Long-Term Population Changes of a Fire-Adapted Plant Subjected to Different Fire Seasons

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ABSTRACT: Long-term studies of the responses of plant populations to fire can inform adaptive management of ecosystems. I present results of an analysis of responses of a fire-adapted plant, *Pityopsis graminifolia* (Michx.) Nutt. (silkgrass goldenaster), to season of fire from 2001 to 2005 in a longleaf pine (*Pinus palustris* P. Miller) sandhill community in north Florida. Replicated May-burned and January-burned plots had been burned biennially from 1986 to 2004. Previous work in the early 1990s showed that populations of this species benefited more from fires during the peak lightning fire season (i.e., May) than from January fires. In 2001, however, shoot densities in both treatments were substantially lower than in 1992 and remained relatively low through March 2005. Shoot densities were significantly higher in May-burned plots than in January-burned plots between 2001 and 2005. May fires significantly increased shoot densities in 2002 (relative to January fires), but did not in 2004. Shoot densities in January-burned plots remained remarkably stable between 2001 and 2005. As in the early 1990s, May fires were consistently more effective than January fires at stimulating flowering, which in turn produced higher seedling densities. Seedling survival was low, however, as in the early 1990s. Positive short-term effects of lightning-season fires on long-term population trends in this fire-adapted species appear to be substantially reduced by periodic population crashes, inconsistent short-term effects on clonal growth, and inherently low seedling establishment rates.

Index terms: clonal growth, fire-induced flowering, fire management, fire season, lightning, longleaf pine sandhills, seedling survivorship

INTRODUCTION

Most ecosystems characterized by frequent, low-intensity wildfires require prescribed burning to maintain populations of fire-dependent species. Today, these ecosystems are often highly fragmented, lack effective fire conductivity, and thus cannot be managed by relying on pre-colonial processes (aboriginal people or the unimpeded spread of lightning fires) to burn vegetation (Leach and Givnish 1996, Frost 1998). Because many plants in fire-dependent savannas can survive frequent fires and are adapted for environmental conditions occurring before and after those fires (Platt 1999), the types of fires used might be important in preserving fire-dependent species.

Ecologists disagree about the benefits of using prescribed fire to mimic natural lightning fires. On the one hand, some argue that fire-dependent plants in North America evolved with lightning fires before the arrival of humans (Komarek 1964, Howe 1994, Platt 1999). These ecologists reason that fire-dependent organisms should benefit more from fires that mimic lightning fires (such as those that occur during seasons of high lightning activity) than from those set between lightning seasons. There is some evidence to support this hypothesis for some species. For example, among those species induced to flower by fire, several show greater responses to lightning-season fires than to fires between lightning seasons

(Parrot 1967, Streng et al. 1993, Brewer and Platt 1994a; but see Kirkman et al. 1998). In at least one genus (*Pityopsis*), fire-induced flowering is a heritable form of adaptive phenotypic plasticity that arose early in the evolution of the genus and was then conserved in species restricted to areas of high lightning-fire frequency. It enables plants to endure competition from other groundcover vegetation during fire-free intervals (Brewer 1995, Gowe and Brewer 2005). On the other hand, humans have modified fire regimes for thousands of years in North America (Pyne 1982, Delcourt and Delcourt 1998). In contrast to lightning fires, many of these fires were set outside the peak lightning fire season, especially (but not exclusively) in late autumn and winter (Hilgard 1860, Cushman 1899, Beilmann and Brenner 1951, Cowdrey 1996, Audubon (December 1820) *in* Irmscher 1999). It therefore stands to reason that species that were specifically adapted to lightning-season fires – but were intolerant of fires set outside the lightning season – went extinct long ago. Hence, many fire-dependent species that are still around today might tolerate or even benefit from fires set between lightning seasons (Kirkman et al. 1998, Glitzenstein et al. 2003). If so, using prescribed burning to approximate pre-suppression fire regimes (regardless of the historical ignition source) may be more important to preserving biodiversity than restoring a close approximation of lightning-started fires (Waldrop et al.

1992, Brockway and Lewis 1997, Sparks et al. 1998, Glitzenstein et al. 2003).

