Demographic effects of fire on two endemic plant species in the longleaf pine-wiregrass ecosystem

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Abstract Fire can have dramatic effects on the vital rates of plant species and has been used successfully for management in a number of ecosystems. However, the demographic response of species to fire in fire-dependent ecosystems is variable, making it important to study the effects of fire on rare and threatened species. We quantified the effects of fire on *Astragalus michauxii* and *Pyxidanthera brevifolia*, two rare endemics of the longleaf pine-wiregrass ecosystem of the southeastern USA, by means of periodic matrix models to project the effect of fire frequency on population growth. In contrast to many species in the longleaf pine-wiregrass ecosystem, fire had short-term negative effects on both species, causing reductions in survival, size, flowering, and fruit production. Relative to the three-year fire intervals to which the study populations are currently exposed, more frequent burning is projected to cause population decline, with the most dramatic effects under annual burning. Although the current longleaf pine-wiregrass ecosystem is fire dependent and has experienced frequent fire for at least several thousand years, we propose that the two endemic species may be remnants from a past vegetation assemblage that experienced less frequent fire and thus may be adapted to longer fire-return intervals compared to other species currently in the ecosystem. Despite the short-term negative effects of fire on the vital rates of these species, longer-term benefits such as reduction of woody encroachment and litter removal may be important for the ultimate success of the species.

Keywords Astragalus · Demography · Endemism · Fire · Matrix models · *Pinus palustris* · Pyxidanthera

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Introduction

Fire is a natural disturbance in many ecosystems and can have a profound effect on the population dynamics of plant species (Glitzenstein et al. 1995), which directly influences plant community composition (Morrison et al. 1995) and vegetation structure (Moreira 2000). Under natural fire frequencies, many regions with precipitation and nutrient availability adequate for supporting closed canopy forest are instead maintained as grasslands or savannas (Staver

et al. 2011). Owing to the recurring destruction of aboveground biomass, frequent fires tend to favor plant species of smaller size with less carbon investment in aboveground biomass (Hoffmann 1999), and many areas with high fire frequencies tend to be dominated by herbaceous species. Fire suppression during the 20th century has led to changes in vegetation structure in many ecosystems, including increased density of woody vegetation (Bond et al. 2004), decreased biomass of herbaceous plants, and loss of species diversity, making it one of the primary threats to rare plants in the United States (Schemske et al. 1994).

Prescribed fire has become one of the primary tools for restoring and maintaining fire-dependent plant communities and managing rare plants in the longleaf pine ecosystem of the southeastern United States (Brockway and Lewis 1997). Both representative rare and common plant species in the region have been shown to respond positively to fire, exhibiting increased flowering (Seamon et al. 1989; Gowe and Brewer 2005; Brewer et al. 2009), fecundity (Hartnett and Richardson 1989; Brewer 2001), and seedling establishment (Hartnett and Richardson 1989; Brewer and Platt 1994; Brewer 2001). Based partly on the observed positive responses of many plant species to fire in this system, over the last few decades biologists and land managers have advocated for restoring historical fire regimes in many natural areas as a critical component of rare species management.

Although re-establishing historical fire regimes is a well-intentioned goal, local and regional differences in historical fire regimes are expected due to spatio-temporal variation in fuels, topographic position, and climate. It is also difficult to identify fire frequency over the timeframes within which most plant species are likely to have evolved. As a surrogate for other information (Power et al. 2007), some have used the demographic responses of native plants to infer past fire regimes (Liu et al. 2005; Menges 2007). This is appropriate in areas that have been climatically stable for an extended period of time, but in the northern extent of the longleaf pine ecosystem the situation is complicated because of substantial climatic changes since the Pleistocene (Jackson et al. 2000). Vegetation assemblages in these areas are likely a mixture of species with different evolutionary relationships with fire, for example endemic species that were most likely present through the latter Pleistocene (Wall et al. 2010)

and species that migrated following the end of the Pleistocene (Soltis et al. 2006). Consequently, it is important to specifically understand the demographic response of rare or endangered species to variable fire regimes to make better informed management decisions (Kirkman et al. 1998; Slapcinsky et al. 2010).

It is within this context that we studied the fire ecology of two rare endemic species restricted to the Fall-line Sandhills, an ancient dune system at the eastern edge of the Gulf and Atlantic Coastal Plain physiographic province (GACP) that was historically dominated by the longleaf pine ecosystem. We examined the effects of prescribed fire on the mortality, growth, flowering, and seed production of *Astragalus michauxii* (Kuntze) F.J. Herm. and *Pyxidanthera brevifolia* Wells. We monitored individuals across multiple populations and estimated the effects of fire frequency on the species population growth rates and long-term population viability by matrix modeling and interpreted the results in the context of the climatic and vegetation history of the GACP.

Methods

Study area and species

Astragalus michauxii (Fabaceae) is a perennial, herbaceous legume with populations in North Carolina (NC), South Carolina (SC), Georgia (GA), and Alabama (AL), USA. Flowering occurs in early May with fruit maturation by mid-July. *Pyxidanthera brevifolia* (Diapensiaceae) is an evergreen, woody cushion plant with a range limited to four counties in NC and two counties in SC with over 80 % of extant populations found on Fort Bragg Military Reservation, NC. Flowering occurs from late December through early April with the majority of flowers opening in mid- to late March. Fruit maturation occurs between the last week of April and the first week of May. Anecdotal evidence suggests that both species are relatively long lived perennials that experience low natural recruitment rates since no seedling establishment for either species had been documented before this study. Both species have been designated by the Department of Defense as Species-at-Risk and are considered vulnerable to local extinction in NC (S3).

