plants at all sites, and were not included in demographic analyses for the years adjacent to the dormant year. (Plant dormancy is known in at least two other *S.* species; Lesica & Steele 1994; Kephart & Paladino 1997.) We defined mortality as the disappearance of marked plants for the duration of the study.

Initially, we distinguished four stage categories passed on morphology and reproductive status. Seedlings were identified by cotyledons during their first census. Prior germination experiments suggested no seed dormancy (Menges 1991a); thus seedlings are produced from flowering individuals in one year and no seed stage is needed in demographic models (Caswell 1989). Vegetative plants are non-flowering individuals older than seedlings. The largest class of plants consisted of flowering individuals. We subsequently separated these into stages based on total height (summed over all stems), size variables that best predicted demographic performance. Finally, we specified an ‘alive-undefined’ stage represented by individuals alive but with no size or flowering data, usually as a result of mowing but sometimes due to herbivory.

We implemented the Moloney algorithm (Moloney 1986) to determine the optimal division of flowering plants into stages based on total height. The algorithm specifies category sizes and cut-offs by minimizing the summarized of the sample and distribution errors associated with any classification category, and accounting for differences in transition probabilities among sub-populations and census periods. We used 100 samples to estimate the sample error, and included stages with at least 100 plants. We determined the category size maximum on a non-linear fitted curve between the summed error and category maximum.

Estimating Demographic Parameters

We obtained proportions of plants moving between vegetative and flowering plant stages directly from demographic data. We used actual data from each population and year when possible, but when sample sizes for a stage were less than five, aggregate data (across years, within populations) were used (as in Bullock *et al.* 1994). In cases with fewer than five observations across years within a population, species-level means were used. Of all stage-year-population columns, 172 (70.2%) had specific data for year and population, 47 (19.2%) had data pooled across years, and only 26 (9.6%; mainly large reproductives) had data pooled species-wide.

We compared seedling densities and flowering plant densities to calculate seedlings per flowering plant in an average seedling recruitment year, and partitioned seedling numbers among reproductive plants of various sizes in proportion to their estimated fecundity (number of flowering whorls, on average). These provided fecundity terms for the various projection matrices. Fecundity (seedlings produced per reproductive plant) was not varied to reflect individual populations due to the rarity of seedlings. We assembled population-specific seedling survival rates when sample sizes permitted (for four populations). Otherwise mean seedling survival rates were used for populations grouped by management regime, since management regime affected seedling survival (see the Results).

We formed matrices for individual populations and years, with and without fecundity. A total of 98 separate projection matrices were constructed (individual matrices are available from the first author). A matrix representing a composite population was also formed from data on all plants in the study.

Modeling Population Dynamics and Extinction

We used the program POPPROJ (Menges 1992) to calculate finite rates of increase, with and without recruitment, from the matrices. Rates of increase were checked using the RAMAS-STAGE program (Ferson 1994). For years with recruitment we defined λ_R as the finite rate of increase. For years without recruitment, the rate was λ_N . POPPROJ was also used to simulate late stochastic population dynamics, by simultaneously varying fecundity scenarios (year with or without recruitment) and year to year data on survival and growth. To do this, we alternated matrices representing each pair of years' data (probabilities of each matrix equal), either with recruitment or without (probability based on proportion of years with recruitment). Depending on available data, between two and 12 matrices were alternated for each population. Density-dependence was not modeled.

For each population, stochastic simulations used 1000 replicate runs (cf. Harris *et al.* 1987) of either 100 years or 1000 years each. We based initial population size and non-seedling stage structure on the last field census for the population, with observed proportions in various stages extrapolated to the whole population if only a portion had been sampled. We estimated initial seedling numbers based on species means for the most recent year's seedling production by reproductive plants (by stage), rather than by observed seedling numbers, which were based on limited sampling. Populations were considered extinct if size dropped below one within 100 years or 1000 years.

Relating Demography to Other Factors

We initially used univariate analyses, then multivariate analyses, to relate population viability estimates (median finite rates of increase λ_R and λ_N , extinction probabilities) to management regime, population size, geographic region, degree of isolation, amount of genetic variation and habitat characteristics, using ANOVAs and other statistical tests with SPSS (Norusis 1993). Because the four genetic variation variables (from Dolan 1994) were highly intercorrelated ($r > 0.80$, $P < 0.01$ for all pair-wise comparisons), we used principal components analysis to construct PCA axis 1 scores that served as a single index of genetic variation. Not all co-variate-factor interaction terms could be included simultaneously with only 15 populations, so partial analyses were used to cull non-significant co-variate-factor interaction terms. Final ANOVAs did include all interactions among factors.

Elasticities quantify the proportional effects of small changes in demographic parameters on λ (de Kroon *et al.* 1986; Caswell 1989). We calculated elasticities using the RAMAS-STAGE program (Ferson 1994) for each matrix (representing different populations and years). Composite elasticities representing growth (G, advance in stage), survival (L, stasis or regression in stage) and fecundity (F) were calculated (as in Silvertown *et al.* 1996), and related to λ_R using regression. We also examined the effects of management regime on G, L and F by calculating means of G, L and F across years within populations (including those years where terms involving the alive-undefined stage constituted less than 0.15). Elasticity differences among the three management regimes were tested at the population level using one-way ANOVA with a Student-Newman-Keuls (SNK) test for pair-wise differences when appropriate.