The only way to test whether lightning-season fires are necessary to maintain populations of fire-dependent plants is to manipulate fire season and measure how these plants respond. One major challenge presented by such an approach, however, is deciding which responses to measure, in which species, and for how long. Most studies of responses of plants to fire in fire-dependent ecosystems of the southeastern United States have focused on short-term (sexual or vegetative) reproductive responses in perennial plants (Hartnett 1987; Barker and Williamson 1988; Brewer and Platt 1994a,b; Abrahamson 1999; Carrington 1999; Hiers et al. 2000; Drewa et al. 2002; McConnell and Menges 2002). These studies provide only limited information about long-term population trends in these species, however, due in part to year-to-year environmental variation (Menges and Quintana-Ascencio 2004) and weak relationships between reproductive success and population dynamics in long-lived perennials in pine savannas (Hartnett 1987, Brewer and Platt 1994a). Furthermore, although some fire-dependent species show highly specific short-term responses to fire season (Brewer and Platt 1994a), others do not (Kirkman et al. 1998). The populations of different fire-dependent plant species may therefore respond differently to fire season over the long term. On the other hand, given that few fire-dependent plants of longleaf pine (*Pinus palustris* P. Miller) savannas rely primarily on seedling establishment to maintain their populations, different short-term reproductive responses to fire season may not translate into long-term differences in population responses to fire season (Streng et al. 1993). Regardless of how a plant immediately responds to a given fire, careful consideration of year-to-year environmental variation and plant life history is crucial to assessing the potential long-term consequences of changes in fire season.

The current study is a follow-up to results reported in Brewer and Platt (1994a,b) and begins nine years after the end of those studies. In 1990 and 1992, *Pityop-*

sis graminifolia (Mich.) Nutt. (silkgrass goldenaster) showed higher rates of floral induction, flowering, seed set, seedling emergence, and clonal growth (i.e., increases in vegetatively-derived shoots and ramets) in response to May (early lightning-season) fires than to January (winter) fires. In addition, seedling establishment was slightly greater following May fires than following January fires but was still very low in May-burned plots. Given those findings, Brewer and Platt predicted that shoot densities would continue to diverge between May-burned and January-burned plots, primarily due to different effects on clonal growth. By comparing data from Brewer and Platt (1994a,b) with new data from 2001 to 2005, using the same sampling plots, I test the following hypotheses as they relate to *Pityopsis graminifolia*: (1) May fires consistently increase shoot densities via clonal growth at a higher rate than January fires; (2) May fires consistently induce flowering to a greater extent than do January fires; (3) May fires consistently, but modestly, increase reproductive success (i.e., seedling recruitment) above that of January fires; and (4) As a result of one or more of these effects, treatment differences in shoot densities first observed in 1992 increase over the long term.

METHODS

Study Species
Details of the life history of *Pityopsis graminifolia* have been provided previously (Brewer and Platt 1994a,b). I chose to study this species for three reasons. First, it is one of the most common forbs in the sandhills plots at St. Marks National Wildlife Refuge in north Florida (Streng et al. 1993). Therefore, adequate sample sizes could be obtained. Second, a considerable amount of information about its life history and its responses to fire has already been collected (Brewer and Platt 1994a,b; Brewer 1995). Finally, flowering in this species is strongly induced by fire, especially lightning-season fires. In effect, floral induction in this species depends on fire at these sites. Significantly less than 1% of all shoots bolt in years without fire (Brewer and Platt 1994a). In addition, I previously showed that clonal growth was

stimulated largely by early lightning-season fires rather than by other fires.

Study Sites and Design of Fire Season Experiment

In this study, I examined floral induction, seedling density, and shoot density in December 1992, November 2001, December 2002, March 2004, and March 2005 in replicated May-burned and January-burned plots in a xeric longleaf pine sandhill community (see also Platt et al. 1988; Streng et al. 1993; Brewer and Platt 1994a,b; Glitzenstein et al. 1995). May is one of the peak months for lightning fires in north Florida (Robbins and Myers 1992). Lightning-started fires occur much less frequently in January and other times during the winter, in part because of lower lightning strike frequencies (Hodanish et al. 1997) and in part because of higher precipitation amounts (National Climate Data Center; Robbins and Myers 1992).

Changes in Shoot Densities via Clonal Growth

In May 1990, 25 0.125-m² sampling subplots were established within one of two replicate May-burned and January-burned plots. The same number of sampling subplots was established in the other replicate plot in December 1990. Details of the shoot sampling procedure are provided in Brewer and Platt 1994b. All adult shoots were permanently marked with aluminum wire and tags.