Fort Bragg Military Reservation is located at the northern limit of the Fall-line Sandhills. The landscape

is characterized by rolling hills dissected by numerous streams, which create a matrix of wetland and xeric habitats. For the duration of the study, Fort Bragg was managed with prescribed fire on a fixed, three-year burn interval. Growing-season burns are defined as occurring in April through June. During the course of the study, all growing-season fires were completed by 1st July. Dormant season fires occur from December through March. The flora and vegetation communities of Fort Bragg have been described separately (Sorrie et al. 2006). The study species occur on excessively well-drained upland sandy soils with low nutrient availability, and a priori habitat characterization of the two species suggests that both require a relatively open forest canopy and relatively low ground-level biomass.

Field methods

In summer 2007, we surveyed all known *A. michauxii* populations on Fort Bragg, locating individuals in 39 of the 87 surveyed populations. Population sizes averaged 13 individuals and ranged from 1 to 116 individuals. We placed aluminum tags next to all identified individuals; over the course of the study, we identified and tagged 496 individuals. During winter 2008, we randomly selected 24 of the 277 known *P. brevifolia* populations which were evenly divided into one-, two-, and three-years post-burn. Before the 2008 growing-season burn period (April-June), we surveyed and demarcated the areal extent of the 24 populations and established a transect through the area with the highest population density. We placed aluminum tags next to all individuals within one meter of the established transect. In total, we marked 1042 individuals with sample size averaging 42 individuals per population and ranging from 13 to 71 individuals.

We measured the height (± 1 cm) and number of fruits for the five tallest stems of each tagged *A. michauxii* individual annually during the last 2 weeks in June from 2007 to 2010 (Fig. S1, online resources). We estimated the number of seeds per fruit by counting the number of viable seeds in 466 fruits produced between 2007 and 2010. We established twenty-one 2.25-m^2 seed addition plots (mean number of seeds $= 98.4$) during 2007 and 2008 and monitored for recruitment for four years (2008 through 2011). Size of *P. brevifolia* plants was quantified by

measuring the major and minor axis (± 1 cm) of each tagged individual and estimating the percentage cover within the cushion to the nearest 10 %. Area was calculated as follows: area $= \frac{majoraxis}{2} * \frac{minoraxis}{2} * \pi * \frac{percentagecover}{100}$. We recorded occurrence of flowering and revisited each population to estimate the number of fruits of ~ 10 randomly selected individuals per population. We recensused all populations in 2009 and 2010 before the beginning of the burn season (Fig. S1, online resources). To estimate the number of seeds produced per fruit, we collected and counted seeds of 111 fruits from 12 of the populations in 2008. We established thirty 2.25-m^2 seed addition plots by distributing 100 seeds per plot and monitored for seedling recruitment from 2008 to 2010. No seedlings were observed in any of the *A. michauxii* or *P. brevifolia* seed addition plots, but one *A. michauxii* seedling was identified in the field during the course of the study and 41 *P. brevifolia* seedlings were identified across four populations during the 2010 census.

Vital rates data analysis

We modeled the effects of fire and plant size on the vital rates by means of generalized linear mixed effects models (Pinheiro and Bates 2000) with year and population as random factors for *P. brevifolia* and year as a random factor in the case of *A. michauxii*, as population variance was small and causing convergence issues. We tested for the effects of fire on plant size by means of a linear regression model. Survivorship for both species was modeled by logistic regression. We quantified recovery rates following fire for both species by calculating the ratio of the pre-burn size to post-burn size one and two years post fire and performed an ANOVA to test for differences in recovery rates by pre-burn size. We modeled the effects of fire and plant size on number of fruits produced by means of a Poisson distribution with a log link function. While all the *P. brevifolia* populations were subjected to spring burns, some *A. michauxii* populations were burned in winter so we compared the effects of seasonality of burn [growing (April–July) versus dormant season burns] on the survivorship, post-fire recovery, and fruit production of *A. michauxii*.

Matrix construction and analysis

We classified *A. michauxii* into four height classes based on the tallest stem: small (0.1–20 cm), small-medium (>20–40 cm), medium (>40–80 cm), and large (>80 cm). Because of low numbers, *A. michauxii* individuals were pooled across populations and years to estimate three separate transition matrices based on years post-burn: burned during current growing season, one year post-burn, and two or more years post-burn (Tables 1 and 2, online resources). We classified *P. brevifolia* into ten size classes using area (cm^2):>0–10 cm^2, >10–25 cm^2, >25–50 cm^2, >50–100 cm^2, >100–200 cm^2, >200–400 cm^2, >400–800 cm^2, >800–1,600 cm^2, >1,600–3,200 cm^2, and >3,200 cm^2; an additional age class was recognized for first-year seedlings. We calculated mean seed production by multiplying the mean number of seeds per fruit by per capita fruit production. Seedling recruitment per seed was estimated by dividing the observed number of seedlings at time t by total seed production at time $t-1$. For *P. brevifolia*, seedling survivorship and growth were estimated by tagging and revisiting in spring 2011 the 41 seedlings located during the 2010 census. For *P. brevifolia*, we constructed six separate transition matrices grouped according to years post-burn (one, two, or three years post-burn) and the two times steps (2008–2009 and 2009–2010) by pooling individuals across populations (Tables 3 and 4, online resources). Because the census of *P. brevifolia* populations was conducted before burn season, response data collected one year post-fire represent the first census after fire. We estimated size class survivorship at 0.972 (average survivorship of two largest size classes across all years) for *A. michauxii* and 0.998 (average survivorship of four largest size classes across all years) for *P. brevifolia* when no mortality was observed within a size class during a time step. We did not include a seed bank in the modeling for either species. While we did not directly parameterize the role of the seed bank in the population dynamics, prior work on *A. michauxii* suggests that the size of the seed bank is small (Weeks 2005), and the low overall recruitment rates for both species indicate that the contribution of the seed bank is minimal.

