

Population Trends in Royal Catchfly (*Silene regia*) at Wilson's Creek National Battlefield, Missouri

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ABSTRACT.—Royal catchfly (*Silene regia*, Caryophyllaceae) is a rare, tap-rooted, perennial forb known to occupy Midwestern prairies, glades, and savannas, which are increasingly fragmented. Though not federally listed, it is recognized as rare, threatened, or endangered in six states. We resurveyed 15 populations identified in 1980s–1990s monitoring at Wilson's Creek National Battlefield, Republic, MO. Abundance at each site was collected in 6 y (1988–1989, 1998–2000, 2019); measures of plant height and stems browsed were collected in 4 y (1998–2000, 2019). Fire history and precipitation were also explored. Mean royal catchfly abundance per population declined significantly over the study period, and only five of 15 populations supported extant populations in 2019. Year, site location, and the interaction between the two were highly significant factors in explaining variation of height measures and proportion of stems browsed. Plant height was significantly higher in 2019 than any other year, corresponding with overgrowth of competing vegetation and a wet spring. Prescribed fires became less frequent over the study period, and the mean fire return interval was higher than the historical regime of the region (9.7 y vs. 4–8 y). The decline of royal catchfly at Wilson's Creek National Battlefield and similar sites points to the need for fire management and restoration of prairie and savanna ecosystems for the persistence of this rare species.

INTRODUCTION

Habitat fragmentation and conversion affect nearly every ecosystem type in the United States, yet few as dramatically as prairies and savannas. Once the dominant ecosystems in the Midwest before European settlement, prairie and savanna have been reduced by over 80% (Nuzzo, 1986; Menges, 1995; Anderson, 2006), and remnants have become increasingly fragmented through agricultural conversion, urban sprawl, and fire suppression (Noss *et al.*, 1995; Jefferson *et al.*, 2008; Barrioz *et al.*, 2013). Savannas are particularly vulnerable to degradation, as they are an ecotone between prairie and woodland maintained and structured by frequency and intensity of disturbance (McEwan and McCarthy, 2008). Specifically in Missouri, cultivation, heavy grazing, and cessation of regular fire regimes have resulted in a landscape essentially devoid of savanna, and with very little intact prairie remaining as well (Nuzzo, 1986; Speck, 1992; Jenkins and Jenkins, 2006).

Although agricultural and urban conversions have been arguably the most destructive forces to prairies and savannas, the reintroduction of fire can be a powerful tool for restoring these ecosystems. Fire is a crucial part of the evolution and maintenance of grasslands, encouraging species diversity, keeping cool season grasses and woody plants at bay, and influencing nutrient cycling, pH, and net primary productivity (Jefferson *et al.*, 2008; Bowles and Jones, 2013). Management with fire is frequently cited as the most effective strategy to accomplish restoration of prairies and savannas, and to maintain that restoration in perpetuity (Speck, 1992; Bowles and Jones, 2013; Li and Waller, 2015). However, as knowledge of fire management increases, so too does the understanding that fire effects are

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interwoven with mammalian grazers and climatic factors, which can be difficult to parse (Anderson, 2006; Bowles and Jones, 2013).

In fragmented landscapes, species with specific environmental requirements may be reduced to small isolated populations separated by unsuitable habitat. Previous studies suggest small populations have lower fruit production, lower seed mass, and lower germination success than larger populations (Menges, 1988; Flocca *et al.*, 2004). Small isolated populations are also more likely to experience processes that erode genetic diversity, such as drift, and may be unable to recover from this diversity loss without gene inflow from adjacent populations (Dolan, 1994). For species already patchily distributed, fragmentation may decrease the ability of pollinators to locate their host plants, further exacerbating seed-set and germination issues and diminishing population persistence (Menges, 1988; Schemske *et al.*, 1994).

The royal catchfly (*Silene regia* Sims; Caryophyllaceae), is a rare, tap-rooted, perennial forb known to occupy mesic or wet-mesic prairies, calcareous glades, and cherty savannas, as well as roadsides (Menges, 1988; Dolan, 1994, 1995). It produces red, perfect, hummingbird-pollinated flowers in July to early August, which then mature into dehiscent capsules later in the fall (Menges, 1988; Rabeler and Hartman, 2005). Seeds are gravity dispersed and have no known dormancy period, and no clonal reproduction is known to occur, though individuals may produce more than one stem per plant. The species is characterized by high survivorship, slow annual growth, frequent flowering, and episodic seedling recruitment, often as the result of soil disturbance, fire management, or both (Menges, 1988; Menges and Dolan, 1998).

Royal catchfly is considered native to twelve states in the Midwest and southeast, with the largest concentration of extant populations occurring in southern Missouri and northwest Arkansas (Menges, 1988). Under consideration to be federally listed under the Endangered Species Act during the 1980s, it was concluded in September 1993 that the species had “proven to be more abundant or widespread than previously believed” and was removed (45 Fed. Reg. 242; 58 Fed. Reg. 188). However, it retains a legal status of Rare, Threatened, or Endangered in six states across its range – Arkansas, Georgia, Illinois, Indiana, Kentucky, and Ohio (Ohio Department of Natural Areas and Preserves, 2018; USDA, NRCS, 2019) – and was declared extirpated from Tennessee in 2013 and officially removed from that state’s rare list at that time (T. Crabtree, pers. comm.). Royal catchfly has been known to occur near the study site in Greene County, Missouri since at least 1883, when it was included on a list of botanical collections of the county by Drury University professor Edward M. Shepard (Bush, 1931).