The current study began with a census of all 25 subplots in each of the two replicate May-burned and January-burned plots. All but one subplot (which occurred in one of the January-burned plots) contained at least one shoot at the end of the 1992-growing season. I left in place all the aluminum wire stakes marking live shoots in December 1992. In November 2001, I revisited all the subplots, including those that had been excavated, and counted shoots. I revisited these subplots to count shoots in November 2002, March 2004, and March 2005. These census dates corresponded with the end or the beginning of a growing season in each year. Peak emergence of a year's

cohort of seedlings of this species is not complete until about February. For this reason, I discontinued monitoring shoots in November after 2002 and began monitoring vegetatively-derived shoots in March 2004, which allowed me to monitor seedlings and vegetatively-derived shoots simultaneously once each year.

Reproductive Responses and Seedling Survival

To assess treatment effects on reproduction and seedling dynamics, I measured the proportions of shoots that bolted (i.e., those that produced flowering stalks) in November 2001 and 2002 and in March 2004 and 2005. In March 2003, I marked all seedlings of the 2002 fire-year cohort. In March 2004, I recensused the subplots for seedling survival and marked the survivors with fire-resistant metal wires. At that time, I also determined which, if any, survivors had grown significantly. I considered a seedling to have grown to the size of an established plant if it produced at least one primary leaf that was longer than 8 cm. No seedlings emerged in March 2004 due to a lack of flowering in 2003. I then revisited the subplots again in March 2005 to determine survivorship and count new seedlings from the 2004 fire-year cohort.

Statistical Analyses

I ran two separate repeated-measures analyses to test the main effects of fire and year and their interaction on densities of all shoots (minus those derived from 2002 seedling cohorts). The first analysis examined only 1992 and 2001 densities and included only the 20 subplots that had not been excavated in February 1993. The second analysis examined November 2001 and 2002 and March 2004 and 2005 and included those excavated subplots that had been recolonized by March 2005.

I examined treatment, plot, and year-of-fire effects on proportions of shoots that bolted in each fire year (1992, 2002, and 2004) using log-linear models and chi-square tests of independence. I analyzed the relationship between the incidence of

bolting in a subplot within the May-burned plots in 2002 and 2004 and the number of seedlings within the subplots the following winter using separate two-sample t-tests (assuming unequal variances) for each year. All univariate statistical analyses were done using Statistix 8 (Analytical Software, Tallahassee, Florida). Repeated measures analyses were done using SuperAnova v. 1.11 (Abacus Concepts, Inc., Berkeley, California).

RESULTS

Changes in Shoot Densities via Clonal Growth

Shoot densities in 2001 were about one-fifth those in 1992, irrespective of fire season (Figure 1). The main effect of year (i.e., 1992 versus 2001) was highly significant ($F_{1,78} = 219.3$, $P < 0.0001$). Shoot densities, averaged across both years, were significantly higher in May-burned plots than in January-burned plots ($F_{1,78} = 9.42$, $P = 0.003$). Although declines appeared to be slightly greater in May-burned plots than in January-burned plots (Figure 1), the fire season x year interaction was not statistically significant ($P = 0.14$).

Trends from 2001 to 2005 revealed that

shoot density varied among years (Figure 2; $F_{3, 192.8} = 4.79$, $P = 0.008$) and on average remained higher in the May-burned plots than in the January-burned plots (Figure 2; $F_{1, 90} = 9.41$, $P = 0.003$). There was, however, a statistically significant interaction between year and fire season (Figure 2; $F_{3, 192.8} = 4.18$, $P = 0.015$). A close examination of the components of this interaction revealed a significant effect of fire season on changes in shoot density in the 2002 fire year ($F_{1, 90} = 6.59$, $P = 0.012$) but not in the 2004 fire year ($F_{1,90} = 0.013$, $P = 0.91$). Despite the lack of a significant difference in the effects of May fires and January fires in 2004 on changes in shoot density, shoot density was still higher in May-burned plots than in January-burned plots at the end of the study (Figure 2; $F_{1,90} = 12.22$, $P = 0.0007$).

