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Vegetation Ecology

High survival promotes bunchgrass persistence in old-growth savannas under different fire regimes

Jennifer M. Fill | **Raelene M. Crandall**

School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, Florida, USA

Correspondence
Jennifer M. Fill
Email: jfill@ufl.edu

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Abstract

Clonal perennial grasses are a key functional group in fire-prone, old-growth grasslands and savannas. They are flammable and can resist extinction for decades. Although clonal grasses as a functional group are considered resilient to fire regime variation, data-based research on clonal grass dynamics under multiple different fire regimes is still lacking. We modeled the population dynamics of wiregrass (*Aristida beyrichiana*), an endemic perennial bunchgrass, under very different long-term, frequent fire regimes within the historical range of variation, in two southeastern US pine savanna environments. All wiregrass populations had similar and stable population growth rates. As expected for a long-lived species, survival was nearly 100% in all populations. Given that flowering in wiregrass is fire-stimulated, there was high variability in flowering and seed production between fire and non-fire years. The consistency of results between our study populations lends data-driven support to wiregrass' resilience under fire regimes that differ in frequency and seasonality. The patterns we observed in wiregrass mirror inferences from other studies of dominant grass dynamics in old-growth tropical savannas and support the inclusion of old-growth US pine savannas in global savanna ecology.

KEYWORDS
demography, fire regime, old-growth grasslands, pine savanna, population, resilience, wiregrass

INTRODUCTION

Perennial grasses are a defining feature of the world's ancient tropical grassy biomes. Because they are a dominant group in herbaceous understories and often form feedbacks with fire and grazing, perennial grasses are recognized for their role in ecosystem structure, flammability, and biodiversity (Beckage et al., 2011; Fill et al., 2015, 2016; Nerlekar & Veldman, 2020; Ratnam et al., 2011; Simpson et al., 2022; van Langevelde et al., 2003). Faced with increasing modification from expanding human populations, shifts in climate, and nonnative species invasions, tropical old-growth savannas and grasslands have recently received much attention with respect to their distribution and resilience (Buisson et al., 2019; Noss et al., 2015; Pau et al., 2023; Silander et al., 2024; Veldman et al., 2015). Because perennial grasses are so foundational in the structure and function of these biomes, they have a vital place in our understanding of savanna stability.

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Clonal perennial grasses are a key functional group in ancient grasslands that have persisted for decades to millennia. Stable ecosystems are those that have resilience (i.e., the ability to return to equilibrium after a disturbance over a characteristic period of time) and resistance (the ability to absorb disturbances without changing basic structure; Eriksson, 2000; Pimm, 1984). Clonal grasses can enhance the stability of ecosystems under stress through their longevity, ensuring the continuity of functions such as fire spread, nutrient cycling, mycorrhizal colonization, and species establishment (Eriksson, 2000; Veldman et al., 2015). They can resist extinction for decades, bypassing sexual reproduction and persisting in the vegetative stage of their life cycle (Eriksson, 2000). The known or estimated longevity of clonal grasses ranges from several hundred to thousands of years (De Witte & Stöcklin, 2010). Long-lived clonal perennial grasses may, therefore, provide a buffering effect during periods of disturbance or stress (e.g., fire exclusion, climate variability; Morris et al., 2008).

Although clonal grasses as a functional group are considered resilient to fire regime variation, data-based research on clonal grass dynamics under multiple different fire regimes is still lacking. Current support for this assertion comes mainly from inferences about the lifespan, relative dominance, and typical presence of perennial grasses within reference or unmodified savannas and grasslands. For example, Veldman et al. (2015) synthesized characteristics of old-growth savannas around the world, highlighting the importance of frequent fire and long-lived herbaceous plants and emphasizing the protected meristematic tissue, clonality, and sensitivity to soil disturbance in dominant groundcover plants. Subsequently, Veldman (2016) used data from degraded and reference savannas in Bolivia to identify perennial grass species as an indicator of old-growth savannas. Shearman et al. (2019) and Fill et al. (2021) documented the capability of a dominant bunchgrass to survive and reproduce after more than 50 years without fire in a North American pine savanna. In the same system, Fill et al. (2014) described the dominance of perennial species in the groundcover. Koffi et al. (2022) suggested that long-lived perennial species in an African savanna could live over 80 years, and Hamilton et al. (2002) estimated longevity at 100 years in an established bunchgrass in undisturbed California grassland.