We simulated the stochastic population growth rate (λ_s) of *A. michauxii* and *P. brevifolia* under one- to four-year fire-return intervals by a matrix selection approach, which preserves the correlations between transition elements. The population growth rate provides information on whether a population is likely to increase, decrease, or remain the same through time. To increase the variation of possible λ_s, we constructed nine new transition matrices from the *A. michauxii* dataset divided into three time since fire categories (burned in current year, one year post-burn, and two years post-burn) and three time steps (2007–2010). For *P. brevifolia*, we utilized the six matrices described above. We calculated the average annual λ_s over 200 time steps and 5,000 iterations by the following formula: $\lambda_S = \left(\frac{N_t}{N_0}\right)^{1/T}$ (Lewontin and Cohen 1969). At each time step of the simulation, we first randomly selected one "year" (e.g., either 2007–2008, 2008–2009, or 2009–2010 for *A. michauxii* or 2008–2009, 2009–2010 for *P. brevifolia*). So, under a simulated two-year fire-return interval we randomly selected a year and then multiplied the population vector N_t by the burned matrix and the unburned$_1$ matrix for the randomly selected year; under a three-year fire-return interval, the simulation also included the two-year post-fire matrix from the selected year. To simulate a four-year fire-return interval, we used the two-year post-fire matrix for the fourth year.

Elasticities (de Kroon et al. 1986) were calculated for the estimated *A. michauxii* and *P. brevifolia* matrices based on the deterministic population growth rate (λ). Elasticities provide information on the proportional contribution of the individual matrix elements to proportional changes in the population growth rate (Caswell 1996). We calculated the reproductive value of each size class and the stable stage distribution, which are mathematically defined as the left and right eigenvectors of a matrix, respectively. The reproductive value of each size class is defined as the expected number of offspring for an individual of that size class, relative to the smallest size class (defined as one). For *P. brevifolia*, the reproductive values were relativized to the seedling size class, not the seed class (Goodman 1968). The stable stage distribution refers to the proportional representation of each size class under a stable population structure scaled to sum to one. Stable stage distributions represent long-term population dynamics and can mask underlying transient dynamics, especially in frequently disturbed systems (Stott et al. 2011). We estimated the proportional difference between the observed size distribution at each time since fire and

stable stage distribution of the two year post-fire matrix for both species by Keyfitz's Δ (Keyfitz 1968). This index is a value between one and zero with one representing the largest proportional differences and zero no difference between the observed and stable size distributions.

Fire influences λ through its multiple effects on reproduction, mortality, and growth of individuals. To quantify the contributions of these vital rates to the overall change in λ caused by fire, we performed a life table response experiment, or LTRE (Caswell 1996). We utilized a fixed one-way design to compare the burn matrix with the second year post-fire matrix. The difference in λ between these two matricies ($\Delta\lambda$) was decomposed by the linear approximation: $\Delta\lambda \approx \sum_i \Delta X_i \frac{\partial \lambda}{\partial X_i}$. The overall difference in the population growth rate ($\Delta\lambda$) is approximated as the sum of the differences of the individual contributions $\left(\Delta X_i \frac{\partial \lambda}{\partial X_i}\right)$ of the underlying parameters (X_i) of the transition matrices. This formula is appropriate for any set of parameters that can be used to reconstruct the transition matrices (Caswell 1996); here, we utilized an alternate parameterization (Hoffmann 1999).

All statistical analyses were performed by means of R version 2.10.1 (R Development Core Team 2009); R script is available from the authors on request. Point estimates include standard errors.

Results

### Effects of plant size and fire on vital rates

Mortality was generally low for *A. michauxii* and *P. brevifolia*, averaging 4 and 2 % per year, respectively. Mortality was highest among small individuals for both *A. michauxii* ($X^2_{1df} = 88.1$, $P < 0.01$; Fig. 1) and *P. brevifolia* ($X^2_{1df} = 198.9$, $P < 0.001$; Fig. 1). Burning increased mortality in *A. michauxii* ($X^2_{2df} = 89.7$, $P < 0.01$) and *P. brevifolia* ($X^2_{2df} = 2579.5$, $P < 0.001$; Fig. 1). Burning had a greater effect on mortality of small *P. brevifolia* individuals relative to the larger size classes ($X^2_{2df} = 2303.1$, $P < 0.001$), but in *A. michauxii* all size classes were affected ($X^2_{2df} = 5.83$, $P = 0.05$).