Reproductive Responses and Seedling Establishment

May fires were consistently more effective at stimulating flowering (bolting) than January fires in 1992, 2002, and 2004 (Figure 3). The proportion of shoots that bolted varied between plots following May fires ($\chi^2 = 15.33$, df = 5, $P = 0.009$) but not after January fires ($\chi^2 = 9.16$, $P = 0.103$). So, each May-burned plot was compared with both January-burned plots separately.
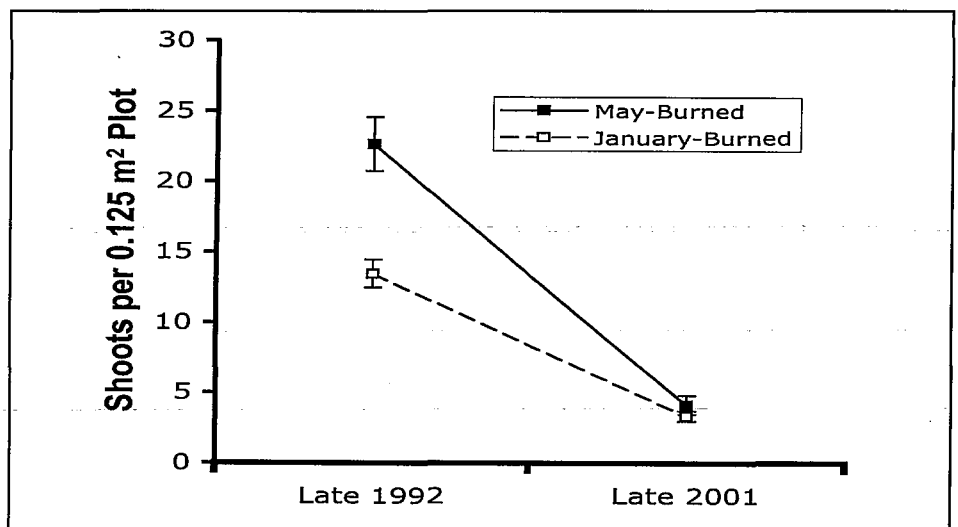

Figure 1. Changes in shoot density in May-burned and January-burned plots between December 1992 and November 2001. Values are mean density per 0.125-m² subplot ± 1 standard error. Plot effects within each burn treatment were not statistically significant and thus subplot errors were pooled (n=40). Five subplots were excluded from each plot, because all had shoots that had been excavated in 1993 from these subplots to determine biomass allocation and rhizome connections.
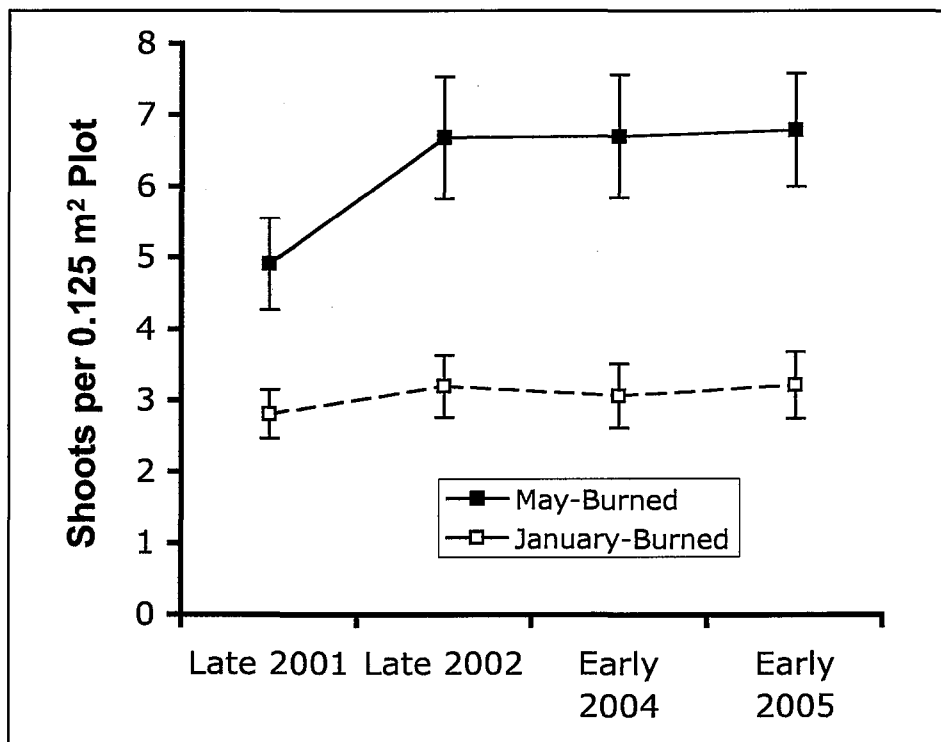
Figure 2. Changes in shoot density in May-burned and January-burned plots between November 2001 and March 2005. Values are mean density per 0.125-m² subplot ± 1 standard error. Plot effects within each burn treatment were not statistically significant and thus subplot errors were pooled (n=45 for the May-burned treatment and 47 for the January-burned treatment).

