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Fire Effects on Demography of the Invasive Shrub Brazilian Pepper (*Schinus terebinthifolius*) in Florida Pine Savannas

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ABSTRACT: Fire is a common disturbance in savanna ecosystems that may either facilitate or impede non-native plant invasions. Although fire can create recruitment opportunities for non-native plants, it can also prevent their invasion if it exerts strong negative effects on their demographic processes. Some savannas may, therefore, be able to resist invasion provided the natural, frequent-fire regime remains intact. We examined the effects of fire on the demography of the invasive shrub Brazilian pepper, *Schinus terebinthifolius* Raddi., which is invading fire-prone slash pine savannas of southern Florida. We studied survivorship, growth, and reproduction of low-density populations of Brazilian pepper in a pine savanna within Everglades National Park to investigate whether fire might suppress Brazilian pepper in the early stages of invasion. We found a significant decrease in Brazilian pepper survivorship following fire, particularly among small individuals. We further found that fire reduced fecundity of surviving Brazilian pepper individuals for at least two years. However, resprouting individuals that survived fire had high relative growth rates the following year, which could facilitate population recovery during inter-fire periods. We used a simple population simulation to show that a low-density cohort of Brazilian pepper may be rapidly eliminated from pine savannas with fire-return intervals of four years or less, but individuals may persist for > 50 years with fire-return intervals of eight years or more. Our study suggests the need to maintain the historical frequent-fire regime in pine savannas in order to prevent their invasion by fire-intolerant shrubs such as Brazilian pepper.

Index terms: demography, fire, invasion, pine savanna, *Schinus terebinthifolius*

INTRODUCTION

Fire is a common disturbance agent in many plant communities and consequently is an important factor in the invasion of those communities by non-native plant species (D'Antonio 2000; Keeley et al. 2003). Fire may create opportunities for colonization and subsequent invasion by removing pre-existing vegetation, but it may also cause mortality or otherwise suppress population growth of non-native species (D'Antonio 2000). Therefore, demographic responses to fire by non-native plants are important in determining their potential invasion success under a specific fire regime (Jacquemyn et al. 2005; Lockwood et al. 2007). A species can invade a fire-prone community if its population growth is enhanced by fire relative to the native community (Buckley et al. 2007), for example, through greater post-fire survival (Bond and Midgley 1995; Rossiter et al. 2003) or by increased fecundity after fire (i.e., through serotiny; Richardson et al. 1990).

Conversely, fire may prevent invasion by non-native plant species if it is frequent or intense enough to cause substantial mortality (Lonsdale and Miller 1993) or reduce reproductive rates (Emery and Gross 2005). While this response to fire is less well documented (D'Antonio 2000), it has been observed in pyrogenic savanna ecosystems, where frequent fires can exclude invasion by woody shrubs (D'Antonio 2000; Bowles

et al. 2007). Fire may be an effective control strategy for such fire-intolerant non-native plant species, but some fire-intolerant species have the ability to reduce fire spread or intensity if they establish at sufficient densities to limit fine fuel accumulation or disrupt fuel continuity (Doren and Whiteaker 1990; Brooks et al. 2004). Therefore, frequent fires are essential to keep these non-native plant populations at low densities and prevent them from reducing the likelihood or intensity of future fires.

In southern Florida, the invasive non-native hardwood shrub Brazilian pepper, *Schinus terebinthifolius* Raddi., may be sensitive to fire at early stages of community invasion. Doren and Whiteaker (1990) showed that small-sized individuals (stems < 2.5 cm diameter) within dense populations of Brazilian pepper growing on disturbed soils were negatively impacted by fire. However, large-sized Brazilian pepper generally survived fire, possibly due to reduced fine fuel biomass under large individuals. Brazilian pepper also invades native pine rockland savannas of southeastern Florida, which historically experienced frequent understory fires (Wade et al. 1980; Loope and Dunevitz 1981). In pine savannas outside Everglades National Park, where fire has been excluded, Brazilian pepper has invaded and achieved very high densities (Loope and Dunevitz 1981). However, Brazilian pepper is generally present only at low densities in pine savannas in Long

Pine Key within Everglades National Park that are managed by prescribed burning (DeCoster et al. 1999), suggesting that frequent fire may prevent invasion of these savannas.

We examined the effects of prescribed understory fires on the demography of low-density populations of Brazilian pepper within pine rockland savannas in Florida. If frequent fire can slow or prevent invasion of pine savannas by Brazilian pepper, then Brazilian pepper should exhibit a negative demographic response to fire at one or more life history stages. We specifically examine the effects of fire on mortality, growth, reproductive maturity, and fecundity of Brazilian pepper. Given the potential for a reduction in fire spread and intensity in pine rockland savannas where Brazilian pepper is present at high densities (Stevens and Beckage 2009), understanding the demography of low-density Brazilian pepper in these savannas is important to preventing its rapid invasion and potential alteration of fire regime characteristics in these savannas.

METHODS

Study Ecosystem and Species

Pine rockland savannas of southeastern Florida are fire-dependent ecosystems (Wade et al. 1980). They are dominated by the canopy species *Pinus elliottii* var. *densa* Little & Dor. (south Florida slash pine), which is resistant to understory fires (Doren et al. 1993). The understory con-

tains a diverse herbaceous flora, including at least 40 south Florida endemic species, a number of which depend on fire to reduce competition from hardwood species (Loope and Dunevitz 1981; Snyder et al. 1990; O'Brien 1998). The historical fire regime was one of understory fires every three to seven years, which occurred at the beginning of the rainy season when increased lightning strikes ignited dry fuels (Beckage et al. 2003; Slocum et al. 2007). These fires suppressed hardwood trees and opened gaps for pine recruitment (Doren et al. 1993; Beckage and Platt 2003). More recently, the fire regime has shifted towards the dry season due to anthropogenic influence (Slocum et al. 2007), and in savanna remnants outside Everglades National Park, fires are typically suppressed and Brazilian pepper has invaded extensive areas (Loope and Dunevitz 1981).