Fruit production was positively correlated with plant size in both *A. michauxii* ($X^2_{1df} = 89.3$,
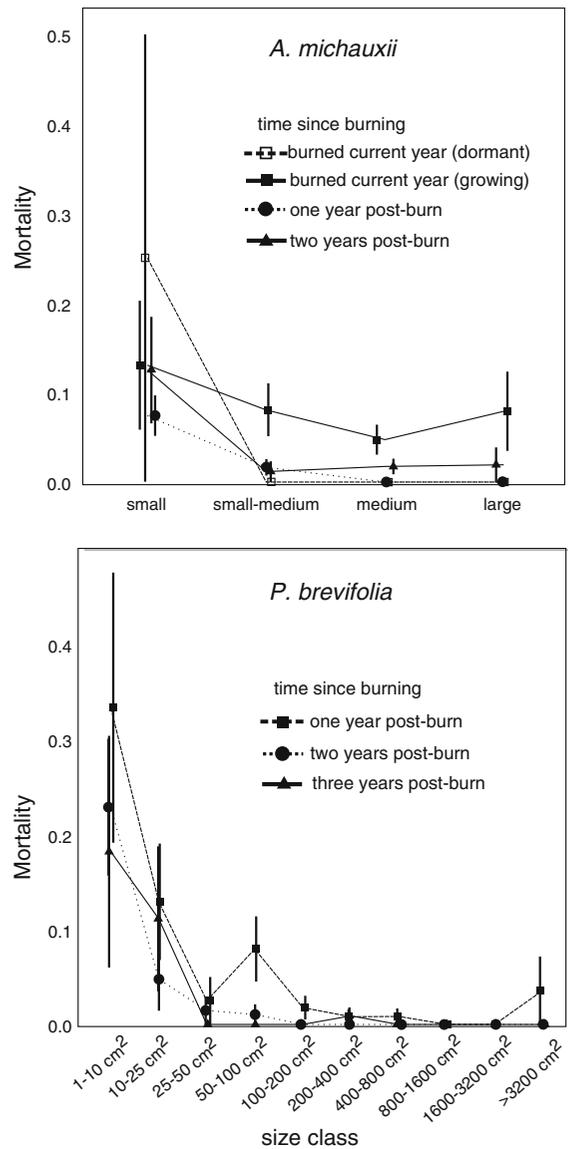
Fig. 1 Mortality of *Astragalus michauxii* (*top*) and *Pyxidanthera brevifolia* (*bottom*) as a function of time since last burn and size class. *Error bars* represent standard error of the mean

$P < 0.001$) and *P. brevifolia* ($X^2_{1df} = 1769.2$, $P < 0.001$; Fig. 2). Burning reduced flowering (not shown) and fruit production (Fig. 2) in both species. Growing-season burns nearly eliminated fruit production in *A. michauxii* across all size classes (Fig. 2) with mean per capita fruit production of 0.2 in years when burned and 9.2 in unburned years ($Z^1_{470df} = 16.6$, $P < 0.001$). Burning reduced flowering in *P. brevifolia* by 48 % in the first-year post-burn ($X^2_{2df} = 639.5$,
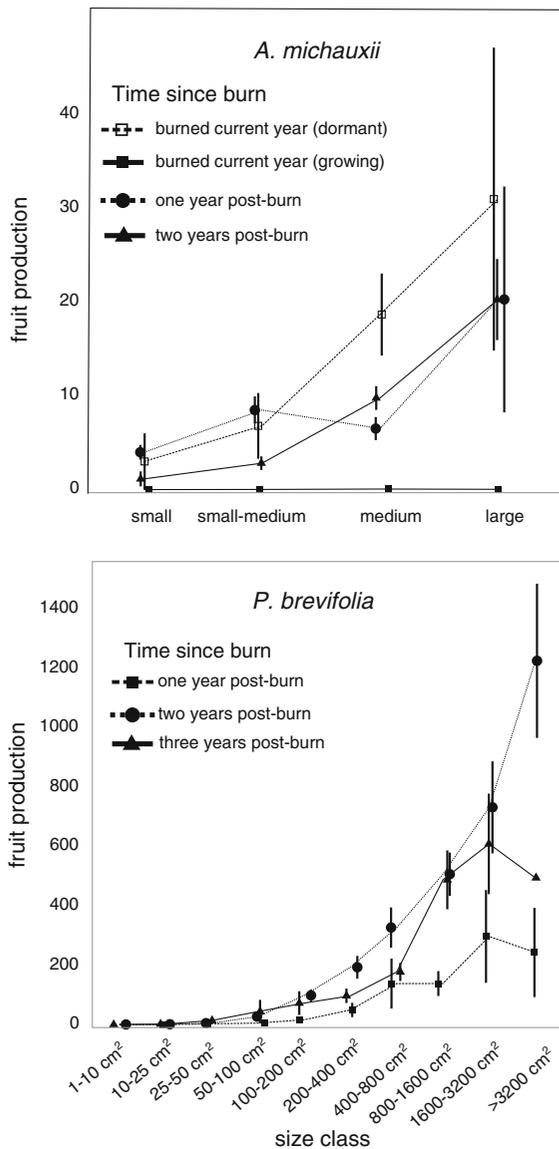
Fig. 2 Mean number of fruits produced as a function of time since last burn and size class for *Astragalus michauxii* (*top*) and *Pyxidanthera brevifolia* (*bottom*). *Error bars* represent standard error of the mean

$P < 0.001$, not shown), and reduced fruit production ($X^2_{2df} = 4816.7$, $P < 0.001$).