Like other grassland species, royal catchfly is threatened by continued loss of habitat to agricultural conversion and urban sprawl; in fact, its rarity in the eastern part of its range (Ohio and Indiana) has been attributed primarily to agricultural conversion rather than dispersal issues or narrow habitat requirements (Menges, 1988; Dolan, 1995). Succession of grassland communities to a more closed-canopy condition is both common under reduced-frequency fire regimes in the Midwest (Jenkins and Jenkins, 2006; Barrioz *et al.*, 2013; Li and Waller, 2015) and potentially harmful to herbaceous species richness and occurrence of uncommon species like royal catchfly (Schemske *et al.*, 1994; Barrioz *et al.*, 2013). Specifically, encroachment of eastern redcedar (*Juniperus virginiana*) in the absence of periodic fire can profoundly affect light availability and soil processes, and has been identified as a threat to grassland flora both regionally (Harr *et al.*, 2014) and at the study site (John Milner Associates, 2004).

We revisited the 15 populations of royal catchfly identified at Wilson's Creek National Battlefield to observe how regional threats, shifting park management regimes, and steadily increasing deer populations have affected abundance and plant attributes over the nearly twenty years since they were last monitored. Specific objectives were to (1) document changes in abundance, stem height, and percentage of stems browsed across the park's populations, and (2) evaluate the relationship between these changes and environmental and management factors, specifically prescribed fires and precipitation.

METHODS

STUDY AREA

Wilson's Creek National Battlefield is located in Greene and Christian counties in southwest Missouri (37°6'56"N, 93°25'11"W), on the southern edge of the unglaciated Springfield Plateau (Fig. 1; Speck, 1992). The park was established as a unit of the National Park Service in 1960 and formally dedicated in 1961 with the purpose "to commemorate the Battle of Wilson's Creek [August 10, 1861] and to preserve the associated battlefield" (NPS, 2003; John Milner Associates, 2004).

Bearss (1979) and Gremaud (1986) both identify the pre-European settlement vegetation character of the area as a mixture of prairie, open savanna, and woodland, with many areas "thinly timbered" with oak species (*Quercus* spp.) and little to no underbrush. However, the landscape was considerably altered by agriculture, domestic grazing, fire suppression, and town and railroad development from early European settlement (ca. 1818) through the present. The result is a vegetative community that "today scarcely resembles the one that existed at the time of settlement, or even at the time of the battle" (John Milner Associates, 2004).

Native prairie grass restoration began in the late 1960s and continued through the mid-1990s, with the removal of excess woody and exotic species beginning in the late 1970s and continuing to the present day (John Milner Associates, 2004). Through this period of natural communities restoration, the park's recreational features were also being developed – removal of excess structures on park lands (late 1960s), rehabilitation of the historic Wire Road (late 1970s), removal of county roads within park boundaries (late 1970s–mid-1980s), creation of the vehicle Tour Road (mid to late 1980s), trail construction (mid to late 1980s), etc. – resulting in ongoing soil and vegetation disturbance for much of the late 20th century (John Milner Associates, 2004). Prescribed fires were also reintroduced to the landscape around the same time, with records of management units burned beginning in 1988 and accurate on-the-ground maps of areas burned beginning in the mid- to late-1990s (S.A. Leis, pers. comm.). Although prescribed fire and the treatment and removal of woody and exotic species continues today, park-scale soil and vegetation disturbance tapered off considerably through the late 1990s into the early 2000s as the park's infrastructure was completed (John Milner Associates, 2004).

DATA COLLECTION

From 1986–1989 Missouri Department of Conservation staff assisted the park in conducting preliminary surveys for rare plants, including royal catchfly, during a period of management plan development and restoration (John Milner Associates, 2004). Fourteen populations were identified, and their locations described and marked on paper maps; locations were later taken on Global Navigation Satellite Systems (GNSS) units for most populations. Data collected in the 1988 and 1989 surveys (hereafter "the late 1980s")