Brazilian pepper is native to southeastern South America, and was introduced to Florida in the 1890s (Austin 1978; Morton 1978). A hardwood evergreen shrub, Brazilian pepper can produce multiple stems that create a dense shade canopy and it has numerous advantages over native hardwood species (Ewel et al. 1982). For example, seed germination rates in undisturbed habitat range from 30% to 40% of seedfall, a rate 10% to 35% higher than the native pine rockland species *Ilex cassine* L. and *Myrica cerifera* L. (Ewel et al. 1982). Among adults, Brazilian pepper has a growth rate up to twice as high as many of its native competitors, both under

normal growing conditions (Pattison et al. 1998) and following fire (Snyder 1999). Brazilian pepper is pollinated by generalist insects, is capable of producing flowers year round, and can reach reproductive maturity rapidly, often within three years of germination (Ewel et al. 1982). Brazilian pepper is dioecious, uncommon among invasive plants, with an equal ratio between genders (Ewel et al. 1982). It is capable of resprouting (Snyder 1999) and has very high fecundity, with mature females capable of producing tens to hundreds of thousands of single-seeded fruits annually (Ewel et al. 1982).

Fire Effects on Brazilian Pepper: Field Methods

We located populations of Brazilian pepper within six fire management units, or "burn units", of pine savanna in the Long Pine Key area of Everglades National Park, Florida (25.398 N; 80.644 W). Brazilian pepper grows at low densities in Long Pine Key, where pine savannas are managed under a system of prescribed burning (Loope and Dunevitz 1981; DeCoster et al. 1999). Three of the six burn units we sampled were burned during our study (Table 1). We established belt transects 20 m wide through each burn unit, and tagged each Brazilian pepper within a transect with a stainless steel tag around the largest stem. Every 20 m along the transect, we conducted a thorough visual search for five minutes. We extended a transect through the length of each burn unit until we en-

Table 1. Transects used for Brazilian pepper (BP) sampling. Transect names correspond to burn-unit identifications used by Everglades National Park. Three transects burned during the period of our study and three did not. Not all plants in each transect burned, due to the patchy spread of the fires. 47 of 61 plants burned in 2006. 45 plants of 61 burned in 2007. Density is given as (plants/1000 m²), where each transect was 20 m wide. NA=Not Applicable.

Transect Name	Transect Length (km)	Initial # BP	Year Burned	# BP Burned	BP Density (plants/1000 m ²)
H	1.5	61	2006	47	2.03
I2	2.15	31	2007	31	0.72
B	2.6	30	2007	14	0.58
A	2.25	13	NA	0	0.29
F1	1.5	21	NA	0	0.7
E	2.25	8	NA	0	0.18
Total:		164		92	

countered 30 individuals. If the transect did not contain at least 30 individuals, we established a second transect through the burn unit. Total transect lengths in each burn unit varied from 1.5 km to 2.6 km (Table 1). If we did not find 30 individuals after two transects, we did not establish a third transect in that burn unit. All burn units had two transects except for burn unit H (Stevens and Beckage 2009).

We conducted a summer census of each tagged plant for two years (July 2006 and June 2007). Initial densities in 2006 were very low across all transects (Table 1). Everglades Fire Management conducted prescribed burns in late July of both study years. Large portions of savanna in two of the three transects scheduled to be burned did not burn completely due to patchy spread of the fires (Table 1); however, Brazilian pepper individuals in these transects that were not burned were included in our unburned sample.

Approximately five months post-fire, in December of each year, we conducted a winter census. During each census, we noted mortality and resprouting (resprouting individuals consisted of old charred stems and new green stems generally less than 0.5 m tall). We also measured the basal diameter of the tagged stem on a north-south axis. We measured fecundity (fruit production) by counting all fruits on each plant during the winter censuses. We assumed the measured fruit count was near 100% of total fruit production (i.e., that no fruits had been dispersed), because early December is the beginning of the fruiting season for Brazilian pepper (Ewel et al. 1982) and fruits were just beginning to ripen. Plants without fruits but with persistent pedicels indicating flowering were assumed to be mature males.

Fire Effects on Brazilian Pepper: Analysis

We modeled the vector of observed mortalities for all Brazilian pepper plants, \bar{M} as a binomial distribution conditional on predicted mortality probabilities \bar{p} : $\bar{M} \sim \text{Binomial}(\bar{p})$. We estimated the logit (log odds) of \bar{p} as $\text{logit}(\bar{p}) = \mathbf{X}\bar{\beta}$, where

$\bar{\beta}$ is a vector of estimated parameters corresponding to the occurrence of fire and to basal diameter, and \mathbf{X} represents the design matrix. The logit function is given by $\text{logit}(p) = \log(p/1-p)$. We fit our models using maximum-likelihood in the R statistical software package (<http://www.r-project.org>), and compared the likelihood of different models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

We calculated annual diameter increments $G = d_{t+1} - d_t$ for all plants from December 2006 to December 2007, where d_t is the diameter measured during the December 2006 census and d_{t+1} is the diameter measured during the December 2007 census. We used AIC to compare the likelihood of a model where the observed set of growth increments \bar{G} followed a normal distribution $\bar{G} \sim \text{Normal}(\mu_g, \sigma^2)$ with a single μ_g and σ^2 , regardless of fire history, to a model where μ_g and σ^2 were different for plants that had survived the 2006 fire, compared to unburned plants. The plants that survived fire were resprouters, so their initial diameters in 2007 were all < 1.0 cm. Therefore, we also included a model comparing plants that survived fire to only those unburned plants with initial diameters < 1.0 cm (i.e., seedlings), with different μ_g and σ^2 for burned and unburned populations.