Results

Recruitment Terms

Seedling recruitment is episodic in *S. regia* populations. We never observed seedlings in about half of populations studied, and only three populations had seedlings observed in two or more years, despite intense searches during 1990-92. Seedlings were observed in five of the six populations managed using fire, but in only three of 10 populations managed without fire (Fischer's exact test, $P = 0.059$). Seedling recruitment years were also more frequent for sites managed by fire, with or without mowing, compared to unburned sites (Fig. 2).

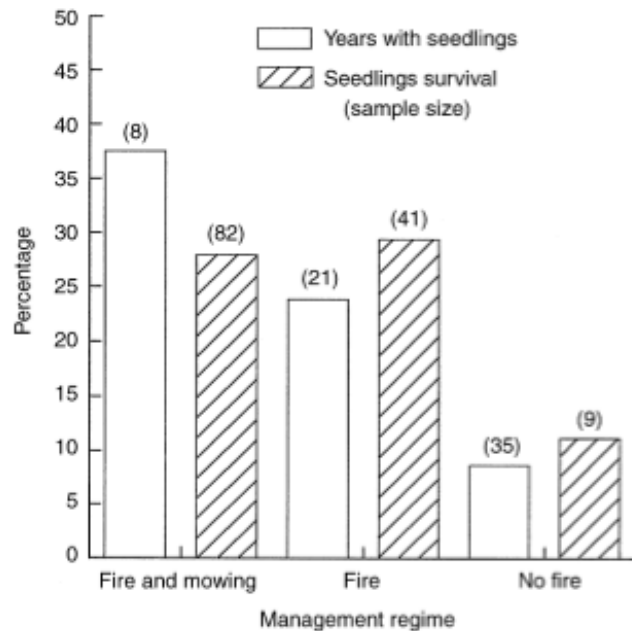


Fig. 2 Percentage of population years with seedlings appearing at a site and percentage annual seedling survival at a site, as a function of management regime, for *S. regia*. Unburned areas are managed with mowing, herbicide, or are unmanaged. Numbers in parentheses represent sample sizes (number of population \times years we search for seedlings or numbers of seedlings followed).

Seedlings were found only four times during intense searches in the narrow belt transects in 1990-92. The overall mean seedling density was 2.2m^{-2} for these cases. Given a mean flowering plant density of 0.29m^{-2} , mean fecundity was calculated to be 7.5 seedlings per flowering plant during recruitment episodes. This rough estimate was used to estimate seedling production from each of the three reproductive stages for the composite population as proportional to mean numbers of flowering whorls. There were not sufficient data to provide seedling density estimates for populations or years individually.

Frequencies of years with seedling recruitment were difficult to estimate from a short-term study of a species with apparently episodic recruitment. An approach of combining

apparently similar populations under similar management was used. We calculated the frequency of seedling recruitment as 0.375 (three out of eight year-site combinations) for burned and mown sites, 0.238 (five out of 21) for burned sites, and 0.086 (three out of 35) for other management treatments (Fig. 2).

Seedling Fates

Annual seedling survival was low and variable (0-33% by population). For populations with more than 10 seedlings in total, population-specific values were used. For other populations, means for populations undergoing similar management were used in modeling. Seedling survival was highest for burned management treatments and lowest for non-fire management (Fig. 2). Mean seedling survival for management regime was used for populations with fewer than 10 seedlings total.

Adult Demography

Silene regia is a long-lived perennial herb with relatively stable demographic parameters. Annual mortality is low, averaging 5-17% by year (Table 2). More than three-quarters of established plants (non-seedlings) flower each year, and these flowering plants usually have less than 10% annual mortality (Table 2). However, established plants do not necessarily grow quickly from year to year and median total height changes were negative in 2 of 6 years with sufficient data. Plants typically have 1-10 stems, and the median change in number of stems was always zero (no change) while mean values were always small and were negative in 4 of 7 years (Table 2).

Table 2 Summary statistics for all *S. regia* plants studied, by year. Beginning in 1990, Missouri and Arkansas populations were added to the study

Statistic	1985-86	1986-87	1987-88	1988-89	1989-90	1990-91	1991-92
Annual mortality (%) total	9.4	5.1	14.8	16.8	9.4	5.7	14.5
Flowering plants—all	6.9	4.6	9.5	11.6	6.6	4.6	13.4
Ohio/Indiana	6.9	4.6	9.5	11.6	6.6	5.6	6.4
Missouri/Arkansas	—	—	—	—	—	2.1	19.7
% plants flowering*	77.1	88.1	58.8	77	74.8	85	79
Median % change in total height**	NA	+13%	-32%	+52%	-8%	+37%	+13%
Median change in number of stems	0	0	0	0	0	0	0
Mean change in number of stems	-0.23	+0.26	-0.18	-0.33	-0.07	+0.29	+0.08

* Of plants with flowering status defined, excluding seedlings, for first year in pair.

** Summed over all stems

Construction of Projection Matrices

The Moloney (1986) algorithm, as implemented, suggested three classes of flowering plants defined by total (summed) height (2-228cm, 229-569cm, > 570cm; total sample sizes number 2796, 1309 and 208, respectively, for the three stages). With the additional previously defined stages of seedlings, vegetative plants and alive-undefined, we modeled *S. regia* population

dynamics using transition matrices with six stages. A total of 98 matrices was formed for combinations of population, year and recruitment vs. no recruitment (each is of the form given in Table 3). Matrices feature both advances and regressions in stage, although modal transitions for most stages represent stasis (as in Table 3).