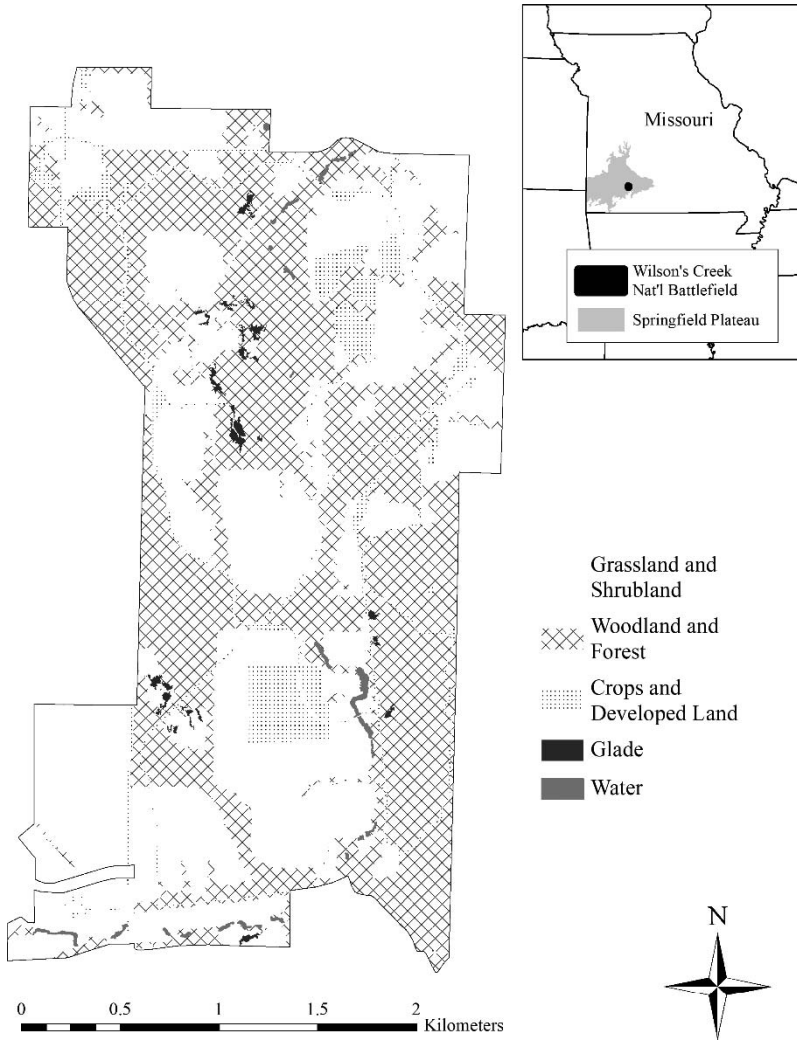


FIG. 1.—Location and vegetation types of Wilson’s Creek National Battlefield, Republic, Missouri. Map inset shows location of park within the unglaciated Springfield Plateau

includes counts of individuals at each site, as well as estimates of percent flowering and percent browsed. Because these estimates of other attributes are subjective in comparison to later efforts, only number of individuals (abundance) contributed to analysis from the late 1980s surveys. Monitoring dates ranged from late July to mid-August.

From 1998–2000 (hereafter “the late 1990s”) most known populations were resurveyed yearly, and two additional populations were identified. One of the new sites (site 15) was later combined with an adjacent known population (site 7), for a total of 15 populations on the park. Data collected during these surveys included qualitative site-level characteristics (vegetation community composition, potential threats to habitat), overall population

characteristics (spatial aggregation, phenology), and individual characteristics (number of stems, height of each stem, number of reproductive structures of all types) for each individual. Observers also noted whether stems showed signs of browse damage from white-tailed deer (*Odocoileus virginianus*). Monitoring dates ranged from mid-July to late August.

In 2019 all fifteen known populations were resurveyed. The locations of sites 10, 11, and 12, which were known only from paper maps in the late 1980s, were estimated in ArcMap 10.7.1 (Environmental Systems Research Institute (ESRI), 2019) and added to the file of other known sites to locate in the field. Due to the gap in monitoring, early season searches were conducted in June to confirm that current habitat conditions could still support populations. Flowering surveys were conducted in late July.

During 2019 flowering surveys the monitoring crew of two to four observers navigated to the site location using a Trimble Geo 7x handheld GNSS system. Beginning at the previously recorded point, observers searched progressively outwards in sweeping arcs for any royal catchfly individuals, using their bright red flowers and distinctive white-cast opposite leaves as the easiest detection characteristics. When an individual was detected, observers measured number of stems, height of each stem, number of leaves, number of flowers, and number of unopened buds, as well as noting if any of the stems showed signs of white-tailed deer browse. A location was collected on the GNSS unit for each individual or cluster of individuals. Qualitative site-level characteristics were also collected, as in the late 1990s surveys. A population was deemed to have no detectable individuals (*i.e.*, no mature plants, flowering or non-flowering) after 20–50 observer-minutes of searching, depending upon habitat complexity and number of observers present.

Despite flowering searches being conducted in a variable 6 wk period across monitoring years, we expect little effect on overall detection of mature plants. All observers were trained to identify flowering and non-flowering royal catchfly individuals, and surveys were conducted after flowers had begun to open each year (attempting to capture “peak” flowering for optimal detection). Timing of searches within this “peak” window depended on weather and staff availability, but in all years both flowering and non-flowering plants were detected. It is important to note, however, that in no year were surveys conducted in such a way to detect seedlings. Menges (1988) observed that seedlings of royal catchfly are not readily detectable in flowering plant searches, and generally require a separate, intensive seedling transect method to detect them reliably. Such transects were not performed in any surveys 1988–2000, and were outside the scope of the 2019 surveys; however, they may be a useful addition to future surveys depending on capacity and monitoring objectives.

STATISTICAL ANALYSIS

Annual abundance trends were analyzed using a one-way analysis of variance (ANOVA) to compare mean population size across years. In the case of a significant effect, a post-hoc Tukey’s honestly significant difference (HSD) test was employed to determine which pairwise comparisons of years are significantly different from one another. Data were analyzed using R statistical software and the RStudio graphical user interface (RStudio Team, 2018; R Core Team, 2019).

For each study year, mean park-level and population-level attributes were calculated from measurements taken at the individual level. Three height characteristics were explored: the maximum height of any one stem on an individual; the sum height of all stems on an individual; and the mean height of all stems on an individual. Another characteristic, the proportion of stems browsed on a given individual, was calculated as:

$$PB = NBS/NS$$

where PB is the proportion of browsed stems, NBS is the number of stems observed with browse damage, and NS is the total number of stems on the individual. Differences in the means of these four characteristics were calculated and analyzed among sites and among years using a two-way analysis of variance (ANOVA) with interaction between factors. In the case of a significant effect, post-hoc Tukey's honestly significant difference (HSD) tests were employed to determine which pairwise comparisons of sites and/or years are significantly different from one another. Reproductive structure characteristics were not analyzed as a part of this study, but present an opportunity for future analysis.