We modeled the fecundity schedule of Brazilian pepper using a joint likelihood function that considered both fecundity and survivorship. Our fecundity schedule was dependent on the probability of sexual maturity $P(m|d)$, which increased with diameter d according to the probit model $\Theta(d) = \Phi(d|\mu, \sigma^2)$ where μ and σ^2 are the parameters of the cumulative normal probability density function. We defined the predicted number of fruits $\lambda(d)$ either as a function of the square of diameter $\lambda(d) = ad^2$ (e.g., Clark et al. 1998) or independent of size $\lambda(d) = b$. We then modeled the probability of a female plant with diameter d having its observed number of fruits f as a negative binomial distribution with overdispersion parameter k (Beckage and Stout 2000): $NB(f|d, a, b, k) = \frac{\Gamma(k+f)}{\Gamma(k)\Gamma(f)!} \left(\frac{k}{k+\lambda}\right)^k \left(\frac{\lambda}{k+\lambda}\right)^f$. We choose the negative binomial because

the fruit data appeared to be overdispersed for a Poisson distribution. Since Brazilian pepper is dioecious, the fecundity schedule is dependent on both sexual maturity and plant gender. A plant producing 0 fruits could be immature (with gender unobservable), female and mature but without fruit or pedicels present, or male and mature but without pedicels. We account for this last possibility by modeling the likelihood of a male plant having flowers that are observed with probability θ_{mf} . A mature plant that is observed to be male has 0 probability of producing fruits, but does provide information on the sex ratio and the maturity schedule. The joint likelihood of the observed fruit count f and gender g for a Brazilian pepper individual is given by the joint likelihood function $L(f, g | d, p_f, \theta_{mf}, b, a, \mu, \sigma^2) =$

$$\begin{cases} (1-\Theta(d)) + (p_f \times \Theta(d) \times NB(0|d)) + (1-p_f) \times \Theta(d) \times (1-\theta_{mf}) & \text{for a plant} \\ & \text{of unknown gender with 0 fruits} \\ p_f \times \Theta(d) \times NB(f|d) & \text{for a female plant with } f \text{ fruits} \\ (1-p_f) \times \Theta(d) \times \theta_{mf} & \text{for a plant with male flowers} \end{cases}$$

where p_f is the probability of the individual being female. The likelihood of all observations would then be the product of this likelihood across all individuals. This likelihood function allowed us to estimate the maturity schedule, fecundity, and the sex ratio for the Brazilian pepper plants studied. We maximized the likelihood using an R function that combines evolutionary algorithms with derivative-based methods for optimization (using the R library "rgenoud").

We examined whether fire affected the predicted maturity schedule $\Theta(d)$, the predicted number of fruits $\lambda(d)$, or both demographic processes. We subset the data into two groups: plants that did not burn; and plants that burned in either 2006 or 2007 (Table 1). For each model (null, different maturity, different fecundity, or both different), we compared the corresponding AIC values for models with separate parameters for burned and unburned stems to the AIC value for a model that did not account for burn history.

Simulation Model

We used the demographic parameter estimates to simulate the response of an initial population of Brazilian pepper to

different fire-return intervals. We abstracted important demographic processes, such as subsequent recruitment of new individuals, to focus on the survival of the founding population. We created an initial population of 100 female seedlings with an average diameter of 0.1 cm with a lower limit of 0 ($\sigma = 0.01$ cm), which was the size of the smallest individual from our field data. For simplicity, we assumed the founding female population within our simulated pine savanna to not be pollen-limited despite an absence of males within the population; the high abundance of Brazilian pepper at disturbed sites close to intact pine savannas suggests this is a reasonable assumption (Loope and Dunevitz 1981; Ewel et al. 1982). Each individual could grow, produce fruits, and die at annual intervals. We simulated fire-return intervals of 16, 8, and 4 years, as well as a no-fire schedule. If a fire was scheduled for a given year, it occurred at the beginning of each yearly time-step, and all plants were assumed to burn. Then, each individual experienced a probability of mortality (p) for a given year, as a function of the plant's diameter (d) and of whether or not it burned. We used parameter estimates from our 2007 mortality data (Appendix). We also assumed that all surviving burned plants resprouted; these were assigned to an initial post-fire diameter of 0.38 cm, because this was the mean post-fire diameter for burned plants in 2007. If the individual survived, we assigned it a diameter growth increment G from a normal distribution with mean μ_g and variance σ^2 . We allowed μ_g and σ^2 to vary depending on the initial size of the plant (smaller plants had higher μ_g ; Appendix) and on whether the plant burned in a given year. Our growth function for the simulation was $d_{t+1} = d_t + G * (1 - \frac{d_t}{d_{max}})^2$, a modification of the discrete logistic growth model (Gotelli 2001), where d_{max} is the average maximum diameter of Brazilian pepper stems (10 cm; Ewel et al. 1982). At the end of each annual time-step, we calculated the probability of maturity for each surviving individual as (d_{t+1}), from eq. 1, and if mature, each individual produced (d_{t+1}) fruits (from eq. 2). Following fires, we set the fruit set at 167 for any surviving mature females for two years based on the observed fecundity of plants resprouting after fire (Appendix), and then allowed

them to resume their normal fecundity schedule. We ran each simulation for 50 years and compared the survivorship, average diameter, and total fecundity of the cohort under the four different fire intervals. While our simple model does abstract important demographic processes, which we are incorporating into an individual-based, spatially explicit model that we are currently developing, we believe our results are nevertheless useful.

RESULTS

Post-fire mortality rates measured in low-density Brazilian pepper populations were 42% in 2006 and 31% in 2007. A model of mortality that included fire and diameter had the most support in both years (Table 2) because mortality from fire was size-dependent, with larger plants less likely to die (Figure 1). Depending on the year, the probability of Brazilian pepper mortality

from fire ranged from 74% to 78% for a plant of diameter 0.1 cm; 50% to 56% for a plant of diameter 1.0 cm; 21% to 34% for a plant of diameter 2.0 cm; and 2% to 7% for a plant of diameter 4.0 cm. Gender did not affect probability of mortality in 2007, the only year when plant gender of individual plants was known (Table 2).