Table 3 Example of projection matrix for the *S. regia* population at Milford 1990-91, assuming recruitment. Numbers represent the proportion changing from the stage of the column to the stage of the row. Transitions in bold represent stasis (plants remaining in the same stage). Numbers in the first row represent seedlings produced by flowering plants (see text). Dashes are undefined transitions. Finite rate of increase given recruitment (as shown), $\lambda_R = 1.67$, λ_N (without seedling recruitment) = 0.96. This is one of 98 matrices analyzed; each represents a specific population, pair of years, and recruitment scenario (recruitment, no recruitment)

	Seedling	Vegetative	Small flowering	Medium flowering	Large flowering	Alive undefined
Seedling	—	—	5.32	12.74	30.88	—
Vegetative	0.308	0.111	0	0	0	0
Small flowering	0	0.566	0.506	0.137	0.167	0.367
Medium flowering	0	0.111	0.210	0.608	0.167	0.300
Large flowering	0	0	0.012	0.039	0.667	0.167
Alive undefined	0	0.222	0.198	0.196	0	0.133

Composite Population Behavior

The composite *S. regia* population was projected to decline slightly in the absence of recruitment ($\lambda_N = 0.90$). For years with recruitment, large increases were projected ($\lambda_R = 1.46$) Hence, variation among populations in recruitment rates and the frequency of recruitment are important to understanding population viability in *S. regia* (see below).

Projected Population Dynamics

Projected finite rates of increase for years with no recruitment (λ_N) ranged from 0.445 to 0.986, varied widely across populations, and varied moderately across years (Fig. 3 and Appendix 1). For years with recruitment, median values of λ_R generally exceeded 1, ranging from 0.571 to 1.829, with similar variation at all sites (Table 4). All sites with median $\lambda_R > 1.35$ were burned (and some mowed as well). Other populations received sporadic mowing and/or herbicide but were not burned. The effect of fire management on λ_N is not as clear-cut (Table 4). Similar patterns were seen when ordering sites by λ values predicted from 1990-92 data, a period when almost every population was studied (data not shown).

Given episodic recruitment and year-to-year variation in growth and survival, stochastic simulations are a more realistic way to view *S. regia* population dynamics. Stochastic simulations resulted in three groups of populations. One group of five populations always went extinct within 100 years (Table 4). The remaining 11 populations nearly always persisted for 100 years (extinction probabilities 0.0-0.2%), but only eight of them always persisted for 1000 years. We term the latter as having no extinction risk (Table 4). The three remaining populations (extinction risk-possible) had 1000-year extinction risks of 10.3% (Rescue), 30.2% (Wabash) and 96.4% (Paint Creek). These three populations all tended to have population sizes below 5000

(and usually below 1000) after 100 years, while the populations with no extinction risks had grown much larger. Field populations with ceilings of 5000 or less may be at risk over thousands of years.

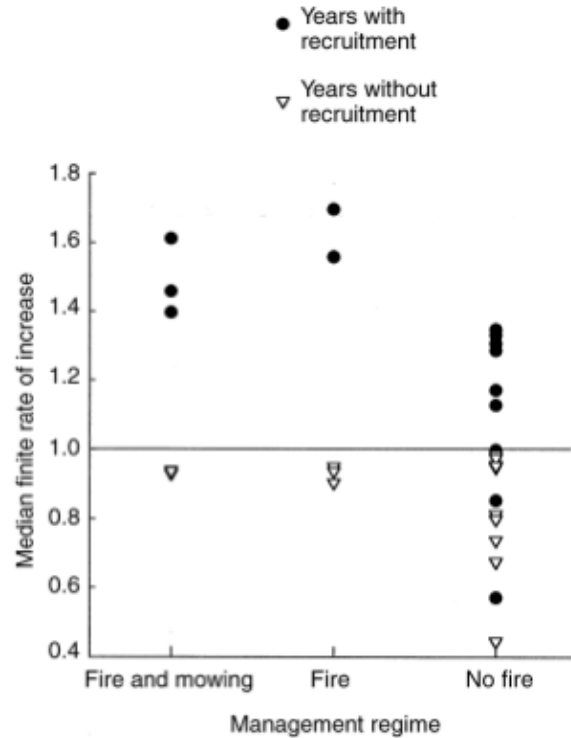


Fig. 3 Median finite rates of increase of *S. regia* populations as a function of management regime, considering recruitment years (λ_R) and non-recruitment years (λ_N). Each symbol represents one site's median. Unburned management regimes include mowing, herbicide or are unmanaged.

Univariate Effects of Management

The three groups of populations classified by 1000-year extinction risk (Table 4) also corresponded closely to prairie management regimes. No sites in the group with extinction assured within 100 years were managed using fire or for conservation purposes, although sporadic mowing and herbicide use occurred at these sites. The group with no extinction risk in 1000 years included all six of the sites that were managed using fire or a combination of fire and summer mowing; five of these six sites were managed for conservation goals. The intermediate group with possible extinction in 1000 years was mown and herbicided regularly.

Table 4 Predicted median finite rates of increase (λ_R = recruitment; λ_N = no recruitment) and extinction possibilities for all studied *S. regia* populations. Populations are ordered by extinction probability and (within extinction risk class) by median . For λ values for individual years, see Appendix 1.

