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Pyrogenic flowering of *Aristida beyrichiana* following 50 years of fire exclusion

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Abstract. Fire-stimulated or pyrogenic flowering is one of many traits that enable plants in fire-prone ecosystems to persist or dominate following frequent fires. Obligate pyrogenic flowering has long been observed in wiregrass (*Aristida beyrichiana*), a foundation bunchgrass in frequently burned longleaf pine ecosystems in the southeastern United States. Widespread fire exclusion in this ecosystem has contributed to well-documented declines in plant and animal biodiversity prompting the need for restoration efforts. We studied the effect of fire reintroduction on the flowering of wiregrass in northern Florida, USA. Prescribed fires were ignited in a 50-yr unburned site and an adjacent frequently burned site in the summer of 2017. Wiregrass was measured eight months after the burns in both stands. As expected, the frequently burned stand had higher density, basal area, and percent flowering of wiregrass tussocks. Logistic regression revealed that wiregrass initiated flowering at significantly larger sizes in the long-unburned stand. Despite these differences, wiregrass size distributions were similar in both stands, with the long-unburned stand lacking tussocks in the largest (100+ cm^2) size class. We did not find differences in the number of flower culms per unit of mass between the two stands. Even though diminished in nearly every measure, the ability of wiregrass to flower after five decades of fire exclusion, and presumably no sexual reproduction, provides evidence of resilience of the dominant herb of these ecosystems.

Key words: ecological resilience; ecosystem restoration; fire regime; fire-stimulated flowering; *Pinus palustris;* plant traits; wiregrass.

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INTRODUCTION

Plants associated with fire-prone ecosystems often have fire-adapted traits that confer persistence in a flammable environment. For example, fire-stimulated or pyrogenic flowering has been observed in many angiosperms in fire-maintained grasslands, savannas, and woodlands throughout the world (Gill 1981, Bytebier et al. 2011, Lamont and Downes 2011). Species that initiate flowering after burning may gain an important fitness advantage over obligate resprouters or those that flower without pyrogenic cues. The synchronization of flowering after fire may increase chances of pollination and outcrossing (Janzen 1967, Schmitt 1983) as well as improving the chances of germination and seedling survival by satiating seed predators and herbivores (Janzen 1978, Augspurger 1981, Brewer and Platt 1994, Lamont and Downes 2011). Additionally, by restricting sexual reproduction to occur after fire, a species reduces the overall cost of flowering (Brewer 1995, Brewer et al. 2009), potentially avoids competition with other plants (Lamont and Downes 2011) and

capitalizes on the newly available resources (Johnson et al. 1994, Brewer 1995, Lamont and Downes 2011). Pyrogenic flowering can be facultative, where post-fire increases in reproductive output return to pre-burn flowering rate within a few years, or obligate, where species only initiate flowering after fire, remaining in a vegetative state during fire-free periods (Lamont and Downes 2011). Both facultative and obligate pyrogenic flowering have been viewed as evidence of fire-adaptive traits; however, obligate pyrogenic flowering is unique in that it illustrates how important fire regimes are in maintaining the composition and function of these ecosystems.

In frequently burned longleaf pine (*Pinus palustris* Mill.) savannas and woodlands of the southeastern United States, wiregrass (*Aristida beyrichiana* Trin. & Rupr. syn *A. stricta* Michx.) is often a dominant herbaceous component that contributes to the continuity of fuels necessary to spread fire (Clewell 1989, Fill et al. 2016). Parrott (1967) noted that wiregrass will not flower without a disturbance that removes the aboveground biomass, for example, fire or herbivory. Clewell (1989) expanded on the observation of Parrott (1967) suggesting that fire is the primary stimulant for flowering in wiregrass because its highly fibrous leaves are unpalatable to native herbivores. Subsequent studies support that wiregrass is an obligate pyrogenic flowering species with high sensitivity to the season in which it burns; wiregrass primarily flowers following growing season burns (Seamon et al. 1989, Streng et al. 1993, Outcalt 1994, Van Eerden 1997, Mulligan et al. 2002, Fill et al. 2012).