Plant size was reduced in the current year by burning in *A. michauxii* ($X^2_{2df} = 243.2$, $P < 0.001$). The mean height in 2007 for plants burned 3 years previously was 44.2 ± 2.1 cm. At the end of the growing season following fire, the mean height was 26.6 ± 1.4 cm. However, mean stem height had recovered to pre-burn height by the end of the second

growing season after fire (43.2 ± 2.5 cm vs. 44.2 ± 2.1 cm, $P > 0.05$). Plant size was also still reduced in *P. brevifolia* roughly nine months following fire ($X^2_{2df} = 50.6$, $P < 0.001$). The area of *P. brevifolia* individuals across all years averaged 908 ± 72.6 cm^2 before burning, declining to 627 ± 48.1 cm^2 after one year and recovered to 854 ± 49.8 cm^2 2 years after burning. Post-burn recovery (ratio of post-burn size to pre-burn size) varied across size classes with small individuals exhibiting greater recovery than large individuals after 1 year ($F^9_{386df} = 9.5$, $P < 0.001$, Fig. 3) and two years post-burn ($F^9_{386df} = 26.5$, $P < 0.001$, Fig. 3).

Burn season (dormant vs. growing) did not significantly increase mortality in *A. michauxii* across size classes ($X^2_{1df} = 2.4$, $P > 0.05$, Fig. 1); growing-season fires decreased the size of individuals, while dormant season burns did not ($F^1_{376df} = 134.8$, $P < 0.001$). Growing-season burns also decreased *A. michauxii* fruit production relative to dormant season burns ($X^2_{1df} = 3521.0$, $P < 0.001$, Fig. 2); individuals burned during the dormant season produced an average of 17.2 ± 3.8 fruits, while individuals burned during the growing season produced an average of 0.03 ± 0.01 fruits.

Population growth rates, elasticities, and LTRE in relation to fire

Simulations of the long-term population dynamics of *A. michauxii* and *P. brevifolia* predicted that λ_s would decline significantly under annual burning and increase with increasing fire-return interval (Fig. 4) with the greatest increase between one- and two-year fire-return intervals. Two-, three-, and four-year fire-return intervals were similar; but, for both species, λ_S was greatest when the fire-return interval was 4 years. Under fire-return intervals longer than one year, λ_S averaged 0.970 (0.964–0.978 95 % CI) for *A. michauxii* and 1.00 (0.990–1.015 95 % CI) for *P. brevifolia*.

Elasticities under annual burning for *A. michauxii* populations indicated that λ was most sensitive to changes in the survivorship of small individuals. Under longer fire-return intervals, λ was most sensitive to changes in the survivorship of medium- and large-sized individuals (Table 5, online resources). Elasticities for *P. brevifolia* demonstrated similar patterns
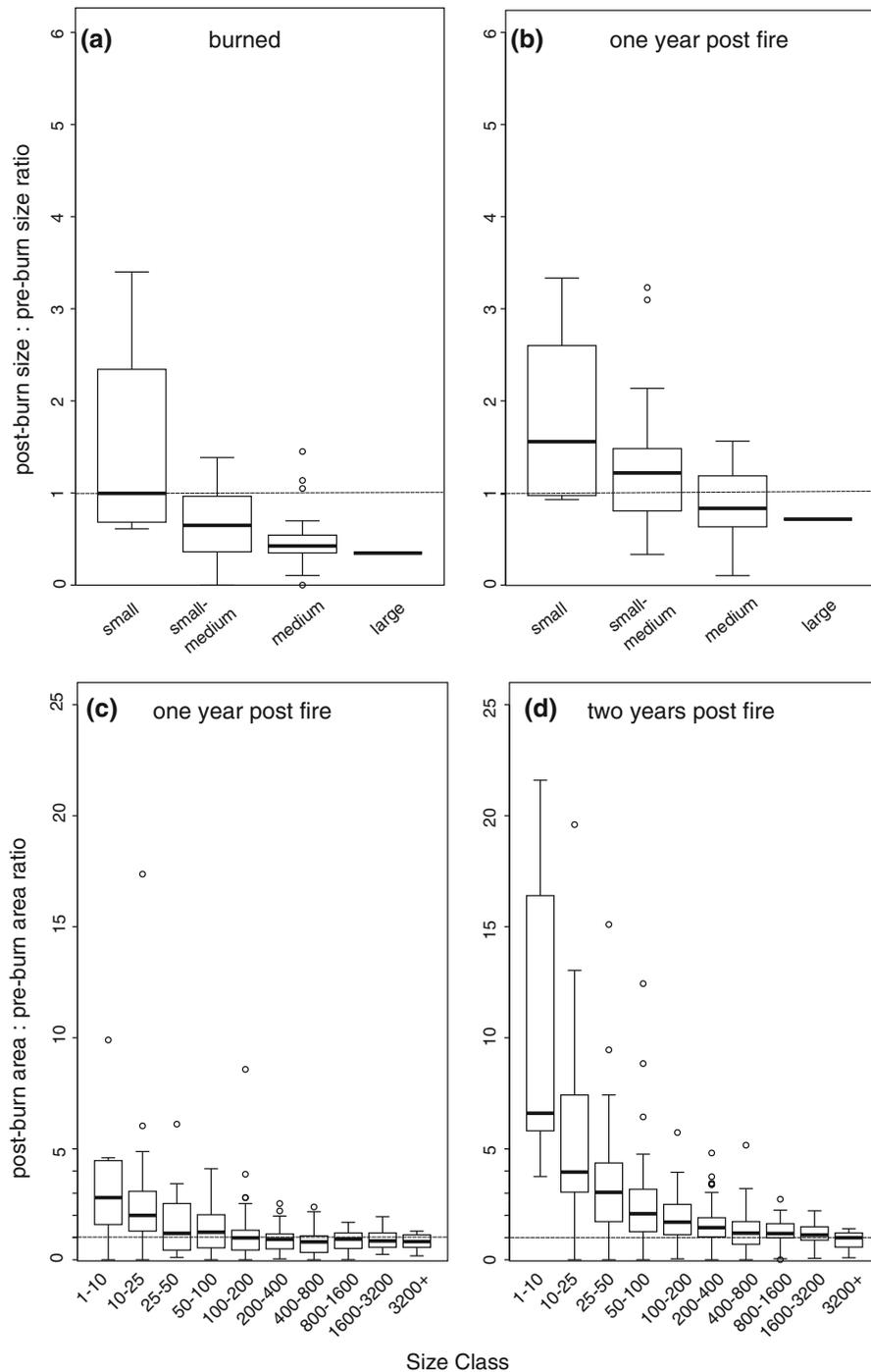
Fig. 3 Modified box plot of post-fire recovery rates for *Astragalus michauxii* (*top*) and *Pyxidanthera brevifolia* (*bottom*) individuals as a function of pre-burn size. *Dotted line* represents recovery to pre-burn size. Smaller individuals recover at a faster rate relative to larger individuals for both species