Population	Management	Median λ_R	Median λ_N	Extinction probability	
				100 years	1000 years
Extinction risk none					
Bigelow	Fire	1.829	0.950	0.0	0.0
Smith	Fire	1.696	0.938	0.0	0.0
Baker	Fire and mowing	1.611	0.931	0.0	0.0
Milford	Fire	1.557	0.905	0.0	0.0
Niawathe	Fire and mowing	1.458	0.934	0.0	0.0
Cox	Fire and mowing	1.396	0.937	0.0	0.0
Rescue	Other	1.346	0.986	0.0	0.0
Ruppert	Other	1.286	0.950	0.0	0.0
Extinction risk: possible					
Rescue A	Other	1.286	0.956	0.0	10.3
Wabash	Other	1.330	0.976	0.0	30.2
Paint Creek	Other	1.306	0.954	0.2	96.4
Extinction risk: assured					
Kendricktown	Other	1.171	0.801	100.0	100.0
Florence	Other	1.128	0.814	100.0	100.0
Stone Bluff	Other	0.998	0.739	100.0	100.0
Selma	Other	0.854	0.676	100.0	100.0
New Marionville	Other	0.571	0.445	100.0	100.0

Prairie management of *S. regia* populations significantly affects population viability (Table 5). Management type (fire, fire + mowing, no fire) was significantly related to the extinction probability group in contingency table analysis (Goodman and Kruskal (tau = 0.372, $P < 0.05$). Fire effects (fire, no fire) were even more highly significant (tau = 0.372, $P < 0.01$). Management type also predicted λ_R (one-way ANOVA, $F = 8.89$, $P = 0.037$), with the difference between burned and other management types significant (SNK test, $p < 0.05$). Management type did not successfully predict λ_N ($F = 0.94$, $P = 0.41$). For fire management as a whole compared to no fire, λ_R differed ($F = 16.14$, $P = 0.0013$) but λ_N did not ($F = 2.03$, $P = 0.176$) (Table 5).

Univariate Effects of Population Size, Isolation and Genetics

Population size and isolation were not significant univariate predictors of population viability (Table 5). Finite rates of increase were positively and nearly significantly correlated with the log of population size ($r = 0.49$, $P = 0.057$ for λ_R , $r = 0.27$, $P = 0.309$ for λ_N). Likewise, the log of population size did not differ among extinction risk groups ($F = 1.71$, $P = 0.219$). Whether a population was isolated did not affect finite rates of increase ($F = 0.38$, $P = 0.548$ for λ_R ; $F = 2.03$, $P = 0.176$ for λ_N) or extinction class (Goodman and Kruskal tau = 0.013, $P = 0.827$).

Genetic variation (data from Dolan 1994) was weakly correlated with demographic estimates of population viability. Spearman correlations of four genetic measures with λ suggested that populations with more isozyme bands had higher median λ_R and λ_N , and populations with higher genetic diversity (Shannon-Weaver diversity index) had high median λ_N (Table 6). However, significant patterns were seen in only three of eight comparisons and

correlations were fairly weak. Measures of genetic variation tended to be higher for populations with no risk of extinction than for the other two groups, but no differences were statistically significant.

Table 5 Summary of importance of individual factors (fire management, isolation and size of populations) on extinction risk group and finite rates of increase for populations of *S. regia* (number of classes in parentheses)

Viability component	Factor (number of classes)			
	Fire (2)	Management (3)	Isolation (2)	Log Size
Extinction risk group†	**a	*a	NS ^a	NS ^b
λ_R	**b	*b	NS ^b	X ^c
λ_N	NS ^b	NS ^b	NS ^b	NS ^c

** $P < 0.01$

* $P < 0.05$

X, $P < 0.1$

NS, $P > 0.1$

† From Table 4

^a Tau statistic

^b One-way ANOVA

^c Pearson's correlation

Table 6 Spearman correlations of relationships between median λ_R and λ_N , and genetic variation for *S. regia* populations, $n = 15$

	Number of bands	Number of phenotypes	PI†	H**
λ_R	0.454*	0.278	0.243	0.404
λ_N	0.498*	0.379	0.265	0.461*

† PI, polymorphic index

* $P < 0.05$

** H, Shannon-Weaver diversity

Multivariate Analysis for Combined Effects of Fire, Population Size, Isolation, Region and Genetics on Demographic Population Viability

Fire, region, genetic variation, population size and isolation all contributed to predicting finite rates of increase (Table 7). Preliminary ANOVAs eliminated all co-variate-factor interactions (except fire by size) from the two final analyses. The strongest variables were fire and geographic region. Higher population growth rates were found in burned areas and in the eastern region. Separate summaries of means confirmed larger λ_R in burned but unmown sites (all of which were eastern). than in burned and mown sites (all western). The effects of regional differences were clearly seen only in burned sites (Fig. 4), indicated by a significant region \times fire interaction in the ANOVA. In addition, λ_R was higher for populations with high genetic diversity, and in larger populations. The population size \times fire interaction was significant (Fig. 5). Isolation was nearly significant as a predictor of λ_R (Table 7), with less isolated populations showing higher λ_R . λ_N responded to similar variables as λ_R , although fire and interaction terms were less important.

Predictions of extinction risk group from the suite of variables was weak overall (Wilks' lambda = 0.19, $P = 0.09$). Region, genetic variation and fire loaded most strongly on axis 1 of a discriminant analysis, while region, population size and genetic variation loaded most strongly on axis 2 (Fig. 6). Classification success was 80%. The group of populations classified as having assured extinction were separated by the first two discriminant functions from the group classified as having no chance of extinction (Fig. 6).