Brazilian pepper individuals that survived fire exhibited rapid growth rates during the year following fire (Figure 2). All individuals in our study populations that survived the 2006 fire did so by resprouting (Figure 2). Therefore, observed plant size was effectively reduced to the seedling class post-fire, but belowground biomass (and energy reserves) would be expected to be greater than for true seedlings (Snyder 1999; Drewa et al. 2002). Because all individuals resprouting from the 2006 fire had small initial diameters in December 2006 (< 1.0 cm), we compared their growth increments to both those of unburned

Table 2. Akaike's Information Criterion (AIC; Burnham and Anderson 2002) values for all models. Model(s) with the most support (where $AIC < 2$) are in bold. Model parameter estimates are given in the Appendix.

Demographic response	Year	Model	- log likelihood	Δ AIC
Mortality	2006	Null	48.7	40.7
		Fire	32.1	9.5
		Fire + diameter	26.3	0
	2007	Null	51.2	23.8
		Gender	49.9	25.3
		Fire + diameter	37.3	0
Growth increment of all plants	2007	No effect of fire.	63.2	8
		Fire	57.1	0
Growth increment of small plants ($d < 1$ cm)	2007	No effect of fire.	19.2	2
		Fire	16.7	0
Maturity and Fecundity	2007	No effect of fire.	364.4	4.9
		Fire		
		Affects maturity	360.6	1.2
		Affects fecundity	362.8	8.8
		Affects maturity and fecundity	359	0

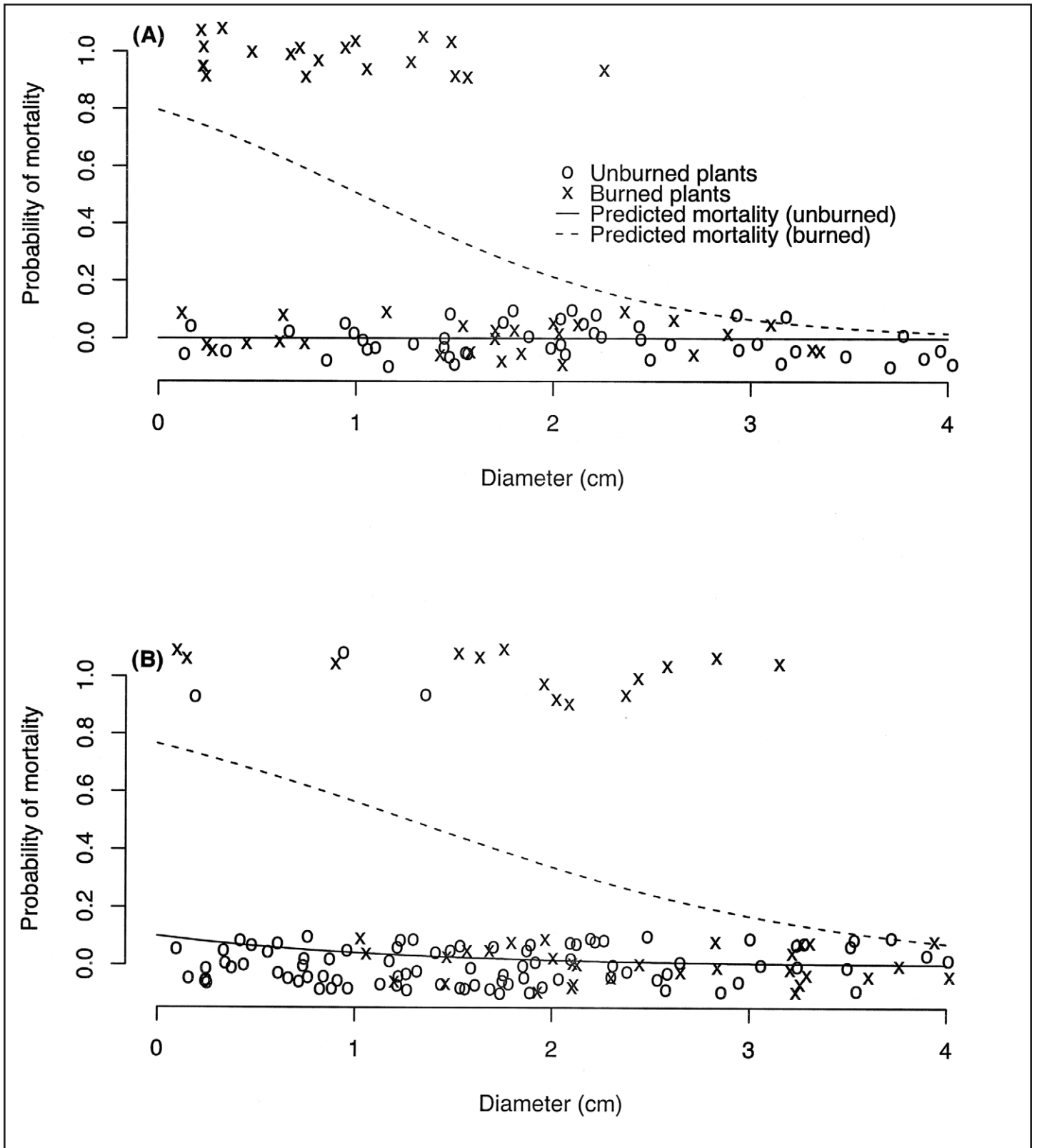


Figure 1. Size-dependent mortality of Brazilian pepper in (A) 2006 and (B) 2007. Points represent individual plants, plants in the upper portion of the figure died, while plants in the lower portion of the figure survived. Curves represent predicted probability of mortality of both burned and unburned plants, using logistic regression models derived using maximum likelihood. Points were jittered in the y-direction for clarity.

plants < 1.0 cm diameter and to all unburned plants of any diameter. The mean growth increment was higher among plants recovering from fire (0.69 cm/yr) than it was among unburned plants less than 1 cm diameter (0.42 cm/yr) and among unburned plants of any size (0.33 cm/yr). The model allowing for differences in mean growth increments between burned and unburned plants had more support than the null model of a single mean growth increment, both for small plants and for all plants (Table 2).