Although fragmented and undergoing restoration, old-growth pine savannas of the southeastern United States were once widespread from Virginia to Texas (Figure 1a). Pine savannas are characterized by an open canopy of widely spaced pine trees and an understory of diverse herbaceous and woody species, with few trees in the midstory (Gilliam et al., 2006; Noss et al., 2015). Fire return intervals that historically maintained these open-canopy ecosystems averaged fewer than 5 years (Huffman, 2006; Rother et al., 2020; Stambaugh et al., 2011), with lightning ignitions occurring primarily during the late dry and early wet seasons (Huffman, 2006; Platt et al., 2015; Robbins & Myers, 1992). Fires set by Native Americans, and more recently, by early settlers and present-day land managers, increased the representation of early-dry or winter season fires in pine savanna fire regimes (Rother et al., 2020). Logging, fragmentation, and soil disturbances greatly reduced the southeastern pine savanna extent. Fire suppression also contributed to changes in ecosystem function; sustained fire return intervals longer than 4 or 5 years allow increases in midstory recruitment, establishment of fire-sensitive species, shading, litter accumulation, and eventually savanna mesophication (Ryan et al., 2013). Thus, pine savanna stability is supported by vegetation–fire feedbacks between the flammable herbaceous understory and fires ignited by lightning and humans (Fill et al., 2015; Platt et al., 2015).

Wiregrass (*Aristida beyrichiana* and *A. stricta*) is a perennial C4 bunchgrass in pine savannas (Figure 1b). Geographically widespread, endemic, and locally dominant, the species is associated with high biodiversity (Baruzzi et al., 2023), promotes understory flammability (Fill et al., 2016), and survives long periods without fire (Fill et al., 2021; Figure 1e), and resists increases in shrub establishment (Fill et al., 2017), thereby perpetuating a vegetation–fire feedback. Regrowth after fire is rapid via vegetative reproduction (clonal growth), which occurs through the propagation of closely spaced ramets (Figure 1b). Sexual reproduction in plants older than a few years is stimulated by fire and may occur without fire in first-year plants. Inflorescence and seed production and viability are variable but typically greater after fires in the late dry and early wet or summer seasons (May–July) than after those in the early dry or winter season (January–March; Figure 1f; Fill et al., 2012). Flowers and seeds are produced about 6 months after fires, and seeds germinate the following spring. Seed banking has yet to be documented, although wiregrass is suspected to have a 1-year seedbank. Wiregrass longevity is unknown but is projected to be hundreds, if not thousands, of years, as death of established plants is rarely observed except after extreme events such as extended flooding or widespread soil disturbance (Clewell, 1989; Michener et al., 1995; Parrott, 1967).

We modeled wiregrass population dynamics under different long-term fire regimes in two pine savanna environments, dry uplands and mesic flatwoods. We predicted long-term population persistence (stable or increasing population growth) or resistance to extinction