The incidence of bolting was much higher in both May-burned plots than in the January-burned plots (χ^2 = 360.6, df = 5, $P <$ 0.0001 and χ^2 = 282.7, df = 5, $P <$0.0001, for each May-burned plot comparison, respectively). Overall, the incidence of bolting did not vary significantly among years after controlling for fire season (χ^2 = 9.2, df = 6, P = 0.16), nor was there a significant year x fire season interaction (χ^2 = 5.81. df = 4, P = 0.21).

Seedling densities in subplots were strongly associated with the incidence of bolting in the plot as a whole and with the incidence of bolting in subplots in the preceding fire year. No seedlings were observed in the January-burned plots in either 2002 or 2004, nor were there any seedlings in May-burned subplots in March 2004 (following a year with no fire). In March 2003, seedling densities in May-burned plots were significantly higher in those subplots that contained at least one bolting shoot at the end of the 2002 fire year (7.52 ± 1.15 seedlings per subplot versus 0.94 ± 0.48 seedlings per subplot, respec-

tively, t = 4.74, P < 0.0001). I observed a similar pattern in March 2005 (8.57 ± 1.30 seedlings per subplot versus 3.81 ± 1.34 seedlings per subplot, respectively, t = 2.55, P = 0.015).

Seedling survivorship over a two-year period from March 2003 to March 2005 was low in both May-burned plots. Seven out of 234 seedlings marked in March 2003 were still alive in March 2005. Of those seven, four produced at least one primary leaf that was longer than 8 cm. The remaining three showed no evidence of growth (at least aboveground) and yet all seven managed to survive the fires in 2004. None of the seedlings had reached reproductive maturity by March 2005.

DISCUSSION

The results of this study show that population densities of *Pityopsis graminifolia* are not likely to diverge dramatically in response to fire season over the long term. Short-term responses to season of fire, although perhaps reliable indicators of

seasonal cues associated with fire, do not provide a reliable indicator of long-term population trends in this species. Differences in the effects of May and January fires on clonal growth rates in two of three fire years in which they were measured (1992, 2002, 2004) did not translate into increasing disparity in shoot density between May-burned and January-burned plots over time. The major factor that prevented the projected increase in disparity in shoot densities was a population crash in all four plots some time between 1992 and 2001. Consecutive droughts in the late 1990s and 2000 were likely the main causes of this crash, based on the coincidence of low rainfall amounts and the disappearance of less common species from sampling plots during that time (Jeff Glitzenstein, plant ecologist and consultant, pers. comm.). In addition to the effects of the population crash, there was no significant effect of fire season on clonal growth in 2004, which was not a drier than normal year. Furthermore, differences in seedling establishment contributed very little to differences in shoot density.

The lack of a significant fire-season effect on clonal growth in 2004 was unexpected, but I offer the following possible explanation. As in previous years, May 2004 fires were more effective at stimulating clonal growth (i.e., increases in vegetatively-derived shoot densities) than were January fires, but they also resulted in more shoot mortality following flowering of semelparous shoots. In previous years, however, most flowering shoots were replaced at the end of the flowering season by one or more shoots originating from axillary buds. For some reason, this did not occur for most flowering shoots in 2004. The net effect was that the high rate of shoot initiation during the 2004 growing season following May fires was countered by higher shoot mortality at the end of the flowering season, which in turn was not compensated for by the initiation of axillary shoots at the end of the 2004 flowering season. Hence, the net increase in shoot density during 2004 was no greater in the May-burned plots than in the January-burned plots.