Because fire has been identified by many studies as an important ecosystem component for royal catchfly, we examined the fire history of Wilson's Creek National Battlefield over the study period. We followed the methodology for recent fire history determination described by Leis and Short (2019), with one exception. First, we overlaid extant and previously known populations on burn polygons generated from prescribed fire monitoring in the park in ArcMap (ESRI, 2019). After constructing 30 m radius circular buffers around population coordinates, we evaluated the buffers against the burn polygons year-by-year from 1995–2019. A site was marked 'burned' if >50% of the buffer was within the burn polygon; Leis and Short (2019) considered sites burned if >30% of the buffer was within the burn polygon, but given the patchy nature of royal catchfly populations and the uncertain accuracy of site locations taken in the 1990s, we elected to increase the threshold to 50%. From this yearly burned / unburned designation, we were able to determine the number of fires each population received during the last 25 y, the number of years since the last fire at a site for any given year, and the mean fire return interval for each site. Mean fire return interval (MFRI) was calculated as:

$$MFRI = NY/NF$$

where NY is the total number of years in the study period (in this case 25 y) and NF is the number of fires observed at the given site. Differences in the mean number of fires and mean MFRI between populations extant and extirpated in 2019 were examined using two-sample *t*-tests.

While some studies suggest that growing season precipitation does not have a significant effect on stem height for perennial grassland forbs (Menges, 1988; Fay *et al.*, 2002), others find that it does (Morrison *et al.*, 2015). Therefore, we examined precipitation differences among years. Precipitation data for a period of 12 mo prior to flowering in each sampling year (previous September–present August) in nearby Springfield, MO were sourced from the National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information (2019) and analyzed using a one-way ANOVA to assess any significant differences over the monitoring period.

RESULTS

During the period 1988–2019, nine to 15 royal catchfly populations were surveyed in each of six monitoring years on Wilson's Creek National Battlefield (Table 1). Mean abundance per population significantly declined over the monitoring period ($F = 3.61$, $P < 0.01$) from 79.7 individuals per site in 1988 to 4.1 individuals per site in 2019. The single largest population observed was 249 individuals at site 2 in 1988; this site remained the largest population in the 2019 survey with 45 individuals. Number of extant populations in the park was reduced from a peak of 14 in 1989 to five in 2019.

TABLE 1.—Number of individuals observed at each royal catchfly site during six monitoring years, 1988–2019. Dashes indicate a population was not visited during the survey year

Site	Year					
	1988	1989	1998	1999	2000	2019
1	175	215	18	27	27	3
2	249	162	23	68	68	45
3	12	3	-	9	34	0
4	5	4	6	8	15	0
5	120	149	62	48	69	9
6	60	69	61	31	19	4
7	60	77	17	34	41	0
8	34	52	0	-	-	1
9	2	2	-	-	-	0
10	-	1	-	-	-	0
11	-	4	-	-	-	0
12	-	13	-	-	-	0
13	-	20	44	71	10	0
14	-	*	37	12	12	0
16	-	-	3	33	7	0
Yearly Total	717	771	271	341	302	62
No. of Sites Surveyed	9	13*	10	10	10	15
Mean No. / Site	79.7 a	59.3 a	27.1 ab	34.1 ab	30.2 ab	4.1 b

The asterisk (*) for site 14 in 1989 indicates plants were observed, but the number of individuals was lost; this site is therefore not included in the total number of sites surveyed. Population 15 was identified in 1998 but subsequently combined with adjacent population 7. Values in the Mean No. / Site row which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey’s HSD test)

Across all four attributes (maximum stem height, sum height of all stems, mean height of all stems, and proportion of stems browsed), year, site, and the interaction between the two were highly significant factors (Table 2). All measures of height followed similar trends over the 4 y included in the analysis, with height decreasing slightly from 1998–2000 and

TABLE 2.—Summary of ANOVAs for the effects of year and population site on individual plant attributes with interaction

Attribute	Source of variation	df	MS	F	P
Max. Height	Population (A)	10	17271	24.773	0.000
	Year (B)	3	33607	48.205	0.000
	A*B	20	3532	5.066	0.000
Sum Height	Population (A)	10	38430	11.586	0.000
	Year (B)	3	117463	35.414	0.000
	A*B	20	8407	2.535	0.000
Average Height	Population (A)	10	16321	25.140	0.000
	Year (B)	3	26726	41.170	0.000
	A*B	20	3401	5.240	0.000
Percent Browsed	Population (A)	10	3.093	22.191	0.000
	Year (B)	3	14.316	102.704	0.000
	A*B	20	0.582	4.177	0.000

TABLE 3.—Mean ($\pm$ SE) of individual plant attributes for monitoring years across sites. Values in a column which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey’s HSD test)

Year	Max. height of a stem per ind. (cm)	Sum height of all stems on ind. (cm)	Mean height of all stems on ind. (cm)	Proportion of stems browsed per ind.
1998	70.4 $\pm$ 1.5 a	85.1 $\pm$ 2.8 a	68.0 $\pm$ 1.5 a	0.35 $\pm$ 0.03 a
1999	68.5 $\pm$ 1.7 a	88.8 $\pm$ 3.4 a	65.8 $\pm$ 1.7 a	0.14 $\pm$ 0.02 b
2000	64.8 $\pm$ 1.9 a	80.3 $\pm$ 3.5 a	62.7 $\pm$ 1.8 a	0.69 $\pm$ 0.03 c
2019	110.8 $\pm$ 3.5 b	170.7 $\pm$ 12.4 b	103.1 $\pm$ 3.7 b	0.11 $\pm$ 0.04 b

increasing significantly in 2019 (Table 3). The only departure from this trend is in the sum height of stems on an individual, where 1998 has a lower mean than 1999, though not significantly lower. Significant differences among sites for the three height measures separated populations into groups which were relatively similar no matter the metric (Table 4). For extant populations in 2019, plants at site 1 were significantly shorter than those at sites 2, 5, and 6 regardless of metric. However, a complex interactive effect between year and site is also present, suggesting population height differences are at least somewhat influenced by year.