Fire exclusion, along with timber harvesting and land conversion, has resulted in the substantial decline of longleaf pine ecosystems, with reported losses of up to 97% in their historical range (Noss 1989, Frost 2006). Longleaf pine ecosystems are notable for very frequent pre-settlement fire regimes, with fire scar studies revealing fires every 2.2 yr on average and evidence of sub-annual fires (Stambaugh et al. 2011, 2017). Without frequent fire, substantial changes occur in species composition (transitions from herbaceous to woody understory; Gilliam and Platt 1999, Kush and Meldahl 2000), stand structure (from open to closed canopy forests; Varner et al. 2005), and forest floor conditions (from scant litter to deep litter, fermentation, and humus accumulations; Varner et al. 2005, Hiers et al. 2007, Kreye et al. 2014).

Soil disturbance in longleaf pine ecosystems is particularly damaging to wiregrass populations, presumably due to the shallow root system of wiregrass tussocks (Parrott 1967). For instance, Wells and Shunk (1931) reported that wiregrass did not reestablish in long-abandoned old fields despite abundant populations adjacent to the disturbed area. Barring soil disturbance, wiregrass is able to resprout after fire even after prolonged periods of fire exclusion. This ability to persist is evident in an account described by Clewell (1986, 1989) in which a 25-yr fire-excluded site with a saw palmetto (*Serenoa repens* [Bartram] J.K. Small) and gallberry (*Ilex* spp.) understory was covered in wiregrass weeks after reintroducing fire to the stand, presumably resprouting from dormant tussocks. Beyond vegetative resprouting, it is unknown what effect, if any, long periods of fire exclusion have on the flowering of wiregrass.

Ecosystems with frequent fire regimes are suggested to be in an alternative stable state maintained by the recurring fire that promotes an open understory and sparse overstory of fire-tolerant tree species (Beisner et al. 2003, Nowacki and Abrams 2008). Larson et al. (2013) found that a single wildfire in a long-unburned ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forest led to the establishment of a dense population of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm). A second fire eight years later eliminated the lodgepole pine and returned the ecosystem to its putative former woodland state with a low density of large ponderosa pines and an open herbaceous understory. Larson et al.'s (2013) study emphasizes that restoring the fire regime is important, rather than simply reintroducing a single fire. The resprouting of wiregrass after extensive periods of fire exclusion is an indication of possible latent resilience of longleaf–wiregrass ecosystems and that restoring a frequent fire regime can return the system to its previous stable state (Beisner et al. 2003, Larson et al. 2013).

In the summer of 2017, prescribed fires were conducted in a fire-excluded and an adjacent frequently burned longleaf pine site in Florida, where soils were not previously disturbed (i.e., intact herbaceous layer). We observed wiregrass flowering in both sites, which provided a unique

opportunity to compare the long-unburned site with the adjacent site with a multi-decade history of frequent fires. The objective of this study was to quantify the pyrogenic flowering response of wiregrass after a long period of fire exclusion. We hypothesized that the extensive fire-free period, well beyond that of the historic fire regime, in the long-unburned stand would have negative consequences on the reproductive output of wiregrass. Results of this study offer insight into the resilience of the understory dominant in longleaf pine ecosystems, but also add to the mounting evidence of the importance of fire in grasslands, savannas, and woodlands.

Methods

Study location and site descriptions

Burning was conducted at the Ordway-Swisher Biological Station in northern peninsular Florida, USA (Putnam County, N 29°40′, W 81°74′). The climate consists of long humid summers and short mild winters, with average annual temperatures of 20°C, and average precipitation of 1432 mm (Readle 1990). Soils consist of deep, excessively well-drained hyperthemic, uncoated Lamellic Quartzipsamments in the Candler series (Readle 1990).

We compared post-fire flowering of wiregrass in two adjacent sites, one with a long history of fire exclusion (ca. 50 yr), the other managed with frequent prescribed fire (approximately every 2–3 yr for at least two decades). The frequently burned site consisted of a scattered overstory of mature longleaf pines (approximately 26-m^2/ha basal area), herbaceous groundcover, and a sparse layer of recently cast litter (Oi horizon 5.7 cm deep at pines and 2.3 cm deep in open sites; J. K. Kreye, J. M. Varner, and L. N. Kobziar, *unpublished data*). The long-unburned stand consisted of a similar longleaf pine overstory (approximately 34-m^2/ha basal area) with a dense midstory of oaks (*Quercus laevis* Walt., *Quercus geminata* Small, and *Quercus hemisphaerica* Bartram ex Willd.) and thick organic forest floor horizons (Oi, Oe, and Oa, 15.3 cm at pines and 3.8 cm in the open; J. K. Kreye, J. M. Varner, and L. N. Kobziar, *unpublished data*). Wiregrass was present in both sites, being dominant in the frequently burned stand, but less abundant in the long-unburned site. Prescribed fires were conducted in both sites in June 2017, within days of each other, when fire is known to stimulate wiregrass flowering (Clewell 1989, Fill et al. 2012).