(Table 6, online resources). Stable stage distributions of *A. michauxii* and *P. brevifolia* indicated that annual burning would result in a larger proportion of individuals in smaller size classes (Tables 1 and 2), but the two species had different growth responses following fire. For *A. michauxii*, *Keyfitz's Δ* decreased
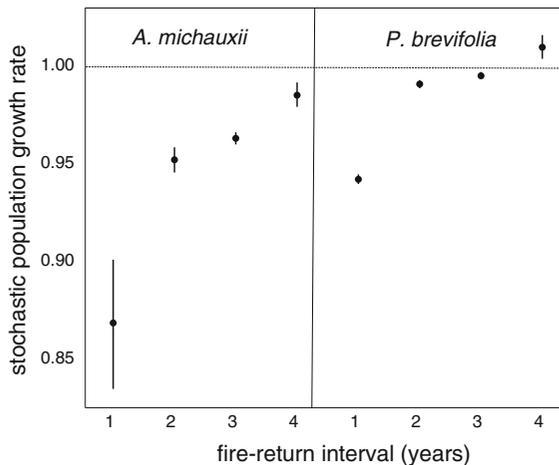
Fig. 4 Projected stochastic population growth rates under different fire-return intervals (1–4 years) for *Astragalus michauxii* (*left*) and *Pyxidanthera brevifolia* (*right*) using a matrix selection approach. *Error bars* represent bootstrapped 95 % confidence intervals

from 0.68 in the year burned to 0.09 in the first year post-burning and 0.05 in the second year, indicating that burning altered the stage distribution; but, by the second year there was essentially no difference in the observed stage distribution and the stable stage distribution. Recovery to the projected stable stage distribution was slower in *P. brevifolia* with $\Delta = 0.38$ one year post-burning and $\Delta = 0.31$ three years post-burning, indicating that *P. brevifolia* may take a longer time than the current three-year fire-return interval to reach a stable stage distribution.

LTRE results indicated that decreased mortality ($0.025 \ \Delta\lambda$) and increased growth ($0.027 \ \Delta\lambda$) of *A.*

michauxii individuals in the "small-medium" size class accounted for 51 % of the difference in λ between burned and unburned projection matrices (Fig. 5). Overall, individual growth made the greatest contribution to the difference in λ with fecundity making only a minor contribution. For *P. brevifolia*, increased survivorship of the smallest individuals ($0.038 \ \Delta\lambda$) and increased growth of medium-sized individuals ($0.040 \ \Delta\lambda$; Fig. 5) made the greatest contribution to the difference in λ. As with *A. michauxii*, fecundity contributed very little to the overall difference in λ ($0.003 \ \Delta\lambda$).

Discussion

In the short term, fire caused increased mortality and reduced size and seed production of *A. michauxii* and *P. brevifolia,* two rare, endemic species of the Fall-line Sandhills, USA. This is in contrast to many common and rare plant species in the Gulf and Atlantic Coastal Plain (GACP) that demonstrate short-term positive responses to burning (Brewer 2001; Kesler et al. 2008; Kirkman et al. 1998; Spier and Snyder 1998). The reduced flowering in *A. michauxii* following fire contrasts with other members of Fabaceae in the longleaf pine ecosystem that generally flower in the same season following fire (Hiers et al. 2000). While species in fire-dependent ecosystems may demonstrate a trade-off in vital rate responses to fire (Menges and Quintana-Ascencio 2004), such trade-offs were not evident in the study species. Recruitment was low for

Table 1 Population growth rates, stable stage distributions, and reproductive values for the three transition matrices (burned, one year post-fire, and two or more years post-fire) estimated for *A. michauxii*