A more complicated pattern emerges in the proportion of stems browsed per individual; 1998 and 2000 are significantly different from all other years, including each other, while 1999 and 2019 are similar (Table 3). Proportion of stems browsed was highest in 2000, with >68% of royal catchfly stems across the park browsed. Significant browse proportion differences among sites separate populations into groups that are similar, but not identical, to the grouped means of the height measures (Table 4). A notable difference is among extant populations in 2019, in which sites 1 and 5 have similar proportions of browse that are significantly higher than sites 2 and 6. As was the case for height measures, the interactive effect between year and site is significant, suggesting browse differences among populations are at least somewhat influenced by year.

TABLE 4.—Mean ($\pm$ SE) of individual plant attributes for 10 populations across monitoring years. Populations with fewer than 2 individuals observed 1998–2019 are excluded from this table (including extant site 8 [only one individual]). Values in a column which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey’s HSD test)

Population	Max. height of a stem per ind. (cm)	Sum height of all stems on ind. (cm)	Mean height of all stems on ind. (cm)	Proportion of Stems Browsed per ind.
1	44.1 $\pm$ 2.2 a	55.8 $\pm$ 3.6 a	41.9 $\pm$ 2.1 a	0.54 $\pm$ 0.06 a
2	74.9 $\pm$ 2.3 b	102.2 $\pm$ 5.7 b	71.1 $\pm$ 2.2 b	0.19 $\pm$ 0.03 b
3	82.6 $\pm$ 6.6 bc	107.6 $\pm$ 15.1 b	79.3 $\pm$ 6.3 bc	0.62 $\pm$ 0.07 a
4	66.9 $\pm$ 5.2 bd	72.0 $\pm$ 6.1 ab	66.7 $\pm$ 5.3 bc	0.59 $\pm$ 0.09 a
5	77.7 $\pm$ 5.2 bc	99.7 $\pm$ 4.5 b	74.3 $\pm$ 2.0 bc	0.40 $\pm$ 0.03 ac
6	78.0 $\pm$ 2.4 bc	99.5 $\pm$ 5.5 b	75.1 $\pm$ 2.4 bc	0.13 $\pm$ 0.03 b
7	49.7 $\pm$ 2.5 ad	57.9 $\pm$ 3.1 a	48.6 $\pm$ 2.5 ad	0.71 $\pm$ 0.05 a
13	84.6 $\pm$ 2.7 c	99.4 $\pm$ 4.8 b	83.0 $\pm$ 2.7 c	0.29 $\pm$ 0.04 bcd
14	65.0 $\pm$ 3.0 b	82.1 $\pm$ 4.9 ab	61.4 $\pm$ 2.8 bd	0.39 $\pm$ 0.06 ad
16	46.4 $\pm$ 4.4 a	71.7 $\pm$ 10.1 ab	43.9 $\pm$ 4.3 a	0.42 $\pm$ 0.07 ad

TABLE 5.—Number of fires and mean fire return interval (MFRI; 1995–2019) for each population site. Asterisks (*) denote extant populations in 2019; average across sites noted in the rightmost column. Site 8, which did not have any fires during the monitoring period, is displayed with an MFRI of >25.0 y although it could not be strictly calculated (divide by zero error)

	Site number															
	1*	2*	3	4	5*	6*	7	8*	9	10	11	12	13	14	16	Ave.
No. of Fires, 1995–2019	3	5	1	3	4	9	5	0	4	3	4	9	4	1	5	4
MFRI, 1995–2019	8.3	5.0	25.0	8.3	6.3	2.8	5.0	>25.0	6.3	8.3	6.3	2.8	6.3	25.0	5.0	9.7

The mean number of fires experienced by royal catchfly sites during the period 1995–2019 was four, and ranged from zero to nine (Table 5). Although there was no significant difference between extant and extirpated sites ($t = 0.18$, $P = 0.86$), extant sites had a slightly higher mean number of fires (4.2 versus 3.9, respectively). Interestingly, extant populations in 2019 occur at both the site with the fewest fires (site 8, zero fires) and one of the sites with the most fires (site 6, nine fires).

The mean number of years since fire for sites as of the 2019 growing season was 12 y and ranged from one to over 25 (Table 5). By plotting number of years since fire against year for each site during the period 1995–2019, an increasing pattern emerges, corresponding with less frequent fires at these 15 sites (Fig. 2). The mean fire return interval across all sites ranged from 2.8 to over 25 y, with a mean value of 9.7 (Table 5). Means for extant and extirpated populations were very similar (9.5 versus 9.8, respectively) and not significantly different ($t = -0.07$, $P = 0.94$).