Fire altered the reproductive response of Brazilian pepper, causing a more narrow size range at maturity and lower fecundity (Figure 3). Of the plants that had been burned between 6 and 18 months earlier, we observed 17 of 58 Brazilian pepper individuals in flower in December 2007 (Figure 3A). Of these 17 burned individuals that flowered, the four largest were burned in July 2007 but retained a portion of their above-ground biomass; therefore, they were not complete resprouts. The remaining plants were resprouts from both the 2006 and 2007 fires that had regained sufficient biomass to produce flowers. Our model showed that Brazilian pepper recovering from fire exhibits a steep increase in probability of maturity with increasing size, from less than 20% at 0.8 cm diameter to more than 80% at 1.0 cm diameter (Figure 3A). However, these mature, post-fire individuals generally produce fewer fruits than do unburned plants of similar sizes (Figure 3B). In fact, we found that while fruit production increased with plant size in unburned plants, our best-supported model of fruit production for burned plants showed no effect of plant diameter on fecundity (Figure 3B). Our joint likelihood model had the most support when it allowed both maturity and fecundity to be affected by fire (Table 2). Single-effect models that allowed either maturity or fecundity to be affected by fire, but not both, still had more support than a model without any fire effects (Table 2). We estimated the fraction of female plants to be between 0.50 and 0.51 in all our models, consistent with the 50% fraction of females estimated by Ewel et al. (1982).

Our simulation of a founding female cohort

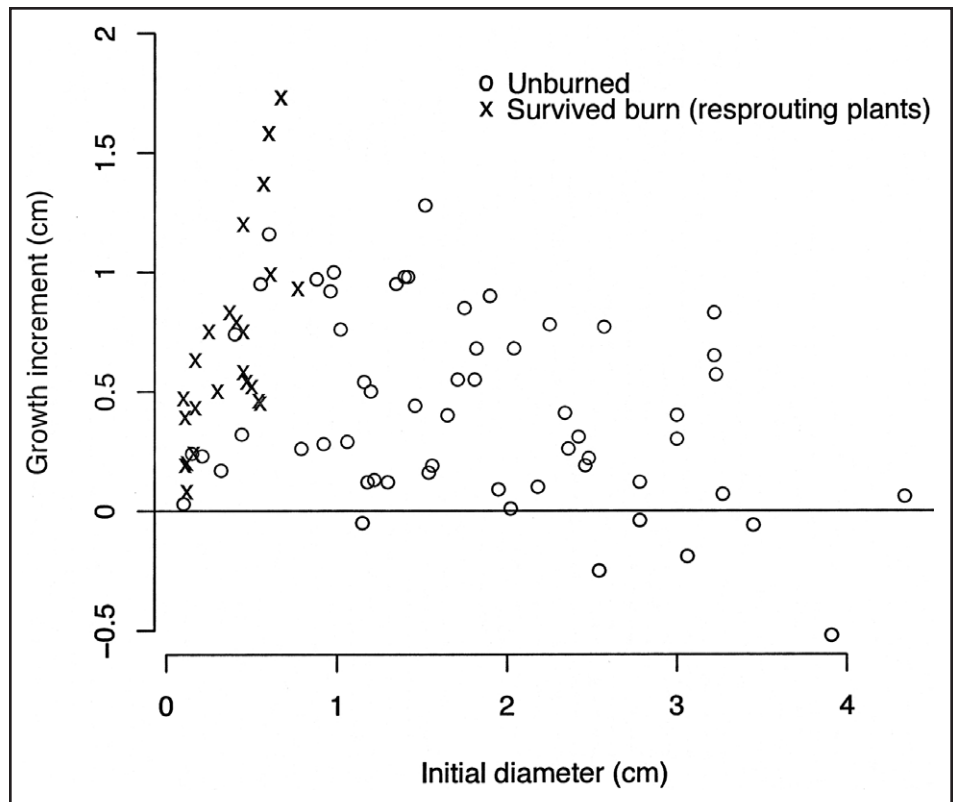


Figure 2. Fire effects on growth increment of Brazilian pepper. Annual growth increments were calculated for 2007 as final 2007 diameter – initial 2007 diameter. Small initial diameters of burned plants reflect resprouting that occurred after the 2006 fires. The mean growth increment of burn-surviving plants (0.69 cm/yr) is higher than that of unburned plants, both for all diameters (increment = 0.41 cm/yr) and at diameters < 1 cm (increment = 0.48 cm/yr). Negative growth increments in Figure 2 are likely small positive values affected by measurement error.

of Brazilian pepper predicted that shorter fire-return intervals could lead to the extirpation of the cohort, but that the population would stabilize with infrequent fires or in the absence of fire (Figure 4). When fire was absent from the system, the cohort stabilized at > 80% of its initial population size (82 individuals) within 10 years, by which time total fruit production of this cohort exceeded 268,000 fruits. Under a simulated 16-year fire-return interval, the initial cohort had 40% survivorship after 50 years, and fruit production, following an initial post-fire decline, recovered to levels seen in the absence of fire (Figure 4B). Under a simulated 8-year fire-return interval, total fruit production was reduced by more frequent fires and a declining population, but > 20% of the initial cohort still persisted after 50 years (Figure 4C). However, a simulated 4-year fire-return interval resulted in extirpation of the initial cohort after 25 years, with a dramatic decrease in the population following the

first fire, because plants were still relatively small four years after establishment and thus more vulnerable to fire (Figure 4D).