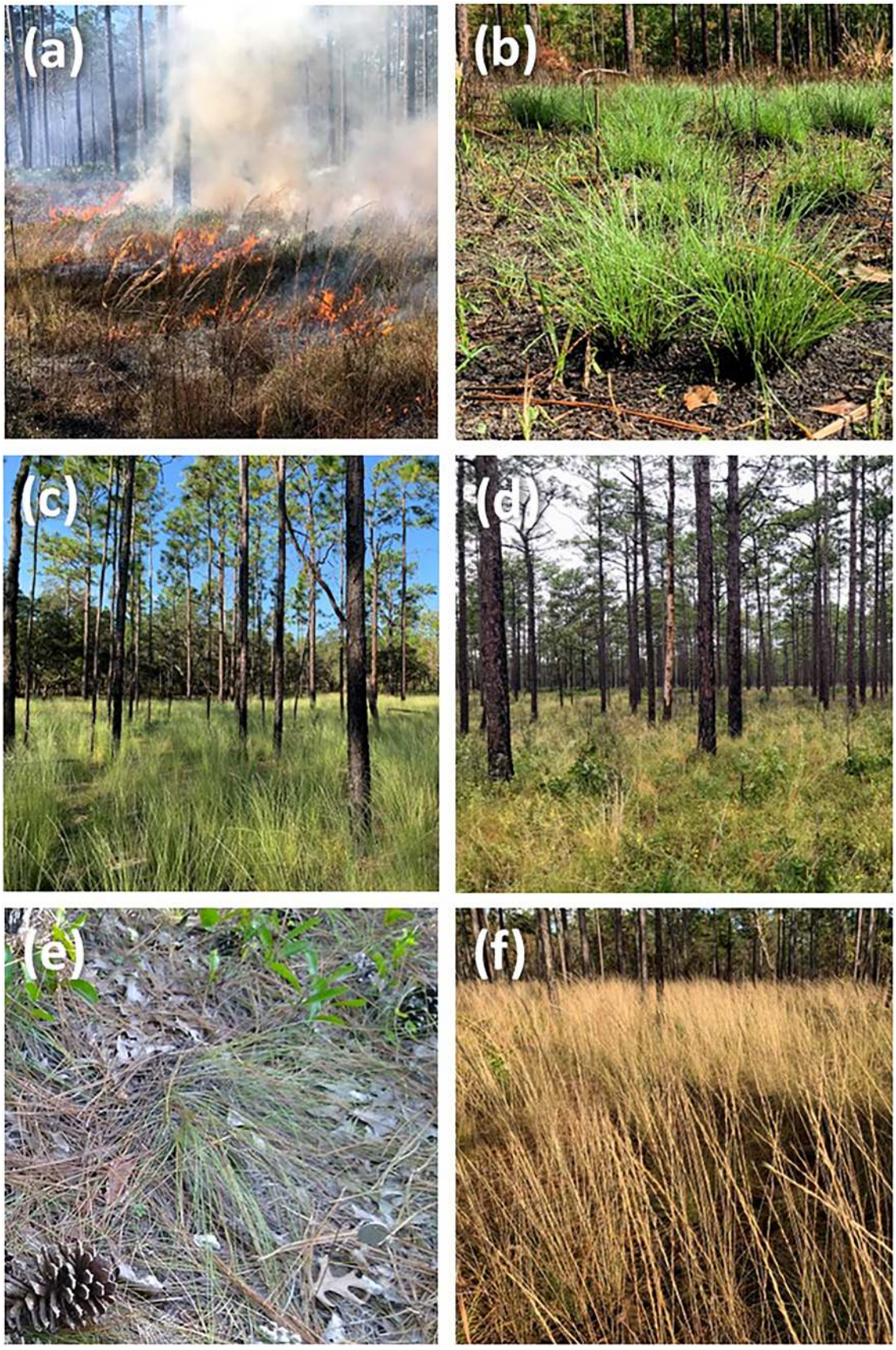


FIGURE 1 (a) Representative surface fire in a southeastern US pine savanna. (b) Wiregrass, *Aristida beyrichiana*, a widespread, endemic perennial bunchgrass in southeastern US pine savannas. (c) Dry sandhill pine savanna. (d) Mesic pine savanna stand. (e) Wiregrass after 30 years without fire in a dry sandhill pine savanna. (f) An understory of wiregrass flowering after a summer fire. Photos by RM Crandall and JM Fill.

(very slow population decline) under fire regimes that vary in seasonality and frequency. Our study thus contributes to our understanding of long-term savanna ecology.

MATERIALS AND METHODS

Study sites

We monitored wiregrass populations on two properties with different soil types, about 20 km apart, in North Central Florida (Figure 1c,d; Table 1). Ordway Swisher Biological Station (29.4°1 N, 82.00°W), the dry site, is a 3845-ha mosaic of mixed-pine uplands, xeric sandhills, and hardwood hammocks, interspersed with wetlands and open fields (Figure 1a). Elevation ranges from 28.7 to 55.5 m NGVD (i.e., National Geodetic Vertical Datum of 1929). We collected data at the highest elevations on deep sandy soils (Candler and Apopka) in units with similar histories of frequent fire and variable fire seasonality (Table 1).