For the 12-mo period before August of each survey year, total rainfall in Springfield, MO averaged 119.4 cm across the six monitoring years and ranged from 96.0 cm to 144.3 cm. Mean monthly rainfall averaged 9.9 cm across monitoring years and ranged from 8.0 cm to 12.0 cm. Although total rainfall in 1988 and 2019 were considerably higher than other years, no significant difference among years was detected ($F = 4.462$, $P = 0.879$). Rain was unevenly distributed throughout the 12-month period, but no single month was significantly different from any other ($F = 1.765$, $P = 0.081$).

DISCUSSION

Over the monitoring period 1988–2019, we observed a significant decline in the number of royal catchfly individuals per population at Wilson’s Creek National Battlefield. Two thirds of historically recognized populations at the park have been extirpated, including populations that once had >70 individuals. Plant dormancy has been observed in two other perennial *Silene* species, but it has not been directly observed in *S. regia* (Menges and Dolan, 1998); therefore, it is likely that these individuals are truly deceased rather than dormant, especially for populations lost in the late 1980s. Declines in extant populations have been reported in other states across the range of the royal catchfly; for example, Dolan (1995) was only able to relocate eight of the 23 previously known populations in Indiana during the 1992 and 1993 monitoring seasons.

In 1989, observers noted that all park populations of royal catchfly were located in successional edge communities. During 2019 surveys, we observed that several of the sites had succeeded to either shrub thicket (*e.g.*, sites 7 and 14) or a more closed-canopy forest condition (*e.g.*, sites 3 and 13); royal catchfly was extirpated from all such sites. Qualitative

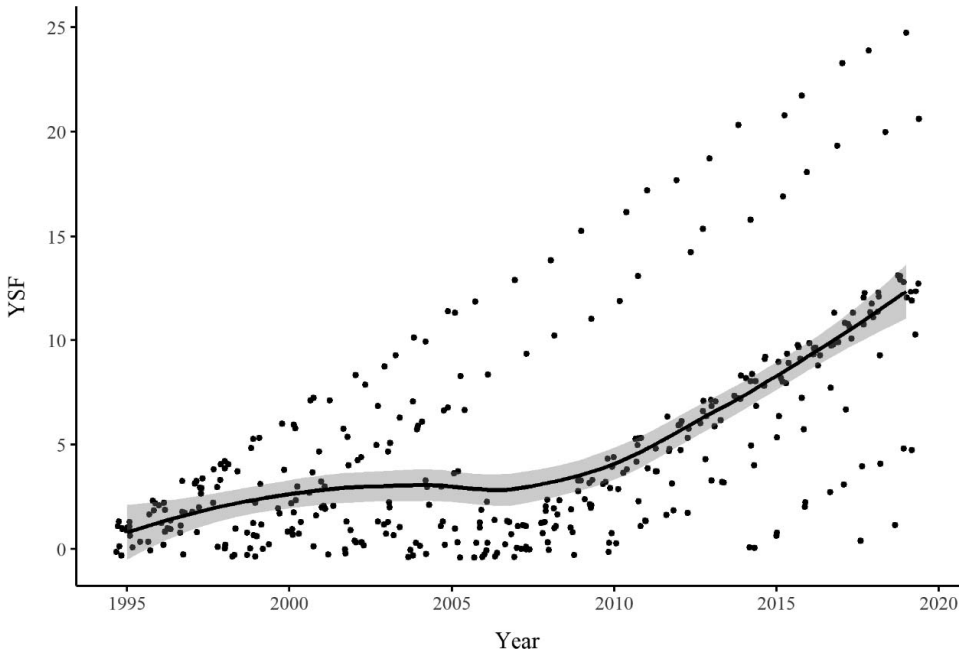


FIG. 2.—Number of years since last fire (YSF), 1995–2019, for fifteen populations of royal catchfly at Wilson’s Creek National Battlefield. If a population was not burned in 1995, a value of ‘1’ was assigned (as if the last fire had occurred in 1994). Data points are plotted with a small, random jitter to prevent masking of overlapping points. The trend line represents the Loess (Locally estimated scatterplot smoothing) conditional mean ($\pm$ SE) and does not include the jitter in its calculation

site descriptions of many sites in the late 1990s mention eastern redcedar (*Juniperus virginiana*) and honeylocust (*Gleditsia triacanthos*) encroachment, increasing height and density of sassafras (*Sassafras albidum*) and sumac (*Rhus* spp.) thickets, and invasion of exotic grasses, forbs, and shrubs (e.g., *Bromus* spp., *Lespedeza cuneata*, *Lonicera* spp.) as threats to the integrity of royal catchfly sites. The effects of these threats are evident today in the nearly impenetrable understories of multiflora rose (*Rosa multiflora*), brambles (*Rubus* spp.), and buckbrush (*Symphoricarpos orbiculatus*) located at some sites, and the loss of populations therein. Sericea (*L. cuneata*) also appears to be on the rise – noted at 10–20% of sites in the late 1990s, it was observed at >50% of sites in 2019, and often in high concentrations.

The drivers of royal catchfly population loss at Wilson’s Creek National Battlefield are likely complex and interactive. The apparent decline of suitable habitat may be the result of an altered disturbance regime on the park, incorporating less frequent fires, increasing deer populations, and the cessation of park-wide soil and vegetation disturbances that could have contributed to larger populations during the period of restoration and development (late 1960s–mid-1990s; John Milner Associates, 2004). Possible support for this hypothesis is that all measures of height were significantly higher in 2019 than in the late 1990s surveys (Table 3) and vary among sites that have differential disturbance regimes today (Table 4). A portion of this effect may be due to the wet spring of 2019 (May 2019 saw >33 cm of rainfall, the wettest single month during the monitoring period), but it may also be the result of increasing shrub and vine competition at overgrown sites.