DISCUSSION

The low-density populations of Brazilian pepper that we examined in the two years of our study exhibited a negative response to fire. Brazilian pepper mortality rates increased from < 5% for unburned individuals to > 30% for burned individuals. The increase in mortality rate is size-dependent (Figure 1), with smaller-diameter individuals being more susceptible to mortality in fires. This suggests that frequent fires may slow invasion of Brazilian pepper by preventing juveniles and newly established populations from recruiting into reproductive size classes. Furthermore, fire causes a decrease in fecundity at all sizes for at least 1.5 years following fire (Figure 3), in large part because reproductively mature individuals that survive fire tend

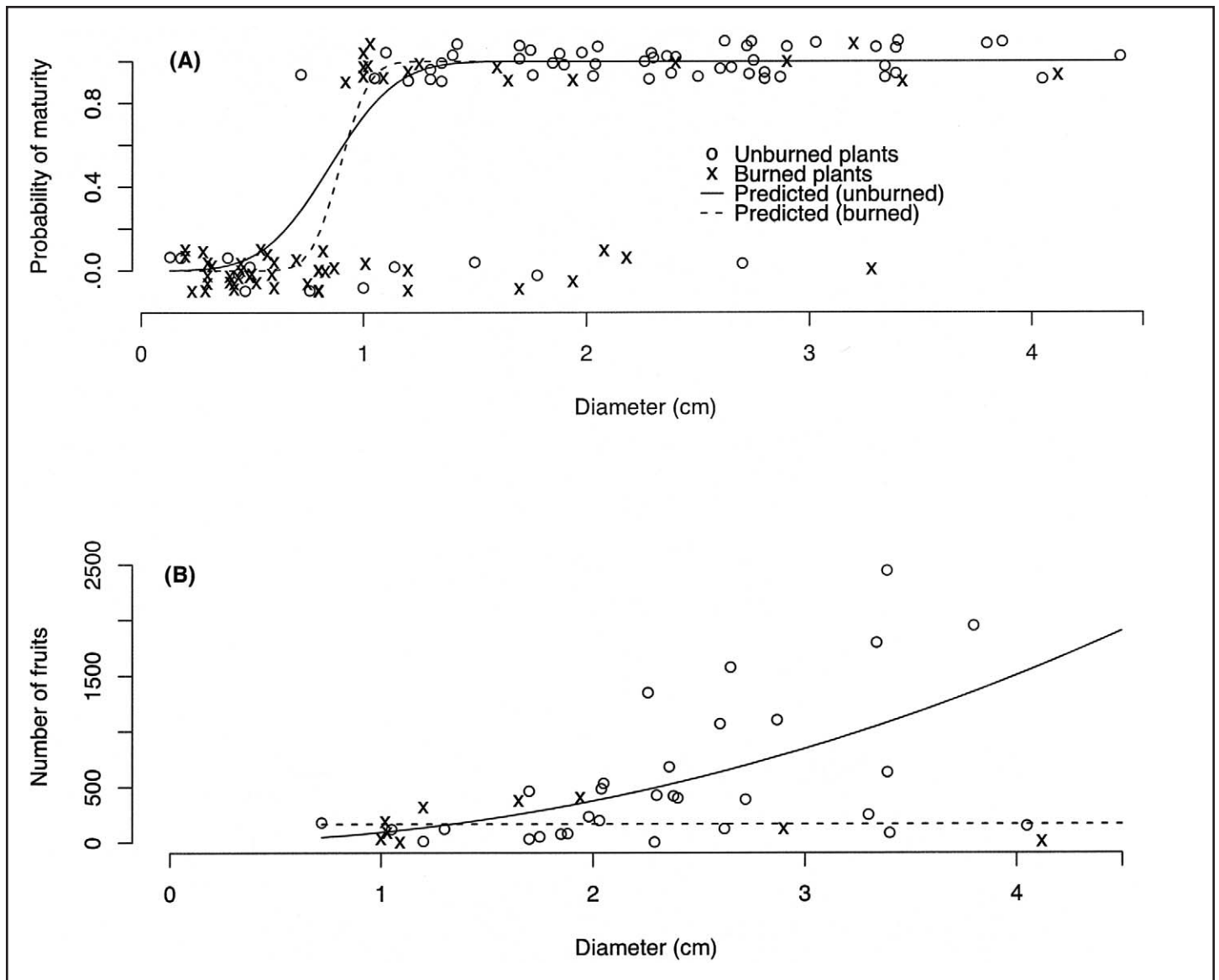


Figure 3. Effects of fire on 2007 reproductive maturity (A) and fecundity (B). The curves in (A) represent predicted probability of reproductive maturity as a function of diameter d . Points represent observed maturity, where 1 represents a mature plant that produced flowers; points are jittered in the y-direction for clarity. Plants recovering from fire have a narrow maturity threshold diameter of ~ 0.9 cm, above which they are more likely to produce flowers than unburned plants of the same size. All points in (B) represent individual fruit sets > 0 . The curves in (B) represent best-fit models of fecundity, as a function of d^2 if unburned (solid line), and independent of d if burned (dashed line). Plants recovering from fire generally exhibit lower fecundity than unburned plants of the same size. Plants were burned between 6 and 18 months prior to the fruit census.

do so by resprouting, and appear to use resources for growth (Figure 2) rather than for reproduction. Thus, while large, reproductively mature Brazilian pepper might be more likely to survive fire by resprouting, they still suffer negative demographic consequences.