Table 7 ANOVA for finite rate of increase with recruitment (λ_R) for *S. regia* populations

Source of variation	Sum of squares	d.f.	Mean square	<i>F</i>	Significance of <i>F</i>
Co-variates	0.162	3	0.054	38.282	0.002
Genetic variation (PCA axis score)	0.058	1	0.058	41.028	0.003
Fire × population size	0.118	1	0.118	83.243	0.001
Log population size	0.059	1	0.059	42.087	0.003
Main effects	0.880	3	0.293	207.534	0.000
Isolation	0.006	1	0.006	4.153	0.111
Region	0.140	1	0.140	99.277	0.001
Fire	0.105	1	0.105	74.144	0.001
Two-way interactions	0.019	3	0.006	4.502	0.090
Isolation × region	0.008	1	0.008	5.475	0.079
Isolation × fire	0.000	1	0.000	0.139	0.728
Region-fire	0.005	1	0.005	3.612	0.130
Three-way interactions	0.004	1	0.004	2.914	0.163
Isolation × region × fire	0.004	1	0.004	2.914	0.163
Explained	1.467	10	0.147	103.802	0.000
Residual	0.006	4	0.001		
Total	1.473	14	0.105		
Co-variate	Raw regression coefficient				
Genetic variation	0.355				
Fire × population size	-0.001				
Log population size	0.430				

Elasticity Patterns

Among the 98 matrices, elasticities were often highest for seedling growth to vegetative plants, for vegetative plant advance to small reproductive plants, for survival (stasis) of small reproductive plants, and for fecundity of small- and medium-stage reproductive plants. Elasticities were nearly always minute for large reproductive plants and the alive-undefined category. With very few exceptions, all individual elasticity values were less than 0.25, implying that many life-history elements contribute to overall demographic processes. Elasticity varied only modestly among years within populations.

In growing populations, growth elasticities (G) and fecundity elasticities (F) were relatively high. Correlations with λ_R were significant and positive for F ($r^2 = 0.647$) and G ($r^2 = 0.499$), and significant and negative for survival elasticities L ($r^2 = -0.571$). Elasticity patterns

also varied predictably as a function of management regime. Areas managed using fire had higher composite elasticities for growth (G) and fecundity (F) and lower composite elasticities for survival (L) than unburned areas (Fig. 7). In one-way ANOVAs, G values differed among management treatments ($F = 7.33, P = 0.007, \text{d.f.} = 15$) and L values were weakly different ($F = 3.15, P = 0.077, \text{d.f.} = 15$). For G, significant pair-wise differences ($P < 0.05$) were found between unburned populations and each of the two burned treatments (burned, burned and mowed).

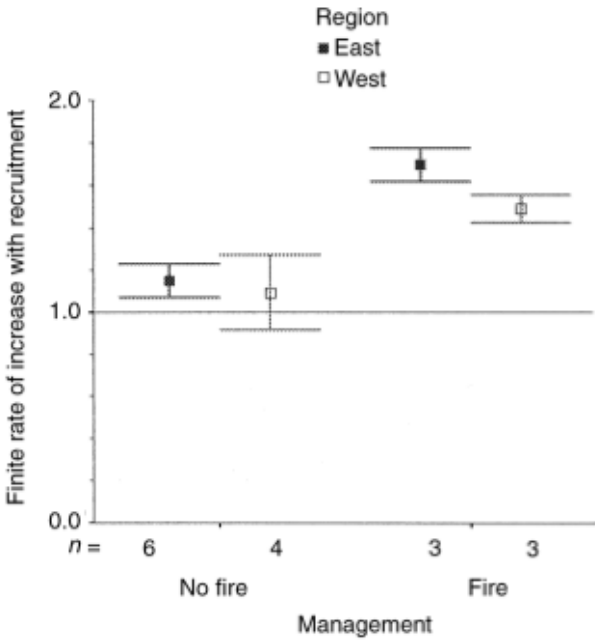


Fig. 4 Median finite rate of increase with recruitment (λ_R) of *S. regia* populations as a function of fire management and region. Shown are means and standard errors across populations. Fire, region and their interaction were significant predictors of λ_R in ANOVA.

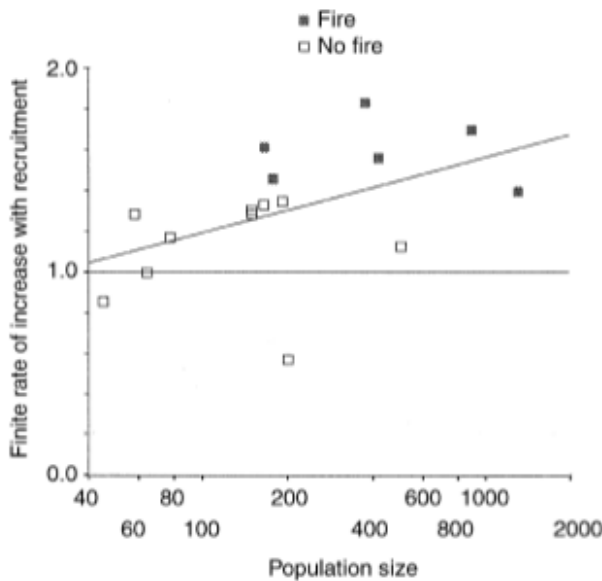


Fig. 5 Median finite rate of increase with recruitment (λ_R) related to *S. regia* population size (log scale) and fire management. Each square represents one population. The regression line is for both burned and unburned populations, $r^2 = 0.2354$. The population size \times fire interaction was significant in ANOVA predicting λ_R .