Qualitative site observations from the late 1990s through 2019 consistently listed overgrowth and woody encroachment among the top threats to royal catchfly populations on the park (noted at 40–80% of sites in the late 1990s, and 87% of sites in 2019). Menges (1988) found that high vegetation cover was significantly correlated with taller plants, and tallest stem heights were found at unburned and overgrown sites. Given the increasing number of years since fire at sites across the park (Fig. 2), it is not surprising that woody species are increasing in height and perennial forbs, such as royal catchfly, are forced to grow taller in order to compete for sunlight. However, increased growth is not without consequence; Menges (1988) found reduced survivorship year-to-year in individuals growing in thickets, pointing to a possible accumulating effect of suboptimal growth conditions and the stress of producing taller stems.

Over the monitoring period, prescribed fires became less frequent across population sites, particularly after the year 2007 (Fig. 2). Although we found no significant difference between extant and extirpated sites in terms of either number of fires or MFRI during the study period, it is likely that fire remains one of a suite of disturbances that maintain suitable habitat and benefit royal catchfly overall. As a species of prairies and savannas, royal catchfly evolved and adapted to a landscape shaped by fires, which historically returned every 4–8 y in southwestern Missouri (Guyette *et al.*, 2012). The MFRI across sites (9.7 y) is higher than the historic interval, with multiple sites experiencing return intervals of approximately 25 y. Curiously, one of these sites is an extant population – site 8 – at which a single plant was observed in 2019, after no individuals had been observed since 1989. Site 8 occurs in a small patch of grassland between a park maintenance road and a visitor-use horse trail. Adjacent grassland patches across the road have a considerably higher component of exotic species (*e.g.*, *Sorghum halepense*, *L. cuneata*), and the presence of deer was obvious throughout (trails through vegetation, bedding sites). Although this site was not burned during the period 1995–2019, the presence of a single individual suggests that the alternate disturbances here (including either mowing, brush-hogging, or both) have created a suitable enough habitat for royal catchfly to persist. However, this individual also had very tall weak stems and showed signs of insect herbivory, suggesting its habitat may not be ideal.

Royal catchfly populations respond well to management regimes involving fire, not only in terms of annual survivorship, but in reproductive output and recruitment as well (Menges, 1988, 1995). Unlike some prairie plants whose germination is stimulated by vegetation-derived smoke (Jefferson *et al.*, 2008), royal catchfly responds instead to repeated management with fire over the short-term effects of a single burn. In one study, royal catchfly seedlings were only ever located at sites that had been managed with prescribed fire (Menges, 1988), suggesting the habitat conditions resulting from fires are favorable to germination. Management with prescribed fire can reduce litter depth, reduce cover of fire-sensitive woody species, and introduce habitat heterogeneity (Bowles and Jones, 2013; Ryan *et al.*, 2013); high litter depth and high vegetation cover have both been found to have significant inhibitory effects on royal catchfly growth, particularly in thicket sites (Menges, 1988). Increased fire management has also been repeatedly identified as crucial to the restoration and preservation of the natural landscape within Wilson's Creek National Battlefield (Speck, 1992; John Milner Associates, 2004).

Although the trend observed in proportion of stems browsed is less straightforward than in measures of height, it is no less interesting. Proportion of stems browsed varied across the four monitoring years, and was significantly higher in 1998 and 2000 than in 1999 and 2019 (Table 3). Browse proportion varied significantly among sites (Table 4) with multiple populations averaging >50% browse during the study period, including both currently

extant (site 1) and extirpated (sites 3, 4, and 7) sites. Deer browse and presence at royal catchfly populations were consistently noted in qualitative site descriptions throughout the park; deer are listed as a threat in 80% of sites in each year 1998–2000 and in 93% of sites in 2019. However, as observed browse on royal catchfly individuals is not quite as high as the perceived threat to their local habitats, we suggest that other factors are determining how frequently and severely white-tailed deer browse on royal catchfly.

Unlike bison (*Bison bison*), which graze almost entirely on grass, white-tailed deer selectively browse forbs over grasses and sedges during late spring and summer (Anderson *et al.*, 2001; Anderson, 2006; Crider *et al.*, 2015). Palatability of forbs – which may be determined both by their nutrition content and the concentration of structural (*e.g.*, lignin) and secondary (*e.g.*, phenolics) compounds – influences how often white-tailed deer browse a particular species. However, it is browse tolerance that determines how well an individual plant responds to and survives a browse event (Augustine and McNaughton, 1998). The ability to compensate for aboveground biomass loss following browsing does not necessarily confer continued survival, as it has been shown that browse events that have no effect on aboveground biomass can still reduce belowground biomass significantly as browse intensity increases (Russell *et al.*, 2001).