	Size class	Burned	One year post-fire	Two years post-fire
Lambda		0.88713	0.98575	0.98167
Stable stage distribution	Small	0.66093	0.01604	0.02866
	Small-medium	0.32035	0.06017	0.16736
	Medium	0.01873	0.41549	0.56245
	Large	0.00000	0.50827	0.24153
Reproductive value	Small	1.00000	1.00000	1.00000
	Small-medium	1.08080	1.07018	1.19493
	Medium	1.14716	1.08065	1.20540
	Large	1.14053	1.040736	1.20786

Stable stage distribution values represent proportions and sum to 1; reproductive values are scaled to the smallest size class, which is equal to 1

Table 2 Population growth rates, stable stage distributions, and reproductive values for the six transition matrices (two time steps and burned, one year post-fire, and two years post-fire) estimated for *P. brevifolia*

|		2008–2009			2009–2010		
		Burned	Unburned$_1$	Unburned$_2$	Burned	Unburned$_1$	Unburned$_2$
Lambda		0.962	0.998	0.998	0.932	1.054	1.028
Stable stage distribution	Seed	0.00000	0.00000	0.00000	NA	NA	NA
	Seedling	0.00000	0.00000	0.00000	0.00919	0.10267	0.05637
	1–10	0.04282	0.00000	0.00017	0.13832	0.02591	0.02232
	10–25	0.06043	0.00000	0.00193	0.08807	0.02531	0.01641
	25–50	0.14323	0.00000	0.00430	0.21885	0.02428	0.01801
	50–100	0.19675	0.00000	0.00540	0.17427	0.03737	0.04711
	100–200	0.21877	0.00000	0.03405	0.15895	0.06177	0.07351
	200–400	0.14286	0.00000	0.06381	0.12035	0.07190	0.09077
	400–800	0.12078	0.00000	0.05523	0.03548	0.11870	0.16012
	800–1,600	0.05526	0.00000	0.14046	0.01192	0.13478	0.13090
	1,600–3,200	0.01026	0.00000	0.26529	0.01573	0.22025	0.12853
	>3,200	0.00885	1.00000	0.42936	0.02886	0.17703	0.25594
Reproductive value	Seed	NA	NA	NA	<0.0001	<0.0001	<0.0001
	Seedling	NA	NA	NA	1.0	1.0	1.0
	1–10	0	0	0	7.5	1.9	2.0
	10–25	0	0	0	4.2	2.0	1.9
	25–50	0	0	0	6.5	2.1	2.0
	50–100	0	0	0	6.2	2.3	2.1
	100–200	0	0	0	6.8	2.4	2.1
	200–400	0	0	0	7.3	2.5	2.2
	400–800	0	0	0	7.6	2.6	2.4
	800–1,600	0	0	0	8.5	2.8	2.6
	1600–3,200	0	0	0	7.9	2.9	2.7
	>3,200	0	0	0	1.3	3.2	3.8

Stable stage distribution values represent proportions and sum to 1; reproductive values are scaled to the smallest size class, which is equal to 1.Stable stage distribution does not include the seed stage and the reproductive values are scaled to seedling stage

both species throughout the fire cycle and did not compensate for the increased mortality and reduced reproduction following fire.

The reduction in plant size caused by burning increased the proportion of smaller individuals in the stable stage distribution for both species relative to unburned populations (Tables 1 and 2) and increased the elasticities of smaller size classes (Appendix A, Fig. 4). This shift indicates that under annual burning the population growth rate would be more sensitive to the vital rates of the smaller size classes and that survivorship and growth of smaller individuals would make the greatest contribution to the differences in λ between burned and unburned populations. Although individuals from both species experienced size

reduction following fire, recovery to pre-burn size was faster in *A. michauxii* relative to *P. brevifolia*. By the first growing season after fire, *A. michauxii* had roughly the same observed size distribution as the projected stable stage distribution in the absence of burning. The recovery of *P. brevifolia* was much slower; by the third year post-fire, the proportional difference between the observed size distribution and the stable stage distribution was still quite different. These results support anecdotal observations that the species is slow growing and that frequent fire leads to a greater proportion of small sized individuals, relative to populations that are burned less frequently.