Austin Cary Forest, the mesic site, encompasses 826 ha of pine flatwoods, hardwood stands, planted pine stands, and a small area of dry sandhills. All populations were on poorly drained soils of the Pomona and Lochloosa series, except those in the planted pine stand, which included soils of the better-drained Millhopper series. Stands varied in fire frequency and history over the last 30 years, ranging from annual to triennial frequency and seasonality of either winter (January–February) or summer (March–July).

Data collection

For each of nine populations, we individually tagged 99–150 plants at the start of the first transition, which varied by management unit (Table 1). Plants were sampled over two to four transitions, which we designate sequentially as transitions 1–4 for all populations (Table 1). In order, transitions encompassed the period from (1) March/April 2018 to March/April 2019; (2) March/April 2019 to November/December 2019; (3) November/December 2019 to October–December 2020; (4) October–December 2020 to October–December 2021.

We individually tagged plants within each management unit across a range of sizes. We determined basal area of each plant to be an accurate measure of size (Appendix S1: Figure S1). We quantified the size of each marked individual at the beginning of the study and at the end of each transition (year) in the fall when plants were flowering. We first surveyed some populations in the spring (Table 1) but subsequently adjusted to a fall measurement schedule. Because wiregrass growth rate is slow, we were not concerned about this 4-month difference (November vs. March/April) in adjusting the data collection. We quantified survival and fecundity in the fall of each year. Winter-burned populations (AW, BW) flowered in June. We did not document this for the first two transitions for AW, for which fecundity was assessed in the fall. For the other transitions, the fecundity of plants in these management units was assessed in June.

We measured wiregrass size, survival, and fecundity for each transition. To determine plant size, we measured

TABLE 1 Characteristics of *Aristida beyrichiana* populations sampled for demography in a mesic site and a dry site.

		Transition					
Unit	*n*	Before sampling	1	2	3	4	Unit fire history
Dry							
T1	109		F (Jun)	PF	NF		Triennial for last 20 years, primarily Apr–Jul
T2	108		F (Mar)	PF	F (Apr)		Triennial for last 20 years, primarily Mar–Jun
BS	129		NF	F (Jun)			Nearly biennial for the last 20 years, mostly Apr–Jul
VW	120	F (Jan)	PF	NF			Variable frequency, mostly Jan/Feb
Mesic							
AS	156	PF/F (Jul)	PF (Jul)	PF (Jun)	PF (Jul)		Annual summer fire (Jun/Jul) since the 1970s
AW	137	PF/F (Jan)	PF (Jan)	PF (Jan)	PF (Jan)	PF (Jan)	Annual winter fire (Jan) since the 1970s
TS	150		F (Jul)	PF	F (Jun)	PF	Every 2–3 years for the last 20 years, mostly April–July
BW	99		F (Jan)	PF			Every 2–3 years Jan–Feb for the last 10 years
PL	121	F (May)	PF	F (Jun)			Planted and thinned; every 2–3 years since 2016, May–Aug

Note: Each transition represents a 1-year timestep, with either fire (F; population was burned during that transition), post-fire (PF; first transition after fire), or no fire (NF; at least one transition since the fire). For units AS and AW, PF is also a fire year because these units were burned annually, but we simplify to PF. Names of management units within each site are intended to reflect the frequency and seasonality of the fire regime. Numbers of plants are sample sizes at the start of analyses.

the length of the longest axis and the axis perpendicular to the longest axis, calculating the basal area as the area of an ellipse. Plants were counted as dead if no green tillers were visible. If plants were not located 1 year but found the next, all data except survival was entered as "NA." Fecundity measures included whether a plant was reproductive (0/1) and the number of seeds produced. We considered a plant reproductive if it had at least one flowering culm. To estimate the number of seeds, we collected and measured 20–30 flowering culms, each from a different plant, and counted the glume pairs of each inflorescence. We regressed the number of glume pairs on inflorescence length to obtain an equation for calculating seed number from inflorescence length for each population and transition. We measured the inflorescence lengths of all culms on each plant and used the equation to calculate the number of seeds per plant.

