Journal of the Torrey Botanical Society 145(2): 121–125, 2018.

Habitat fragmentation, low seed germination rates, and herbivory impede conservation efforts for a prairie relict wildflower[1]

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Abstract. Fire exclusion, agriculture, and the extirpation of large herbivores have contributed to the loss of early successional plant communities and species across the southeast USA. Georgia aster (*Symphyotrichum georgianum* (Alexander) G.L. Nesom), a wildflower endemic to the southeast Piedmont, is one species that is thought to have experienced a notable decline. To document the status of *S. georgianum* in an area in which Piedmont prairie plant communities were historically present (Clemson Experimental Forest, Central, SC), we inventoried patches and flowers and collected seeds for a germination study. We found 37 patches across this 7,082-ha forested landscape, with an average of 25 flowers/patch. Seed germination rates were low, averaging 11%. In addition to fragmentation and low seed-germination rates, camera traps suggest herbivory from eastern cottontail rabbits (*Sylvilagus floridanus* J.A. Allen) further constrains the population. We conclude that forest management that creates, maintains, and connects early successional habitat is crucial in the conservation of *S. georgianum*.

Key words: conservation, eastern cottontail, Georgia aster, habitat fragmentation, restoration

Before European settlement, plant-community assembly in the Piedmont ecoregion of the southeastern USA was largely shaped by fire and grazing (Noss 1994, 2013; Delcourt and Delcourt 1997). This natural disturbance regime—later coupled or replaced with anthropogenic fire and livestock grazing—resulted in a mosaic of plant communities ranging from open prairies to dense, closed-canopy forests (Noss 1994, 2013). However, widespread agricultural conversion (and later abandonment), fire suppression, and even-aged silviculture has resulted in the development of single-species plantations and late-successional forests that are seen today (Davis *et al*. 2002; Nowacki and Abrams 2008). When dense, closed-canopy forests predominate across the landscape, herbaceous, light-demanding, disturbance-tolerant ground cover is often lost. Today, isolated remnant-prairie populations sometimes persist along clear-cut areas, such as power-line rights of way; along railroad tracks; and around fence lines (Davis *et al*. 2002).

One species that has experienced a notable decline in the region is Georgia aster (*Symphyotrichum georgianum* (Alexander) G.L. Nesom). A perennial herb in the Asteraceae, it has large, composite flowers (up to 6 cm across), with dark bluish-violet ray flowers and disk flowers that range from white to dark purple. It is an obligate outcrosser, and although it is pollinated by many different insects, it is favored by butterflies and moths (Jones 1978). Flowering from October through November, *S. georgianum* can grow up to 100 cm tall, with involucrate seedheads containing 20–50 wind-dispersed seeds each. It can exist as either dense, clonal patches or scattered, individual stems (Gustafson *et al*. 2016). Because of its rarity and the scarcity of available information related to its ecology and management, *S. georgianum* is currently part of a candidate conservation agreement (CCA) between the US Fish and Wildlife Service, Clemson University, and many other institutions in its range. The purpose of the CCA is to establish a formal agreement for land managers to cooperate on actions that conserve, manage, and improve *S. georgianum* populations, with the goal of preclud-

[1] This study was supported by the Calhoun Honors College at Clemson University. We thank the individuals who contributed to fieldwork, especially Knight Cox, Dr. Patrick McMillan, Nic McMillan, Amanda Williams, and several members of the Clemson Camera Trapping Creative Inquiry class.

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doi: 10.3159/TORREY-D-17-00020.1

Received for publication May 29, 2017, and in revised form August 18, 2017; first published March 6, 2018.

ing the need to list it under the Endangered Species Act (USFWS 2014).

In support of the CCA, we conducted a study to assess the status of, and threats to, *S. georgianum* in a forested landscape in the South Carolina Piedmont. Our specific objectives were the following:

- Inventory relict *S. georgianum* patches across a forested Piedmont landscape in which it was once common.
- Assess patterns of seed germination rates across a highly fragmented *S. georgianum* population.
- Assess the role of herbivory on *S. georgianum*.