The reduced stochastic population growth rates (λ_s) under simulated annual burning are not surprising, as
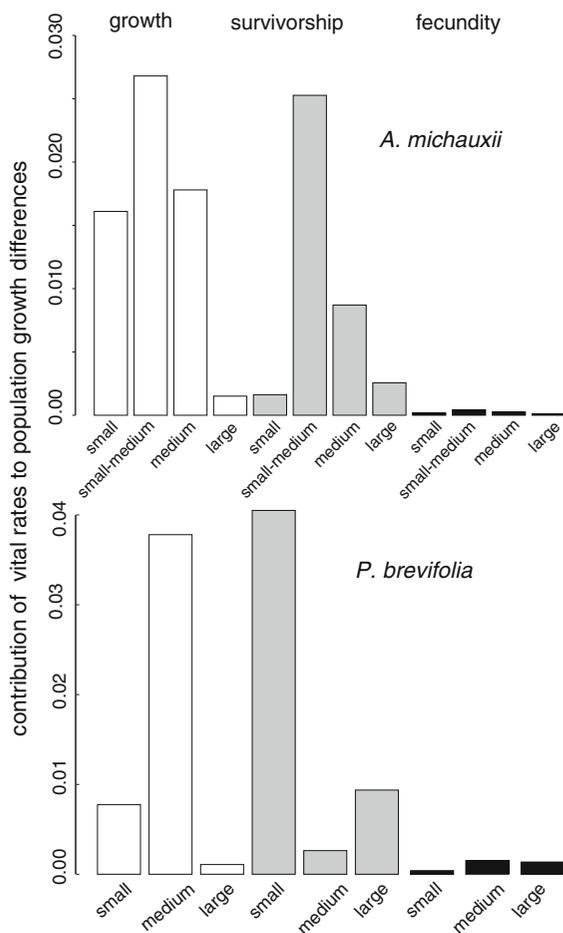
Fig. 5 Contributions of growth, survivorship, and fecundity by size class to the difference in the population growth rate between unburned and burned *Astragalus michauxii* (*top*) and *Pyxidanthera brevifolia* (*bottom*) populations. Size classes for *A. michauxii* are small = 1–20 cm, small-medium = >20–40 cm, medium = >40–80 cm, and large = >80 cm. Size classes for *P. brevifolia* are small = 1–50 cm², medium = >50–400 cm², and large = >400 cm²

demographic studies. The vital rates of *P. brevifolia* and *A. michauxii* most likely vary extensively through time (Hairston et al. 1996) with episodic recruitment and aperiodic bonanza years that could greatly influence long-term population viability (Ludwig 1999). During the course of the study, the area was under a drought for most of the study and annual rainfall averaged 85 % of the 30-year normal rainfall of 120.7 cm (State Climate Office of North Carolina, http://www.nc-climate.ncsu.edu). In addition, seedling detection probabilities are most likely less than one for *P. brevifolia*, and we may have missed a number of seedlings that established near maternal plants, as they are difficult to distinguish from the below ground stems of existing individuals (W. Wall, pers. obs.). Finally, the seed bank for both species may play a role in the long-term population dynamics of both species, especially during bonanza years, but the low recruitment rates did not allow us to parameterize the seed bank over the course of the study as we did not observe any recruitment in the seed addition plots. Thus, recruitment is most likely higher than estimated in *P. brevifolia* and possibly *A. michauxii*, and $\lambda_s < 1$ are not necessarily a cause for immediate concern. Despite this, our results provide valuable information on fire effects because population growth rates in these species are most responsive to changes in growth and survival rather than reproduction.

While fire has negative short-term effects on the vital rates of these two species, fire is necessary under present climatic conditions to reduce competition and allow for population persistence. Long-term fire exclusion in the longleaf pine ecosystem has been shown to have deleterious effects on population dynamics and plant biodiversity (Brockway and Lewis 1997). Fort Bragg is burned on a fixed, three-year fire-return interval so we were unable to observe the effects of fire suppression after 3 years. By the second year post-burn, *A. michauxii* fruit production was decreasing for small and small-medium sized individuals. Observations of *P. brevifolia* populations on adjacent lands that are under long-term fire suppression suggest that fruit production is substantially reduced, relative to the number of fruits produced in populations that are regularly burned (W. Wall, pers. obs.). As with other studies of the responses of plant species to fire in the longleaf pine ecosystem (Hiers et al. 2000), a fire regime that includes variation in frequency and seasonality may be the optimal management strategy.

fire-dependent ecosystems are most likely composed of species adapted to different fire frequencies and other species in fire-dependent ecosystems have demonstrated similar results (Gross et al. 1998; Kaye et al. 2001; Menges and Quintana-Ascencio 2004). However, even under the three-year fire-return interval to which these populations are currently exposed, simulations predict a gradual population decline for both species and only under a regular four-year fire-return interval was λ_s greater than one for either species (Fig. 4). We strongly caution against using this particular result to inform a change in management policy, owing to uncertainty inherent in short-term

It is likely that *A. michauxii* and *P. brevifolia* have persisted in the Fall-line Sandhills in dry, open habitats that have certain characteristics, such as sparse tree cover and low productivity, in common with Pleistocene landscapes (Watts 1980; Webb et al. 1998). Climatic reconstructions for the region suggest a Pleistocene environment with exposed soil and a dry, windy environment (Ivester et al. 2001; Leigh 2008); these conditions most likely reduced plant productivity and biomass accumulation. As climatic conditions became progressively warmer and wetter, *A. michauxii* and *P. brevifolia* may have been isolated to deep sand habitats in the Fall-line Sandhills where competition was reduced because of the extreme xeric conditions. The two endemic species could be viewed as remnants from a past vegetation assemblage that is not currently present. The end of the Pleistocene also led to the northward migration of many plant species out of one or more refugia in the southeastern United States (Soltis et al. 2006) resulting in a mixture of species adapted to variable fire-return intervals. Thus, it is not surprising to discover that two species endemic to a currently fire-prone landscape do not appear adapted to one year fire-return intervals.

Climatic and vegetation changes over the last 20,000 years in the GACP are complex, and more research is warranted to understand the interplay among fire, climate, and the demographic responses of species. While many species in fire-dependent ecosystems may respond positively to increased fire frequency, we should not expect that all species will do so. A thorough investigation of the effects of fire on rare plant species in fire-dependent ecosystems and a better understanding of the evolutionary history of targeted species are critical to both understanding the role of fire in determining the population dynamics of rare species and the development of successful management and recovery plans.

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