Field methods

We measured post-fire flowering response of wiregrass in February 2018, eight months following burns. Within each site, a main transect of 37 m (the approximate length of the long-unburned unit) was established parallel to a road that divided the two stands and occurring 1 m into each unit. Five belt transects (1 m wide) were located at random points along the main transect oriented perpendicular to the main transect. In the long-unburned site, each belt transect spanned from the main transect to 1 m from the opposing firebreak, ranging from 17 to 21 m in length. The frequently burned site was larger in area than the burned portion of the long-unburned site, so the same random points and distances used in the long-unburned site were used for the frequently burned site. We measured the basal diameter of each wiregrass plant within the belt transects by first measuring the widest diameter of the base and then measuring the diameter perpendicular to the first measurement. These measurements were used to calculate the basal elliptic area of each tussock using the formula:

$$\mathrm{BA} = \pi \times r_1 \times r_2 \quad (1)$$

where r_1 and r_2 are the long and perpendicular radii of the tussock base, respectively. Wiregrass tussocks can expand radially via tillers or rhizomes (Parrott 1967), often making it difficult to distinguish individuals (Clewell 1989). We considered a tussock to be an individual as long as there was a measurable basal diameter without any gaps, so although some of our individuals may be genetically identical fragments, the basal area of wiregrass is an accurate measure of wiregrass in each stand. Expanding tussocks eventually develop a central area absent of vegetation. In these instances, as long as there was continuous growth around the absent vegetation, the basal elliptic area of the hole was also measured and subtracted from the basal area calculations. Overstory tree basal area was measured in one 4 m radius circular plot randomly placed along each of the five belt transects.

We randomly collected flowering tussocks in each site (20 in long-unburned, 18 in frequently

burned), severing them at ground level, and transported them to the laboratory. Individual plants were sorted into live leaves, dead leaves, and flowering culms; oven-dried at 60°C for 48 h; and weighed to obtain dry biomass for each component. Flowering culms were counted for each collected wiregrass clump.

Data analysis

We compared wiregrass flowering characteristics between the long-unburned and frequently burned sites using the R statistical program (R Core Team 2018). To test for differences in wiregrass density, basal area, and percent flowering between stands, we compared mean values of each belt transect using *t* tests. To identify relationships between plant size and flowering, we used mixed-effect logistic regression (using the glmer function in the R package lme4, Bates et al. 2015) to model the probability of flowering based on basal area and site. Three separate models were fit with different random effect structures (no random effects, each belt transect as a random effect, and position along each belt transect in 1-m increments), and model selection was made by choosing the model with the highest Akaike weight (*w*, Wagenmakers and Farrell 2004). Pseudo-R^2 estimates including the marginal and conditional coefficients of determination (R^2_m and R^2_c, respectively) were calculated for the best model using the *r*.squaredGLMM function in the R package MuMIn (Barton 2018). Lastly, we compared the belt transect mean number of flower culms per mass of wiregrass live and dead leaves for each site using a *t* test.

Results

Wiregrass flowered in both stands following the growing season burns, but the frequently burned stand had significantly higher plant density, basal area, and percent flowering. Wiregrass density averaged 3.2 plants/m^2 vs. 1.8 plants/m^2 in the frequently vs. long-unburned sites, respectively (t = 5.0653, df = 7.9945, P = 0.001; Table 1). Density in any given 1-m^2 quadrat along the transect ranged from 0 to 12 individuals in the long-unburned stand and 0–17 individuals in the frequently burned stand. Wiregrass basal area averaged 212.9 m^2/ha in the frequently burned site and only 32.2 m^2/ha in the long-unburned site (t = 5.0841, df = 4.1391, P = 0.006). Wiregrass flowering averaged 57.0% of clumps in frequently burned stand vs. only 10.3% in the long-unburned stand (t = 4.7757, df = 4.7947, P = 0.006; Table 1). Overstory tree basal area was higher in the long-unburned site, with an average of 34.2 m^2/ha per transect, consisting mostly of longleaf pine and sand live oak (*Q. geminata*). The frequently burned stand had an average overstory tree basal area of 28.1 m^2/ha per transect, with less sand live oak.