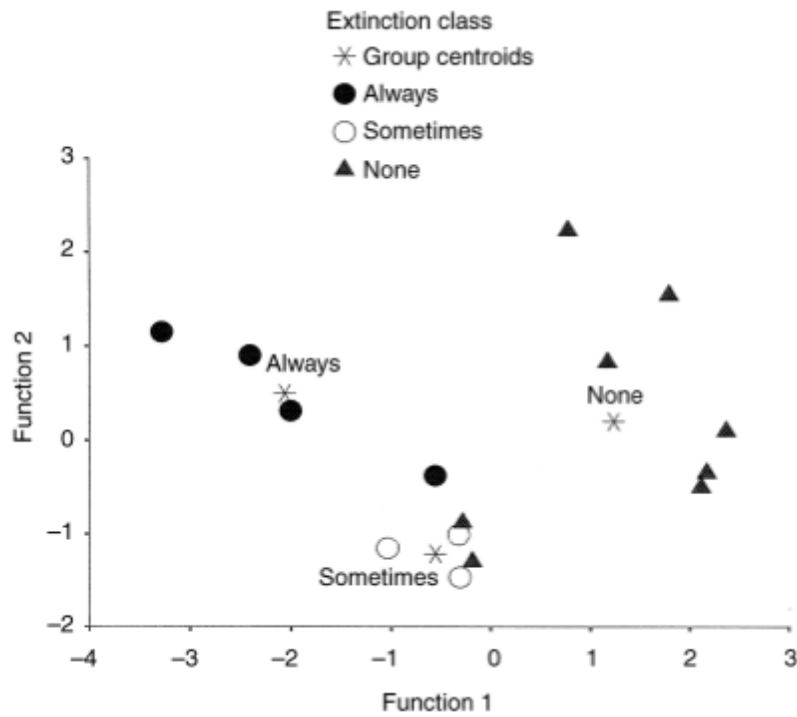


Fig. 6 Discriminant analysis plot showing relationship of *S. regia* extinction probability class to the first two discriminant functions. Group centroids are indicated by asterisks; other symbols represent individual populations coded by their extinction probability class (see Table 4 and text).

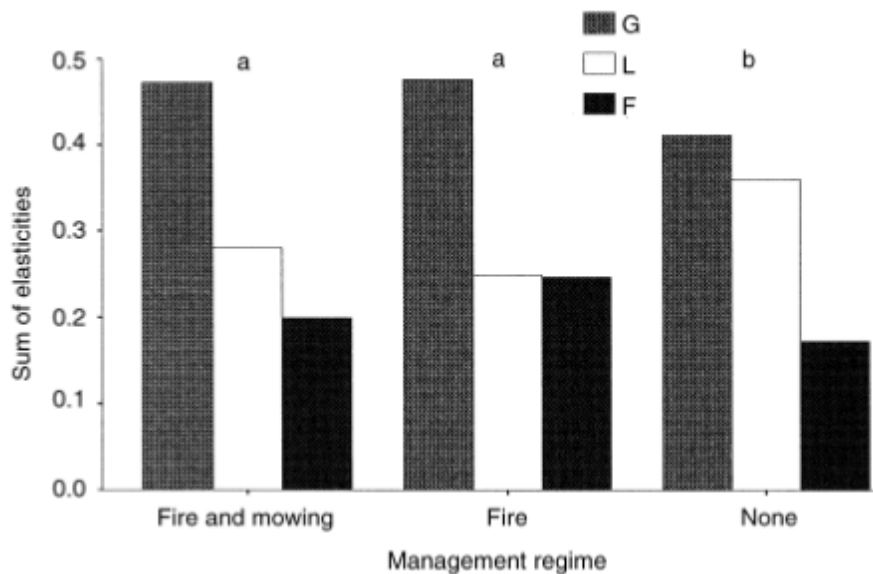


Fig. 7 Variation in composite elasticities G (growth), L (stasis and regression) and F (fecundity) for *S. regia* populations as a function of management regime. Letters indicate significant ($P < 0.05$) pair-wise differences among management regimes on G. No such differences were significant for L and F. The elasticities shown do not sum to 1 because elasticities associated with the alive-undefined stage cannot be classified as G, L or F, and so were not included in the analysis.

Discussion

Demography of Silene regia

For *S. regia* adults, average survivorship is high (usually more than 90%), most plants flower in any year (often 75% or more) and plants often grow slowly if at all from year to year. There is a fairly low rate of population decline in the absence of recruitment (e.g. $\lambda_N = 0.90$ for the composite *S. regia* population). High adult survival and a tendency to remain the same size are also characteristic of *S. douglasii* var. *oraria*, a grassland endemic of the Pacific north-west (Kephart & Paladino 1997).

While adult demographic parameters are fairly consistent at a site over time, seedling dynamics are highly variable. Recruitment was observed in a minority of years even in sites that were relatively favorable for seedlings. Variable seedling recruitment has been documented for another long-lived prairie forb *Ipomoea leptophylla* (Keeler 1991). Lack of recruitment in *S. regia* is not due to failures in seed production or germination. Seed production is high and the average laboratory germination rates exceeded 75% in a study of seeds from 23 prairie populations (Menges 1991a). The observed low establishment rates in the field may be due to frugivory by rodents or ants, germination when environmental conditions are harsh (seedlings seem especially susceptible to desiccation in laboratory studies), or competition for light with established vegetation, especially in unburned areas.

Once *S. regia* seedlings reach the juvenile stage, survivorship is high and individuals appear to be long-lived. These patterns were also evident for *S. douglasii* var. *oraria* (Kephart & Paladino 1997) and other perennial herbs of prairies (Weaver 1958; Platt 1975; Weller 1985; Keeler 1991). The large tap root of *S. regia* may contribute to its longevity by storing resources that can be used to carry a plant through to the next growing season if stems are browsed or broken (as in *Ipomoea leptophylla*; Keeler 1991).