Although the specific palatability and browse tolerance of royal catchfly are unknown, the importance of these factors decrease as deer densities increase, as deer are expected to become less selective about forage when competition is high (Augustine and McNaughton, 1998). Deer monitoring at Wilson's Creek National Battlefield from 2005–2018 shows a moderate (10.5%) yearly increase in the population (Peitz *et al.*, 2018). White-tailed deer may reduce plant population growth rates when deer are abundant and the plant is rare; however, this is an understudied phenomenon (Russell *et al.*, 2001). Repeated high-intensity browse events have been shown to contribute to local extirpation of palatable forbs, including rare species (Waller and Alverson, 1997; Urbanek *et al.*, 2012), but without browse data from the intervening years 2001–2018, it is impossible to say whether the high levels of browse observed in 2000 were sustained or returned to a level more similar to 1999 and 2019. In either case, white-tailed deer may be one of several factors contributing to the reduction of royal catchfly populations across the monitoring period due to locally increasing deer population densities, location of royal catchfly populations in favorable edge habitat, and preferential browsing of deer on forbs in prairies and savannas.

Although royal catchfly is not listed federally, nor in the state of Missouri, its status as a locally uncommon but globally rare species should not be overlooked. The high density of populations in Missouri can be attributed to several factors. First, the unglaciated part of the state (including the Springfield Plateau) likely served as a refugia during the last glacial maximum, which allowed the species to recolonize areas further east and north after glacial retreat (Menges, 1991). The effects of recolonization are reflected in the significantly lower genetic diversity of populations in the eastern part of its range (Dolan, 1994), which may make those populations particularly vulnerable to stochastic events (Menges, 1988; Menges and Dolan, 1998). Second, although land conversion across the royal catchfly's range reduced its prevalence, differential conversion in the east and west informs the current extent of the species. In the east (Ohio, Indiana, and Illinois), prairies were primarily converted to row crop agriculture and subjected to repeated plowing and nutrient extraction. In contrast, the western part of the range, and in particular the Springfield Plateau with its shallow rocky soils, was largely subjected to livestock grazing of various intensities (Menges, 1988). Although some areas were converted to exotic, cool-season grasslands, and still other areas may have been heavily stocked and/or overgrazed, the

mosaic of lightly grazed patches allowed for maintenance of prairie and savanna vegetation, even where degraded (Menges, 1988). In addition, many extant populations in Missouri are located on protected lands and/or lands managed with conservation in mind (Wilson's Creek National Battlefield, Niawathe Prairie Conservation Area), whereas populations in the eastern part of the range frequently occur in cemeteries and railroad rights-of-way. None of the extant Indiana populations found by Dolan (1995) in the 1992/1993 monitoring seasons was located on dedicated natural preserves.

The patterns and locations of royal catchfly populations, both across its range and within Wilson's Creek National Battlefield, indicate an ongoing trend of fragmentation and degradation that is reflected at both scales. Conversion to agriculture has slowed down or halted in many places, but ongoing agricultural land use, exurban development, and fire suppression continue to threaten the suitability and continuity of prairie and savanna remnants. Habitat integrity can easily break down along the edges of grassland remnants, particularly when they abut cropland or other development, and these edges are particularly susceptible to exotic invasion and increasing woody cover (Taft, 2016). Fire suppression can dramatically shift the demographics of a prairie remnant toward a forest (Menges and Dolan, 1998) while maintaining the visual appearance of a quality open site. This illusion of site quality seems to be true at several former royal catchfly populations at the park; the majority of the flora still appears as woodland / savanna species, but the loss of royal catchfly, increasing accumulation of litter, and increasing growth of woody and exotic, invasive species translates to a shift in the fundamental identity of these sites.

Multiple studies (*e.g.*, Menges, 1991; Dolan, 1994) have investigated the demography and genetics of small and/or isolated royal catchfly populations. Threats to populations exist on a variety of scales; small populations have lower germination rates (Menges, 1988, 1991), fewer flowering whorls and lower fruit production (Menges, 1995), and lower rates of population growth from year to year (Menges and Dolan, 1998). Despite these long-term degradations, Menges and Dolan (1998) determined that short-term ecological changes that directly influence individual survival and reproduction pose the greatest extinction risk. Of potential ecological changes to residual populations, this study identifies woody encroachment, variable browse pressure from deer, and reduced fire frequency as possible threats to royal catchfly populations on Wilson's Creek National Battlefield. Lack of fire management may be interpreted as the most poignant threat to this species. When Menges and Dolan (1998) applied stochastic simulation models to sixteen populations with differing management regimes, all of the populations managed with fire had no risk of extinction in the next thousand years, whereas >50% of the populations without prescribed fires were assured extinction within one hundred years.

CONCLUSION

According to English naturalist Thomas Nuttall, the royal catchfly is surely "one of the most splendid species in existence" (Nuttall, 1818). Locally uncommon in Missouri, the state nonetheless contains and protects the greatest abundance of individuals and populations in its range. The marked decline of royal catchfly at Wilson's Creek National Battlefield speaks to the need for reinvigorated fire management and restoration of prairie and savanna ecosystems. Such management not only stands to benefit the royal catchfly; it supports the reduction of invasive species (Menges, 1988), the maintenance of critical habitat for the federally threatened Missouri bladderpod (*Lesquerella filiformis*; Young, 2012), the prevention of succession into thicket or closed woods (Menges, 1988; Speck, 1992), and

the preservation and interpretation of the historic landscape as it might have appeared during the Battle of Wilson's Creek (Speck, 1992; John Milner Associates, 2004). With these goals in mind, we recommend periodic monitoring of royal catchfly populations, particularly as the park undertakes viewshed restoration and other landscape-scale projects over the next several years. By understanding the effects of overstory reduction and reintroduced fire on royal catchfly at Wilson's Creek National Battlefield, the park can continue to steward its landscape to benefit both prairie and savanna ecosystems and this "most splendid" species.

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