Materials and Methods. Field Site Description. The Clemson Experimental Forest (CEF) is a 7,082-ha forest owned by Clemson University that is used for research, education, and recreation (CEF 2017). Annual high temperatures average 22.2 °C (71.9 °F) and annual low temperatures average 9.4 °C (49 °F). Average annual precipitation is 127.4 cm (50.1 inches) (Your Weather Service 2017). The forest consists of a mix of plantation stands (*Pinus* spp.) and late-successional, mixed-hardwood forests. Dominant species in late-successional sites of the CEF are white oak (*Quercus alba* L.), water oak (*Quercus nigra* L.), scarlet oak (*Quercus coccinea* Münchh.), yellow-poplar (*Liriodendron tulipifera* L.), pignut hickory (*Carya glabra* (Mill.) Sweet), and American beech (*Fagus grandifolia* Ehrh.), with basal areas often exceeding 25 m^2 ha^{-1} (Hagan *et al*. 2014). "Open" plant communities, such as prairies and woodlands, were once common—and perhaps predominated—across the area (Barden 1997), but their characteristic ruderal species are now mostly relegated to edge communities along roads, railroad tracks, agricultural fields, and utility rights-of-way within the forest.

Inventorying *S. georgianum* Patches. To inventory extant *S. georgianum* patches, we began with a map of previously known locations provided by the forest manager. At each of those patches, we counted the number of individual flowers and stems. We then characterized each patch as either *right-of-way* or *forest* and collected basal area data with a 10-BAF (basal area factor) prism. These environmental data were used to create a habitat profile for *S. georgianum*, which we used to inform our search for additional patches. Exhaustive searches of the entire CEF, focusing on suitable habitat, were conducted during the period of peak flowering (October 9, 2014 to November 6, 2014) when the plants were easiest to locate because of their distinctive blooms.

Seed Collection and Germination. To collect seeds for germination, we returned to 14 *S. georgianum* patches in late November/early December 2014 and harvested five randomly selected seedheads. Patches with less than five flowers were not sampled. After a 90-day period of cold stratification (40° C) in a refrigerator, seeds were sowed into small pots containing a standard germination soil mix. Four pots were assigned to each patch, with each pot consisting of 10 seeds (40 seeds total per patch). The seeds were then left in a controlled germination room in a greenhouse for 10 wk in spring 2015. Greenhouse conditions (light, temperature) approximated the sunny, open environment where *S. georgianum* would typically germinate. Germinants were tallied twice weekly until no new germinants were observed.

Herbivory. During the seed-collection stage, we noticed that many of the patches had substantially fewer seedheads than the number of flowers recorded in the initial visit. Where the seedheads were missing, the flower stalks appeared to have been cut or browsed. These observations raised the possibility that herbivory might contribute to the rarity of *S. georgianum*. To test that hypothesis, in fall 2015, we selected 10 *S. georgianum* patches of various sizes and monitored flowering phenology for 7 wk (October 1, 2015 to November 20, 2015). During each visit, flowers were classified into six developmental categories (1, unopened flower bud; 2, emerging flower; 3, peak bloom; 4, declining bloom; 5, postdispersal involucre; and 6, browsed). Documenting flowering in this manner helped us to obtain a more-accurate estimate of total flowers (because flowers within a patch may peak at different times) as well as to determine the stage at which they were browsed. On the three largest patches, we mounted three Trophy Cam HD motion-activated cameras (Bushnell, Overland Park, KS). Cameras were set on hybrid mode, taking a photo when triggered by movement, then immediately taking a 10-sec video. Photos and videos were carefully reviewed to identify the species responsible for the herbivory.