The best logistic regression model for predicting flowering in wiregrass included transect position as a random effect (w = 0.975, Table 2). Both basal area and site were significant fixed effects in the model ($P < 0.0001$ for both). The model for flowering probability had the following fixed-effect form:

$$P(\text{Flowering}) = \frac{1}{1 + e^{-(-3.52+0.033\times\text{BA}+2.465\times\text{Site})}} \quad (2)$$

where BA is the basal area of the wiregrass tussock and Site is coded as 0 or 1 for long-unburned and frequently burned, respectively (Fig. 1). Our model suggests that odds of flowering increased by an estimated 3.39% for every 1-cm^2 increase in basal area, holding site constant. Site was also significant with the frequently burned site increasing the odds of flowering by 1076%. For the frequently burned stand, wiregrass clumps had a

Table 1. Comparison of wiregrass (*Aristida beyrichiana*) density, basal area, and percent flowering (and standard deviations) between a long-unburned (50 yr) and a frequently burned stand at Ordway-Swisher Biological Station, Florida, USA.

Measure	Long-unburned	Frequently burned	*t*	*P*
Stand density (plants/m^2)	1.8 (0.4)	3.2 (0.4)	5.0653	0.001
Clump basal area (m^2/ha)	32.2 (10.4)	212.9 (78.8)	5.0841	0.006
Percent flowering	10.3 (6.6)	57.0 (20.8)	4.7947	0.006

Table 2. Model selection table and coefficients for flowering probability of wiregrass.

Model	Intercept	BA†	Site‡	AIC_c§	w¶
Flower# ~ BA† + Site‡ + (1|Position‖)	−3.520	0.033	2.465	386	0.975
Flower# ~ BA† + Site‡ + (1|Transect††)	−3.020	0.030	2.067	393	0.025
Flower# ~ BA† + Site‡	−2.888	0.031	1.893	403	0.000

† Elliptic basal area of tussock.
‡ Binary variable (0 = long-unburned, 1 = frequently burned).
§ Akaike's corrected information criterion.
¶ Akaike weight.
# Binary status of wiregrass tussock (0 = not flowering, 1 = flowering).
‖ Categorical random effect indicating transect and position along transect.
†† Categorical random effect.

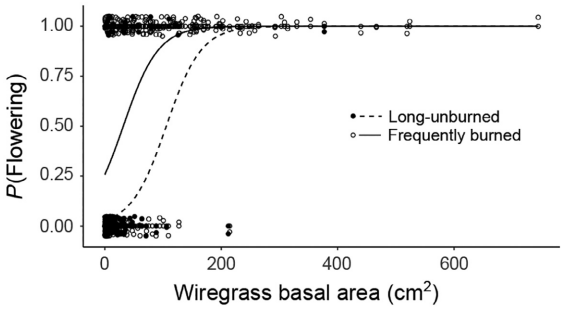


Fig. 1. Results of the logistic regression analysis on flowering of wiregrass (Aristida beyrichiana). Model was fit using basal elliptic area and site as fixed effects and transect as a random effect. Site is a categorical variable with long-unburned (closed circles) being a 50-yr unburned stand and frequently burned (open circles) being a stand that has been burned every 2–3 yr.