Demographic parameters, including matrix transition elements, varied among populations and over time in *S. regia*. Such variation seems to be the rule for plant species (e.g. Bierzychudek 1982; Nult & Gagnon 1993; Horvitz & Schemske 1995; Oostermeijer *et al.* 1996a; Damman & Cain 1998). Finite rates of increase varied widely among populations and across management treatments, but modestly among years within the same population. Median finite rates of increase also varied widely across populations (0.445-0.950 without recruitment, 0.571-1.829 with recruitment). Finite rates of increase for *S. douglasii*, varied more narrowly across years and populations ($\lambda = 0.82-1.12$; Kephart & Paladino 1997) than *S. regia*.

Given this variation, it is appropriate to project *S. regia* demography using stochastic population models that can incorporate observed variation in demographic parameters, especially the episodic nature of seedling recruitment. Such models predict that our study populations fall into three groups: no extinction risk in 1000 years (eight populations), possible extinction between 100 and 1000 years (three), and extinction assured within 100 years (five). Due to uncertainty in parameter estimates, extinction times may be biased in population viability analyses (Taylor 1995), so little weight is given to small differences in extinction risk within the intermediate class of populations.

Life History Analysis

Elasticities vary mainly among populations and less so with time for *S. regia*. Growing populations have higher composite elasticities for growth and fecundity, and lower elasticities for survival, than declining populations. Our analysis of elasticities suggests that burning shifts the environment in ways that are fundamental to the life history of *S. regia*. In populations managed by fire, plant growth and seedling recruitment (fecundity) contribute greatly to population growth and *S. regia* is near the G end of the elasticity triangle (Silvertown *et al.* 1993; Silvertown *et al.* 1996), typical of iteroparous herbs of open habitats. In unburned prairies, the position for *S. regia* is about midway between the G and L apices and at a larger distance from the F apex. This region can be occupied by iteroparous herbs of either open or forested habitats (Silvertown *et al.* 1996). Demographically speaking, lack of burning has made these prairie sites more similar to forests. A similar shift in the GLF spectrum occurs in *Gentiana pneumonanthe* in disturbed (sod cut) sites compared with undisturbed sites (Oostermeijer *et al.* 1996a). A positive relationship of G or F to λ has been found among populations of other species (Silvertown *et al.* 1996). As Silvertown *et al.* (1996) and Oostermeijer *et al.* (1996a) argue, caution is needed in extrapolating from elasticities to management recommendations because reversing declines will require changes in several parts of the life cycle, whereas elasticities calculate changes in λ from individual matrix elements.

Effects of Fire

Silene regia clearly performs best in sites that receive prescribed burning. Recently burned *S. regia* sites have lower woody plant cover and shallower litter than unburned sites (Menges 1988). Extinction-prone populations all occurred on sites with significant woody plant or vine invasion, or severe physical disturbance. The return of fire to unburned *S. regia* populations can have dramatic effects. King (1981) describes sevenfold increases in population size in a decade following the introduction of fire to one of our Ohio study populations. Plants may have been dormant or suppressed by competition and/or frequent mowing prior to burning.

Fire affects most aspects of *S. regia* demography. Seedling recruitment happens mainly in burned sites and seedlings survive better there. Periodically burned *S. regia* populations have higher adult survival and growth (Menges 1988). Finite rates of increase (with recruitment) are significantly higher in burned sites. Prescribed burning therefore emerges as the single most significant factor influencing a population's likelihood of survival. Management using fire or other disturbances that provide opportunities for seedling recruitment will help maintain viable populations of *S. regia*. Substrate manipulation to increase recruitment has also been recommended for other rare plants (e.g. Pavlik & Manning 1993; Oostermeijer *et al.* 1996a), and fire specifically has been demonstrated to increase growth, recruitment and flowering of *S. spaldingii* (Lesica 1994). Similarly, microsites with short vegetation, low cover and shallow soils were associated with relatively high abundance of *S. douglasii* var. *oraria* (Kephart & Paladino 1997). Size-classified matrix models have been used in various contexts to demonstrate the importance of fire on λ (Silva *et al.* 1991).

Regional Differences

In multivariate analyses, region (east vs. west) was the second strongest predictor (after fire) of finite rate of increase. Controlling for fire and other effects (including genetics), population growth was more rapid in eastern populations (Ohio, Indiana) than in western populations (Missouri, Kansas). The strongest regional differences were seen in burned sites. We do not understand the reasons for this result since there are many differences between the regions that are not accounted for in the analysis. One likely difference may be the greater frequency of summer droughts in western sites, which may constrain prairie productivity and make the frequent occurrence of fire less critical than in eastern sites.

Genetic Variation, Population Size, and Isolation

Dolan (1994) examined the relationship between population size, isolation and genetic variation in 18 *S. regia* populations. Based on population genetic theory, smaller, more isolated populations were predicted to have lower levels of genetic variation. These predictions have been upheld in some studies (e.g. Van Treuren *et al.* 1993; Prober & Brown 1994; Raijmann *et al.* 1994; Ouborg & Van Treuren 1995) but not all (e.g. Shapcott 1994). However, these trends were not found in *S. regia* populations from the western part of the species' range (unglaciated sites in Missouri and Arkansas). For populations from Indiana and Ohio, only one of four measures of genetic variation was significantly correlated with population size. Isolation was not significantly correlated with *S. regia* genetic variation in either region. Evidence of greater population differentiation in the eastern populations of *S. regia* was attributed to lower levels of interpopulation gene flow in the fragmented remnant prairies of Indiana and Ohio (Dolan 1994).