Analysis. Histograms were used to determine the frequency distribution of flowers in patches as well as the distribution of patches across a basal

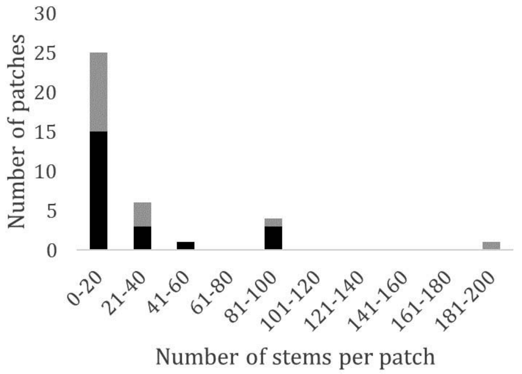

FIG. 1. Histogram showing the frequency distribution of 37 *Symphyotrichum georgianum* patches in the Clemson Experimental Forest by size (number of stems per patch) and habitat (gray = forest/woodland; black = rights-of-way).

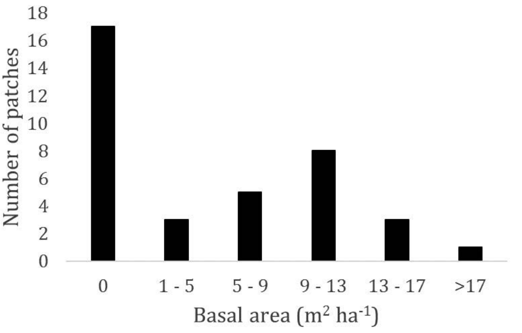

FIG. 2. Histogram showing the frequency distribution of 37 *Symphyotrichum georgianum* patches in the Clemson Experimental Forest by overstory basal area (square meters per hectare).

area gradient. We used regression analyses to assess the relationship between basal area and *S. georgianum* patch size and abundance as well as basal area and seed-germination rates. Germination rates (%) for each patch were calculated by averaging percentage of germination for the four pots. Percentage of herbivory was estimated as the difference between the total number of flowers observed throughout the flowering season and the number of postdispersal involucres remaining at the end of the season. We concluded that this method was more reliable than counting browsed stalks because those stalks were easy to miss and because a single stalk could contain up to 6 flowers. We assumed that herbivory was responsible for any missing involucres because we did not observe any evidence that drought, wind, rain, or other factors were responsible.

Results. Overall, we found 37 individual patches with the average size being approximately 25 stems (range, 1–200 stems). Four patches that had been previously identified in a 2010 roadside survey were no longer present. Twelve (seven in rights-of-way, five in forests) had not been identified in the previous survey. The largest number of patches (18/37) were in rights-of-way with no trees present (basal area = 0), and there was a secondary peak (8/37) in forested areas with basal areas between 9 m^2 ha^{-1} and 13 m^2 ha^{-1}. No patches were found in areas in which basal area exceeded 17 m^2 ha^{-1} (Fig. 1, 2).

Seed-germination rates ranged from 0% to 50%, with a mean of 11% per patch. Five patches (35.7% of total) produced no germinants. Seed germination was not correlated with patch size or the basal area of the site from which they were collected. Because the average number of flowers in a patch was 96 (stems typically had several flowers), and flowers typically had 20–50 seeds, we assume that patches were capable of producing between 0 and 2,400 viable seeds.

One herbivory monitoring patch was destroyed by roadside mowing equipment and was thus excluded from the analysis. Of the nine remaining patches, flower/seedhead consumption ranged from 38.1% to 100%, with a mean of 63.4% (Table 1). Bite marks suggested that eastern cottontail rabbits (*Sylvilagus floridanus* J.A Allen)

Table 1. Subset of 10 *Symphyotrichum georgianum* patches used for an herbivory survey in a forested landscape in the South Carolina Piedmont region. Three patches were monitored with motion-activated cameras.

Patch ID[a]	Total flowers	Unbrowsed flowers (late November)	Browsed (missing) flowers	% lost to herbivory
1	328	203	125	38.1
2	158	72	86	54.4
3*	24	14	10	41.7
4	115	36	79	68.7
5	29	5	24	82.8
6	44	26	18	40.9
7	23	0	23	100.0
8	16	7	9	56.3
9*	125	15	110	88.0
10*	6	0	N/A	N/A

[a] Asterisks (*) denote patches that were monitored for herbivory by motion-activated cameras. Herbivory data are unavailable for patch 10 because that patch was destroyed by road maintenance equipment in November 2015.