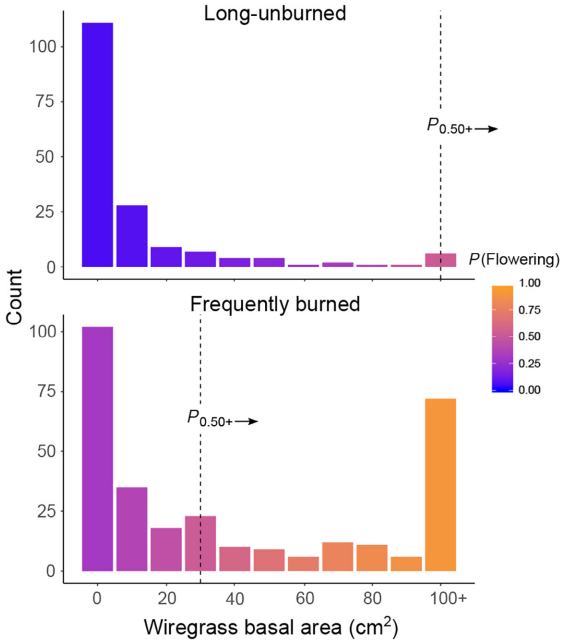


Fig. 2. Size distributions in 10-cm^2 classes of wiregrass (Aristida beyrichiana) in a long-unburned (50 yr) site (top) and a frequently burned (every 2–3 yr) site (bottom). Color of bars indicates the probability that a tussock was flowering based on logistic regression. Dashed line indicates the minimum size class where the probability of flowering was 50%.

50% probability of flowering at approximately 31-cm^2 basal area while clumps in the long-unburned stand reached the same flowering probability at a much larger area, approximately 101 cm^2 (Fig. 1). Pseudo-R^2 values were high with fixed effects explaining approximately 70% of the variation and the random effect of transect explaining approximately 10%.

In spite of these differences, size distributions were remarkably similar between the two stands in all size classes under 100 cm^2 (Fig. 2). Both stands exhibited a reverse-J distribution, with the frequently burned stand having more wiregrass tussocks in the 100 cm^2+ class. We also found no significant difference in the number of flower culms produced relative to the mass of live and dead leaves in the 38 destructively sampled flowering individuals (mean 1.8 and 2.0 culms/g for frequently burned and long-unburned, respectively; $t = -0.27472$, df = 35.954, $P = 0.785$; Fig. 3).

Discussion

Our results highlight the remarkable resilience of wiregrass in a site that had gone unburned for half a century. Despite the protracted fire exclusion, wiregrass, a foundational fire-facilitating bunchgrass in longleaf pine ecosystems, persisted in the forest floor. Although plant density and stature were much reduced, remnant wiregrass was able to flower after reintroducing a

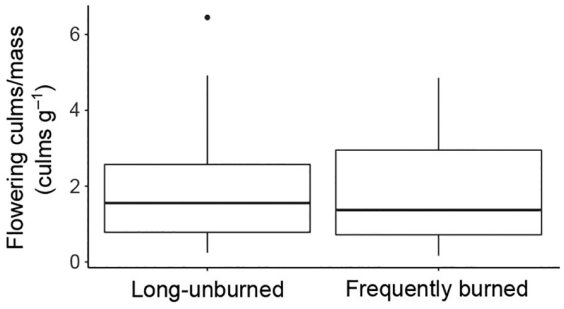


Fig. 3. Comparison of the number of flowering culms per gram of live and dead leaves in approximately 20 flowering wiregrass (Aristida beyrichiana) tussocks. Horizontal bar in each box represents the median.

growing season (June) fire. Clewell (1989) suggested that wiregrass might survive in fire-suppressed sites for 20–40 yr. Our study extends this timeframe revealing that wiregrass not only is capable of persisting, but also is capable of flowering in stands for longer fire-free periods. To our knowledge, no other studies have reported flowering of wiregrass after such a long period of fire exclusion. We did not have the opportunity to quantify viability of seeds produced because the seed had already been dispersed at the time of investigation. The consequences of post-fire seed production and the viability of wiregrass seeds on the burned forest floor are clearly important links that deserve attention.

Restoration potential of these endangered formerly fire-prone ecosystems (Noss 1989) may benefit from the pyrogenic flowering ability of wiregrass. Restoration of wiregrass to longleaf pine old fields, where extensive soil disturbance has resulted in the elimination of wiregrass from the site, generally relies on either direct planting of wiregrass plugs or harvesting wiregrass seed from another location and spreading it at the restoration site (Seamon 1998). Reciprocal transplant studies have revealed that wiregrass exhibits significant population differences due to environmental conditions when young (Gordon and Rice 1998), as well as evidence of local adaptation in older plants (Kindell et al. 1996), which may hinder restoration goals. Our study suggests that reintroducing fire to wiregrass sites that have been fire-excluded, but where soils have not been disturbed, could stimulate wiregrass seed production and may be useful to restoration efforts.