When data from many of the same sites reported in Dolan (1994) were analyzed in this paper, population size had a nearly significant correlation with finite rates of increase. However, when management regime and region were controlled, larger populations had significant higher finite rates of increase. Small populations of this species also had relatively low germination in the laboratory, a finding similarly attributed to inbreeding depression (Menges 1991a). Similarly, seed size, seed germination and regrowth following herbivory were all reduced in plants from smaller populations of *Ipomopsis aggregata*, and this reduction could be countered by addition of pollen from distant populations (Heschel & Paige 1995). Plants from smaller populations of *Geniana pneumonanthe* have reduced fitness attributed to both inbreeding depression and habitat deterioration (Oostermeijer *et al.* 1994a).

When other variables were controlled for, and among unburned populations, isolated populations were more extinction-prone and smaller populations had lower finite rates of increase. Unburned populations were subject to the effects of litter build-up and intense competition from woody plants. They suffered lower survival, lower fecundity and little, if any, seedling recruitment. Isolated populations reduced in size by lack of fire may be at greater risk of genetic erosion.

The univariate relationships between *S. regia*'s genetic variation and demographic viability were fairly weak. However, genetic variation had positive effects on finite rates of

increase and negative effects on extinction probability in multivariate analyses that included the effects of management.

Although there has been a tendency of researchers to study either demographic or genetic aspects of population viability, the two are linked in ways that are difficult to separate completely. Demographically defined population viability in *S. regia* is only weakly correlated with current genetic variation. Current genetic structure may still reflect the higher regional abundance of *S. regia* before habitat loss. Since *S. regia* is long-lived, current genetic variation in small, isolated populations may not be stable, and genetic erosion could affect population viability. Demographic modeling over 100 or 1000 years assumes the current range of conditions, and so ignores effects of future genetic erosion.

Conservation Biology, Management and the Evaluation of Extinction Risk

It is a paradigm of conservation biology that both within-population genetic variation and population viability are expected to increase with population size and to decrease with population isolation (Barrett & Kohn 1991; Ellstrand & Elam 1993; Young *et al.* 1996). For *S. regia*, however, the links between population size, isolation, and genetic variation were significant only in the eastern part of the species range (Dolan 1994), where populations are particularly small and often isolated from neighboring populations. However, regional differences relating to the history of the species' postglacial migration from west to east could also have influenced genetic patterns. Demographically defined measures of population viability (finite rates of increase, extinction probability) strongly support these conservation biology tenets only when the influence of management (mainly fire management) is considered simultaneously. The significance of the effects of isolation, populations size and genetic variation was increased in multivariate analyses with fire management included, relative to univariate analyses.

The overwhelming determinants of *S. regia* population viability (fire management, region) were ecological and historical. Species-specific ecological and biogeographic information will always have a place in evaluating extinction risks of individual species.

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Appendix 1. Summary of finite rates of increase (lambdas); λ by population, year and recruitment for *S. regia*

Population	Recruitment	86-87	87-88	88-89	89-90	90-91	91-92	Median
Bigelow	Yes	1.921	1.371	1.851	1.728	1.882	1.807	1.829
	No	0.989	0.772	0.944	0.963	0.955	0.946	0.950
Milford	Yes	1.715	1.317	1.459	1.415	1.675	1.655	1.557
	No	0.950	0.894	0.868	0.893	0.965	0.916	0.905
Florence	Yes	1.162	1.320	1.094	1.092	—	—	1.128
	No	0.822	0.973	0.805	0.764	—	—	0.814
Selma	Yes	1.196	0.854	0.696	—	—	—	0.854
	No	0.873	0.676	0.504	—	—	—	0.676
Smith	Yes	1.700	1.623	1.701	1.273	1.692	1.710	1.696
	No	0.981	0.972	0.929	0.835	0.919	0.946	0.938
Stone Bluff	Yes	—	1.203	0.914	0.891	0.998	1.088	0.998
	No	—	0.949	0.690	0.636	0.739	0.893	0.739
Paint Creek	Yes	—	—	1.201	1.334	1.279	1.412	1.306
	No	—	—	0.938	0.969	0.933	0.978	0.954
Ruppert	Yes	—	—	—	—	1.268	1.303	1.286
	No	—	—	—	—	0.978	0.921	0.950
Wabash	Yes	—	—	—	—	1.233	1.428	1.330
	No	—	—	—	—	0.959	0.993	0.976
Cox	Yes	—	—	—	—	—	1.396	1.396
	No	—	—	—	—	—	0.937	0.937
Niawathe	Yes	—	—	—	—	1.458	—	1.458
	No	—	—	—	—	0.934	—	0.934
Rescue	Yes	—	—	—	—	1.332	1.359	1.346
	No	—	—	—	—	0.993	0.978	0.986
Rescue A	Yes	—	—	—	—	1.279	1.293	1.286
	No	—	—	—	—	0.988	0.925	0.956
Baker	Yes	—	—	—	—	1.607	1.615	1.611
	No	—	—	—	—	0.961	0.970	0.966
Kendricktown	Yes	—	—	—	—	1.310	1.020	1.170
	No	—	—	—	—	0.990	0.620	0.800
New Marionville	Yes	—	—	—	—	—	0.571	0.571
	No	—	—	—	—	—	0.445	0.445