We searched for but found no naturally occurring seedlings in the field. We also sowed seeds in plots to estimate recruitment, but did not observe seedlings. Thus, we estimated a low recruitment probability in our models (i.e., 0.001). For most fire transitions and populations, we collected seeds in the fall, stored them at approximately 3°C, and germinated them in the lab the following March. Seeds were placed on blotter paper in polystyrene boxes to which we added 5 mL of a 0.002% solution of Plant Preservative Mixture (https://www.plantcelltechnology.com/about-ppm/). We placed the boxes on a lab bench at room temperature (Fill et al., 2021). We defined germination as the elongation of the radicle and epicotyl from the seed coat within 3 months of initiating germination trials.

TABLE 2 Demographic vital rates and definitions used in developing integral projection matrix models for *Aristida beyrichiana*.

Model components	Vital rate	Description
Survival and growth $p(y,x)$	$s(x)$	Probability of individuals of size x surviving to size y
	$g(y,x)$	Probability of surviving individuals growing from size x to size y
Fecundity $f(y,x)$	$f_r(x)$	Probability of individuals of size x producing seeds
	$f_n(x)$	Number of seeds produced by individuals of size x
	$f_d(y)$	Size distribution of seedlings
	f_{est}	Probability of seedling establishment

Data analysis

We used integral projection models (IPMs) to calculate population growth rates for each population and transition. IPMs use continuous, rather than discrete, relationships between size and vital rates to estimate population growth (Ellner & Rees, 2006; Table 2). The detailed description of model development and the demographic functions used for each model component are included in Appendix S1: Tables S1–S9 and Appendix S2: Figures S1–S33.

RESULTS

All wiregrass populations had similar and stable population growth rates regardless of environment or long-term fire regime (Figure 2; Appendix S1: Table S10). As expected for a long-lived species, survival was nearly 100% in all populations and transitions (Appendix S1: Tables S1–S9; Appendix S2: Figures S1–S33), as in a previous long-term study (Laucevicius et al., 2021). Observed causes of mortality included high fuel loading (e.g., Fill et al., 2021) and downed trees or limbs on "unlucky" plants. Furthermore, as expected in a species with fire-stimulated flowering, there was high variability in fecundity; no plants were observed flowering during non-fire transitions. There was very little flowering after fires in winter-burned units, including AW, BW, and VW (up to 20% of plants). In units burned in the late spring and summer, more than half the population generally flowered (e.g., Fill et al., 2012; Laucevicius et al., 2021).

DISCUSSION

Our research indicates that wiregrass population persistence under different fire regimes is driven by high adult survival rather than seedling recruitment. All wiregrass populations experienced little mortality. Although wiregrass plants might not survive severe fires or under extended flooding or drought (e.g., Michener et al., 1995), we found that given environmental conditions that are not extreme, established wiregrass plants are unlikely to experience significant mortality under different fire regimes.

Despite abundant flowering in years with fire, seed germination in the lab was extremely low for all populations, and flowering is meaningful for population growth only insofar as it results in recruits. Wiregrass seedling establishment in intact pine savanna communities is rare (Glitzenstein et al., 2001; Walker & Silletti, 2006). Although we did not observe recruits in the field, nor clonal fragmentation, we know that recruits from