Reduced fecundity alone might be sufficient to cause a decrease in population growth rates of invasive plants following fire. Emery and Gross (2005) showed that annual summer burns reduced population

growth in the invasive forb *Centaurea maculosa*. This reduction was primarily the result of reduced reproduction in *C. maculosa*, which flowers in late summer and disperses seed throughout the autumn (Emery and Gross 2005). Similarly in our study, Brazilian pepper was burned prior to its flowering season, which is generally September through November (Ewel et al. 1982), and the negative effects of fire on fecundity of Brazilian pepper extended at least 1.5 years post-fire. Therefore, we expect that the combination of high mortal-

ity among small individuals and reduced fecundity among larger individuals should produce a negative demographic response to fire among Brazilian pepper populations that are burned.

Plant responses to fire often exhibit tradeoffs in different demographic processes. Bond and Midgely (2001) suggest that species adapted to frequent fire may occupy a “persistence niche”, in which post-fire populations are primarily composed of fire-survivors rather than new recruits.

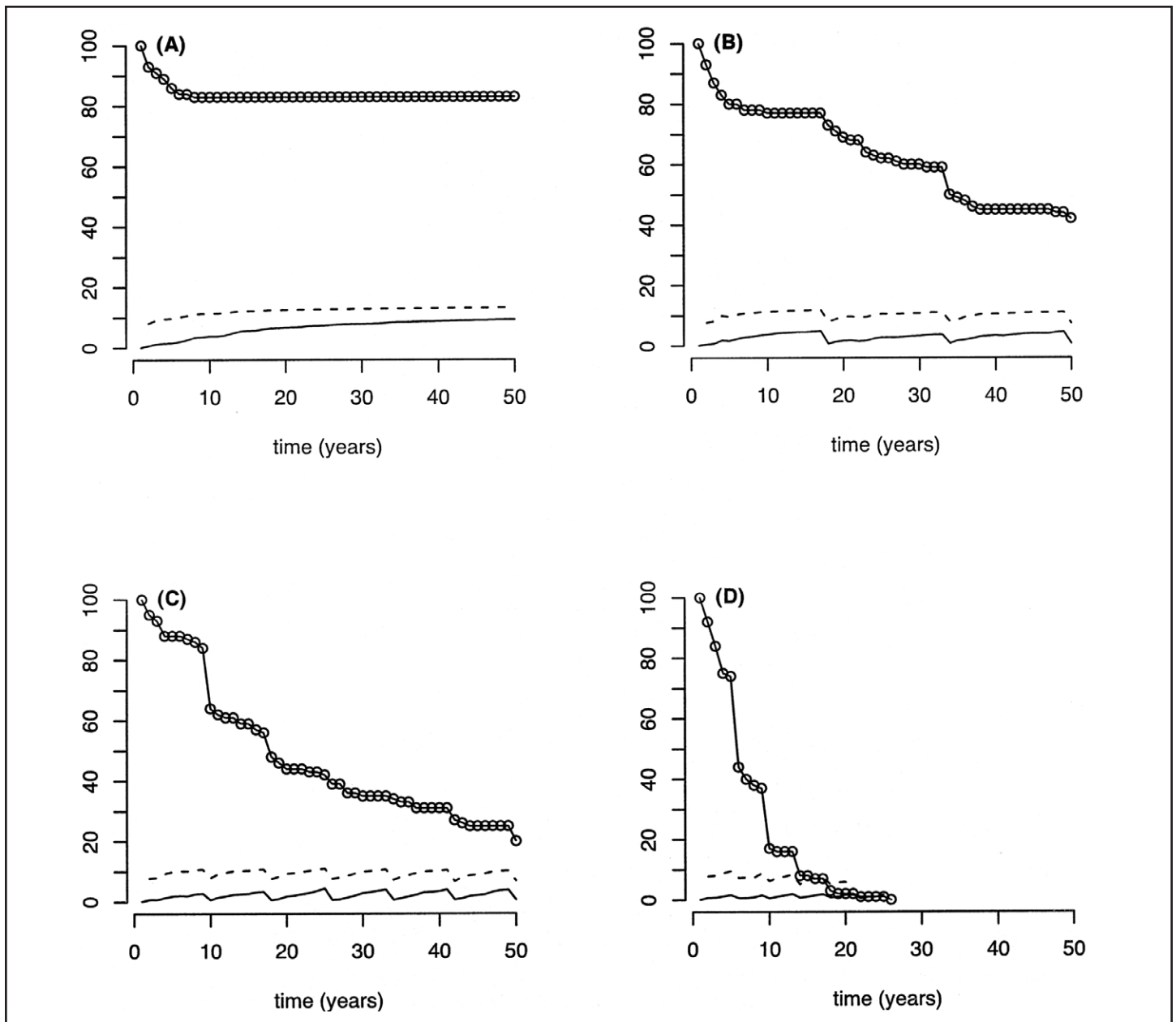


Figure 4. Simulated population models using demographic parameter estimates. Circles represent surviving members of the original cohort of 100 individuals at each annual time step. Solid lines indicate mean basal diameter (in cm) of the population. Dashed lines represent total fecundity of the initial cohort, calculated as $\ln(\sum \text{fruits/individual})$. Fire return intervals are (A) never, (B) 16-year, (C) 8-year, and (D) 4-year. All initial cohort members have been lost after 25 years under a 4-year fire return interval.

Such species, which have high survivorship through resprouting following fire, tend to have relatively low growth rates and fecundity levels in the absence of fire, because they allocate resources to root storage (Bond and Midgley 2001). For example, Keith et al. (2007) showed that the fire-adapted Australian shrub *Epacris barbata* exhibited low mortality after fire, and had low relative growth-rates in the absence of fire. Our work shows that Brazilian pepper

exhibits an opposite response, with high mortality (> 30%) following fire, and a high mean relative growth rate (0.21; Appendix) and high fecundity in the absence of fire (Figure 3). Furthermore, Brazilian pepper individuals that survive fire by resprouting have an exceptionally high mean relative growth rate the year following the fire (1.06; Appendix), but have low fecundity (mean = 101.5 fruits/individual; Figure 3). These results suggest a possible tradeoff

between post-fire growth and fruit production (*en sensu* Keith et al. 2007). The demographics of Brazilian pepper indicate that it is not adapted to fill a persistence-niche as defined by Bond and Midgley (2001); however, high growth rates, especially during the first year post-fire, suggest that Brazilian pepper populations can persist after fire unless repeated fires cause additional mortality and suppress fruit production by survivors.