Wiregrass density, basal area, and flowering were significantly lower in the long-unburned stand compared to the frequently burned stand. These results are consistent with previous studies on wiregrass as well as studies in other ecosystems with frequent fire regimes. For example, Maliakal et al. (2000) also found that wiregrass frequency was lower in long-unburned stands. Similarly, Morgan and Lunt (1999) found that *Themeda triandra* (R.Br.) Stapf, the dominant bunchgrass in a temperate Australian grassland, had reduced tillers per tussock and fewer number of tussocks with fire-free periods of over 6 yr. In Florida scrub habitats, Menges and Kimmich (1996) found that increased fire-free periods led to fewer open patches and increased woody shrubs, which led to low survival, growth, and diminished flowering of the locally endemic *Eryngium cuneifolium* Small. It is unknown what mechanism is responsible for our observed effect of time-since-fire on the growth and flowering of wiregrass. Reduced vigor of individual plants can be due to increased intra- or interspecific competition or being buried by organic forest floor material (Hiers et al. 2007), or possibly a sacrifice of aboveground production for belowground storage of carbohydrates. Wiregrass can exhibit considerable aboveground production following fires even after extended fire-free periods (K. Robertson, *personal communication*), which may indicate a production tradeoff. Given the foundational role of wiregrass in the ecosystems that it dominates (Noss 1989), determining the mechanisms for its persistence and recovery should be given attention.

Clewell (1989) suggested that wiregrass reaches a maximum density of approximately 5 plants/m^2 throughout its range. In our study, both stands had lower average densities than Clewell's estimate, although the number of individuals in any given plot ranged widely. These differences may be due to differences in what is considered an individual as wiregrass often forms vegetative fragments. Clewell (1989) suggested using plotless methods such as point-quarter sampling for estimating density (although his 5 plants/m^2 estimate came from fixed area plots) to avoid having to decide between individuals. Comparing fixed area estimates with point-quarter sampling in bunchgrasses in savannas of southern Africa led Walker (1970) to suggest that density estimates in

bunchgrasses are not useful unless individual size is also considered. We suggest basal area as a better option for estimating wiregrass abundance.

Our results reveal that wiregrass in the frequently burned stand initiated flowering at smaller sizes than those in the long-unburned stand. Thus for similar sized tussocks, the long-unburned stand had fewer resources available for flowering. This finding suggests mast flowering in wiregrass may follow a resource budget model (Yamauchi 1996, Isagi et al. 1997, Crone and Rapp 2014). Resource budget models are hypothesized to be a mechanism for synchronized masting in plants and assume that individual plants will only flower when they reach a certain threshold of stored nonstructural carbohydrate reserves (Crone et al. 2009, Crone and Rapp 2014). Increased fire-free periods have been shown to have a negative effect on live aboveground biomass for a given sized wiregrass tussock (Shearman et al., 2019). Presumably, long fire-free periods would also reduce belowground biomass such as nonstructural carbohydrates. Thus, any advantages of suppressing flowering during the fire-free period (Brewer 1995) may be overridden by habitat changes that occur during that period (i.e., canopy closure, litter, and forest floor accumulation). Future studies are needed to test the hypotheses of whether wiregrass requires a threshold of stored resources to initiate flowering and that habitat change has a negative effect on resource storage.

Although wiregrass in the frequently burned stand was more abundant and had higher reproductive output, the size distributions were surprisingly similar, with the long-unburned stand only lacking larger individuals in the 100+ cm^2 classes. We found no difference between sites in the number of flowering culms per leaf biomass of the plant. Of the flowering individuals collected in our study, larger plants produced more flower culms than smaller plants, a common pattern found among angiosperms (Abrahamson and Gadgil 1973, Samson and Werk 1986). The release from competition that the 2017 fire provided may allow regeneration of seedlings and increased vigor of residual clumps, which may lower the flowering threshold. If a frequent fire regime were to be restored in this stand, wiregrass density and cover may be able to return and reestablish its foundational role in facilitating fire.

Pyrophytic flowering of plants reveals an important component in the life-history strategies of some plants and the role of fire as an ecological process. The fact that wiregrass, a dominant fire-facilitating bunchgrass, seems to rely on burning for sexual reproduction highlights the importance of fire–vegetation feedbacks. Post-fire flowering in remnant wiregrass clumps in a site that had gone without fire for half a century highlights the pyrogenic nature of this species and reveals a remarkable resilience that may be critical for restoration in these once fire-prone ecosystems.

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