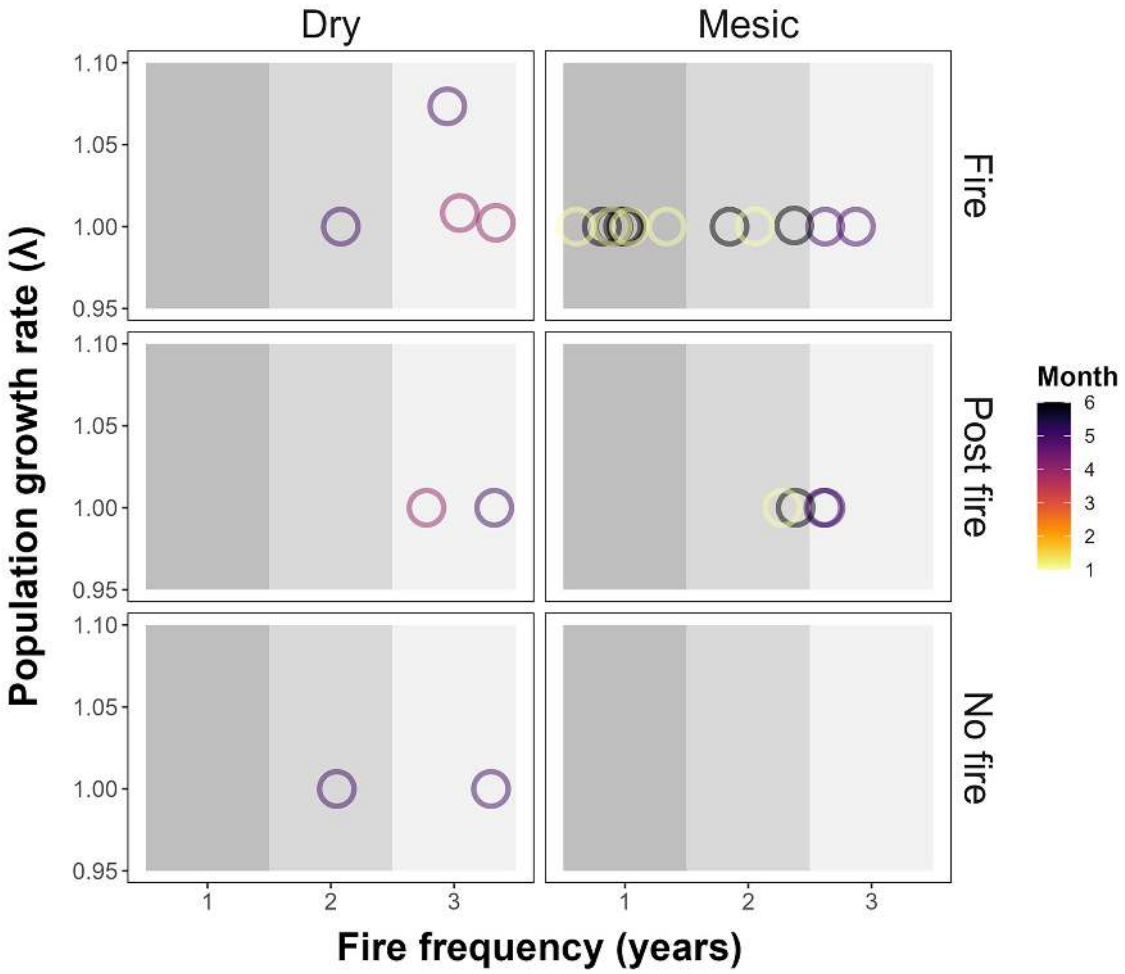


FIGURE 2 Population growth rates (λ) of nine wiregrass (*Aristida beyrichiana*) populations burned under different long-term fire regimes in a dry and a mesic savanna environment. Each circle represents λ in a 1-year time-step; the center of the circle corresponds with the *y*-axis value. Dashed line indicates stable populations. "Fire" indicates a transition in which the population was burned, "post fire" indicates a transition following one with fire, and "no fire" indicates a transition without fire and not immediately following one with fire. Month indicates the month during which the fire occurred. Fire frequency indicates the long-term frequency of the management unit where the population was monitored. Populations were modeled for different numbers of transitions (see Table 1).

seeds do contribute to population trends over decades, especially after spring/summer fires when seed production and viability is high (Fill et al., 2012; Laucevicius et al., 2021). However, there is high interannual variation in factors leading to successful recruitment, such as viable seed production, and fragmentation rates are low (Clewell, 1989; Fill et al., 2012; Laucevicius et al., 2021; Perez, 2014; Seamon, 1998). Certainly, under annual fire regimes, wiregrass seedlings are less likely to survive than under less frequent fire regimes, as seedlings seem to require at least two full years without fire (Mulligan & Kirkman, 2002). Stable population growth under these patterns in survival and fecundity follows previous research demonstrating that as longevity increases in perennial plants, fecundity becomes less influential than survival, and temporal variance in population growth rates decreases (García et al., 2008). Over time, fire regime frequency and seasonality will influence the variable contribution of fecundity to population growth.