FIG. 3. Motion-activated video screenshot of an eastern cottontail rabbit (center) browsing on *Symphyotrichum georgianum*.

were responsible for the herbivory, and this was confirmed by the camera surveys (Fig. 3). The most active period of herbivory was from October 20, 2015 to November 10, 2015, which corresponds to the timeframe between flower senescence and the opening of the involucres to release the seeds. Rabbits were observed consuming *S. georgianum* nearly every night during that period.

Discussion. Light availability is thought to be a primary environmental factor for habitat suitability of ruderal plants, with increased shade contributing to the decline of these species if succession proceeds uninterrupted (Grime 1977). As Piedmont prairies succeed to closed-canopy forests, herbaceous ruderals are replaced by more–shade-tolerant (often woody) species (Bard 1952). *Symphyotrichum georgianum* competes poorly with these woody species (Matthews 1993) and likely cannot persist in the dense shade of a mature forest. These factors likely explain why most of our *S. georgianum* patches were found on, or adjacent to, rights-of-way, where sunlight is abundant, or in woodlands that had large gaps in the canopy from forest thinning, fire, or other disturbances (Davis *et al*. 2002). In the CEF, such habitats are imbedded in a matrix of pine plantations and late-successional forests, often separated from one another by distances exceeding 1 km.

Genetic diversity has a large role in species success and can decline because of habitat fragmentation and subsequent inbreeding depression (Ellstrand and Elam 1993). Low genetic diversity in relict Asteraceae populations was first documented in *Eurybia furcata* (formerly *Aster furcatus*) (Les *et al*. 1991) and was recently observed for *S. georgianum* (Gustafson *et al*. 2016). Because perennial asters are obligate outcrossers and can be highly clonal, the densest patches that we found were most likely a single genetic individual (Jones 1978). This might also explain the poor relationship between patch size and seed-germination rates because large clonal patches provide no greater opportunity for cross-pollination than smaller ones. If sexual extinction (a shift from sexual to asexual reproduction) is occurring for *S. georgianum*, it could be very detrimental to the long-term viability and persistence of the remaining populations (Gustafson *et al*. 2016).

The decline of prairie, savanna, and woodland habitat over the years has largely relegated species such as *S. georgianum* to narrow strips of early successional vegetation between roads and forests (Davis *et al*. 2002). Compounding the effects of fragmentation, low genetic diversity, and low seed-germination rates, herbivory from *S. floridanus* is also cause for concern. *Symphyotrichum floridanus* generally prefers disturbed edge habitats because those areas provide abundant soft mast for browsing as well as cover from predators. The overlapping habitats of these two species, coupled with the affinity that *S. floridanus* apparently has for *S. georgianum*, suggest that the former might further constrain the latter's populations by consuming the flowers/seedheads before the seeds can be released. Interestingly, although anecdotal evidence of *S. georgianum* herbivory has been reported in North Carolina and Georgia, white-tailed deer (*Odocoileus virginianus* Zimmerman) were assumed responsible (USFWS 2014). Our results suggest otherwise; although *O. virginianus* was observed in our camera surveys, no species other than *S. floridanus* was observed browsing on *S. georgianum*.

Conclusion. *Symphyotrichum georgianum* has compounding factors that are contributing to its rarity. A previous study indicated *S. georgianum* has low genetic diversity, and this study showed that it also faces habitat fragmentation, low seed-germination rates, and substantial herbivory from *S. floridanus*. Active forest management that reduces basal area, creates canopy gaps, and promotes connectivity among suitable habitats is crucial to the success of this species. The presence of *S. georgianum* along rights-of-way presents an additional conservation concern because these areas are highly susceptible to impacts from road-maintenance activities.

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