We explicitly modeled population persistence of Brazilian pepper under different fire regimes using a simple simulation model. We simulated the demographics of a hypothetical female-only, non-pollen-limited founder population of Brazilian pepper juveniles in a pine savanna system using our estimated demographic parameters. Our model predicts that a founder population can persist in the absence of fire, with mortality concentrated in early years (Figure 4A). Our model did not include natural mortality from senescence at advanced age because we did not observe any in our populations (Figure 2); however, mature stands of Brazilian pepper have been shown to persist for at least 35 years (Ewel et al. 1982). The corresponding increase in the average reproductive output of this cohort as individual stems grew would be expected to translate into increased population growth, especially in the absence of non-fire, background mortality (Jacquemyn et al. 2005). A simulated 16-year fire-return interval (Figure 4B) resulted in substantial mortality after the first fire, but the initial cohort recovers between fire events. Thus, subsequent fires cause relatively less mortality because of declining fire-related mortality associated with increasing stem diameter. Conversely, when the fire-return interval was as short as four years, the first fire resulted in a 40% decrease in cohort size, and the rapid fire-return caused comparable mortality in each successive fire, eliminating the original cohort within 25 years. Thus, repeated short-interval fires may be effective at controlling low-density populations of Brazilian pepper, and may help to limit large-scale invasions.

While it is common in some communities for fire to promote invasion by fire-tolerant plants (D'Antonio 2000), our study results suggest that fire may also be effective at controlling low-density populations of fire-sensitive invasive plants. Brazilian pepper is moderately fire-intolerant when growing in a graminoid-dominated plant community, exhibiting both increased mortality and decreased fecundity following fire due to an abundance of adjacent fine fuels. Thus, in ecosystems such as pine rockland savannas, which are adapted to frequent fires at 3- to 7-year intervals (Beckage

Appendix. Demographic parameter estimates for fire-effect models. Models in bold had the most support (Table 2).

Mortality response to fire

2006

Null: $\text{logit}(p) = -1.31$

Fire (f^\dagger): $\text{logit}(p) = -13.01 + 12.71 f$

Diameter (d): $\text{logit}(p) = 0.68 - 1.50 d$

Fire and Diameter: $\text{logit}(p) = -14.59 + 15.96 f - 1.34 d$

2007

Null: $\text{logit}(p) = -1.95$

Fire (f): $\text{logit}(p) = -3.38 + 2.58 f$

Diameter (d): $\text{logit}(p) = -1.54 - 0.23 d$

Fire and Diameter: $\text{logit}(p) = -2.20 + 3.38 f - 0.92 d$

Growth increment response to fire

All plants

Null: $\mu_g = 0.42, s = 0.31$

Fire (f): $\mu_g = 0.42 + 0.27 f, s = 0.38$

Small plants ($d < 1$)

Null: $\mu_g = 0.61, s = 0.39$

Fire (f): $\mu_g = 0.48 + 0.21 f; s = 0.41$

Relative growth rate response to fire $\dagger\dagger$

All plants

Null: $\mu_g = 0.45, s = 0.06$

Fire (f): $\mu_g = 0.21 + 0.85 f, s = 0.09$

Small plants ($d < 1$)

Null: $\mu_g = 0.94, s = 0.07$

Fire (f): $\mu_g = 0.65 + 0.41 f; s = 0.14$

Maturity and Fecundity response to fire

No effect of fire: $\Theta(d) = F(d|m) = 0.92, s = 0.15$;

$l(d) = 91.7 d^2$

$p_f = 0.51$

Maturity affected by fire: $\Theta(d, \text{unburned}) = F(d|m) = 0.85, s =$

$\Theta(d, \text{burned}) = F(d;m) = 0.90, s =$

$l(d) = 91.7 d^2$

$p_f = 0.50$

Fecundity affected by fire: $\Theta(d) = F(d|m) = 0.92, s = 0.15$;

$l(d, \text{unburned}) = 94.0 d^2$;

$l(d, \text{burned}) = 167$

$p_f = 0.51$

continued

Appendix. Demographic parameter estimates for fire-effect models. Models in bold had the most support (Table 2).

Mortality response to fire

Both affected by fire: $\Theta(d, \text{unburned}) = F(d|m = 0.85, s = 0.23)$;

$\Theta(d, \text{burned}) = F(d|m = 0.90, s = 0.0015)$

$l(d, \text{unburned}) = 94.0 d^2$;

$l(d, \text{burned}) = 167$

$p_f = 0.50$

† f is an indicator of the occurrence of fire, coded as 1 if there was a fire, and 0 if not.

†† Relative growth rate (RGR) was not used in the model, but was calculated for comparison to Keith et al. (2007) as $G = \log(d_{t+1}/d_t)$, where d_t is the diameter measured during the December 2006 census and d_{t+1} is the diameter measured during the December 2007 census.

et al. 2003), restoring the historical fire regime may be sufficient to slow invasion by fire-intolerant plants (Keeley 2006). However, infrequent fires might allow for sufficient growth during the inter-fire period to reduce the effectiveness of fire for controlling Brazilian pepper (i.e., Figure 4B). Furthermore, if Brazilian pepper populations expand to reach densities of approximately four to six plants within a 5 m radius, they might suppress future fires entirely (Stevens and Beckage 2009). Our data suggest that the frequent occurrence of fire is, therefore, critical to prevent invasion of fire-dependent ecosystems by Brazilian pepper.

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