Our study has several important strengths that indicate wiregrass' contribution to old-growth savanna stability. We modeled populations subjected to different fire regimes in the field (i.e., that differed in their known fire history) instead of simulating different fire regimes using data from one population. Moreover, results of single-year studies of fire effects on tropical perennial grass dynamics are often related more to time-since-fire than to fire regimes. Throughout our study, most wiregrass populations were subjected to frequent fire regimes that varied in seasonality but occurred frequently and within the historical range of variation (Rother et al., 2020; Stambaugh et al., 2011). Although the annually burned populations experienced an invariant fire regime that is unlikely over decades, populations were neither declining

nor increasing. The consistency of results between our study populations lends data-driven support to wiregrass' resilience to regimes that differ in frequency and seasonality. Although wiregrass is resistant to change even under periods of fire exclusion (Fill et al., 2017, 2021; Shearman et al., 2019), our inferences extend to old-growth savannas that have experienced frequent fire regimes for decades. After long periods without fire in old-growth savannas, a single fire does not return the system to a state similar to that of frequent fires (Fill et al., 2021; Morgan & Lunt, 1999). At least several fire cycles would likely be required (Reinhart & Menges, 2004).

The patterns we observed in wiregrass mirror inferences from other studies of dominant grass dynamics in old-growth tropical savannas. There are relatively fewer studies on perennial grass demography in the tropics than in temperate regions. However, one tropical perennial species that has received relatively substantial study is *Themeda triandra*, which is considered a keystone species in Australian savannas (Snyman et al., 2013). Although population models have not been developed, this widespread C4 grass shares many demographic similarities with wiregrass and is similarly considered one of the biome's original dominant grasses (Snyman et al., 2013). It is also clonal, and although flowering is not fire-stimulated, the species does require some type of regular defoliation (burning, mowing, grazing) to persist (Snyman et al., 2013). Similarly, seed production did not contribute much to population growth (Snyman et al., 2013). In a humid West African savanna, three of the savanna's four dominant perennial C4 grasses were sensitive to fire in the late dry season. Still, overall, survival was the most important parameter for population maintenance (Koffi et al., 2022). In contrast, in an annually burned Venezuelan savanna, Silva et al. (1991) found that growth to larger size classes contributed the most to population growth in the C4 perennial grass *Schizachyrium sanguineum*, which was highly sensitive to even 1 year without fire. They postulated that the species was likely promoted by human-driven annual fire regimes (Silva et al., 1991).

Our study supports recognition of old-growth pine savannas in the southeastern United States. Until recently, this region has frequently been omitted from global savanna studies and received a general lack of recognition by the global community (Pau et al., 2023). Species diversity under frequent fire regimes is maintained by fire response strategies related to both survival and recruitment after fire (Brewer, 2023; Pausas, 2019). Many plant species of pine savannas exhibit strategies related to survival, with minimal recruitment (Orrock et al., 2023), and likely contribute to savanna persistence over their long lifespans. Thus, diverse life histories of perennial grasses that co-dominate with wiregrass, such as *Andropogon* spp., *Schizachyrium* spp., and *Sporobolus* spp., might promote old-growth pine savanna persistence under different fire regimes or wider ranges of variation (Gagnon et al., 2012; Silva, 1996; e.g., Prober et al., 2007; Scott et al., 2010).

AUTHOR CONTRIBUTIONS

Both authors contributed to the conception, design, analyses, and writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Fill & Crandall, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.14165603.

ORCID

Jennifer M. Fill https://orcid.org/0000-0002-2301-6676
Raelene M. Crandall https://orcid.org/0000-0002-0229-5418

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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