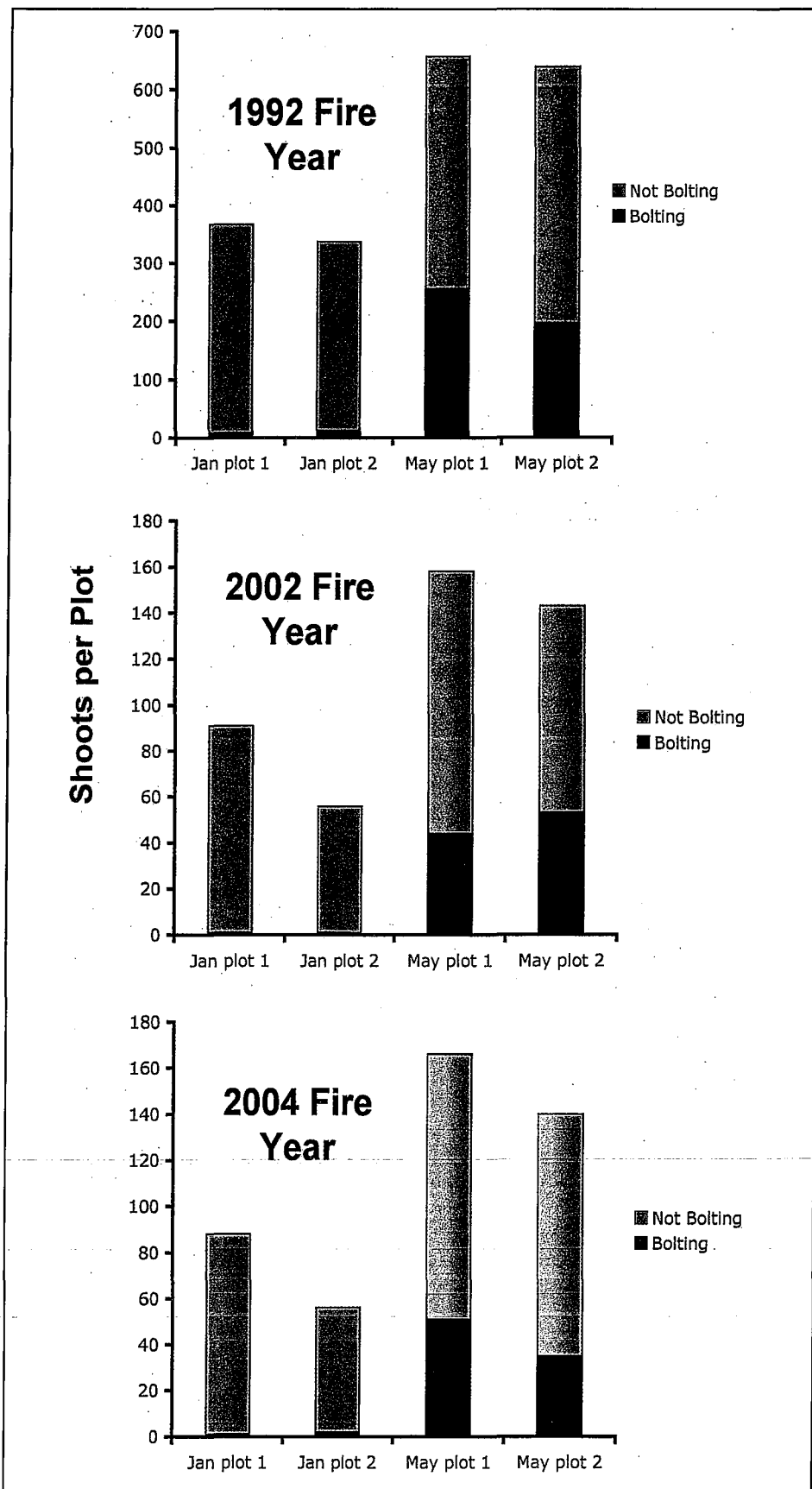The reasons for lower rates of emergence of axillary shoots in plots burned in May

Figure 3. Numbers of bolting (flowering; black bars) and non-bolting shoots (hatched gray bars) in each May-burned and January-burned plot during the 1992, 2002, and 2004 fire years.

2004 remain unknown, but there is likely a limit to how much a genet can increase both the number of flowering and non-flowering shoots before costs associated with sexual reproduction begin to exert some negative effect on shoot survival. The ability of flowering shoots to replace themselves with axillary shoots is size dependent (Brewer and Platt 1994b). Although May fires are more effective at stimulating clonal growth, these increases do not increase the biomass of genets (Brewer and Platt 1994b). In other words, there is a trade-off between the rate at which new shoots are produced and the size of individual shoots in a genet (Brewer and Platt 1994b). This raises the interesting possibility that more frequent sexual reproduction reduces subsequent clonal growth in some years by reducing shoot size.

Consistent with a life history that is typical of long-lived perennials, seedling survivorship in *Pityopsis graminifolia* was quite low (3% over two years after May fires). It is worth noting that the 6% survival rate observed in the May-burned plots in 1992 corresponded with very high rainfall amounts in February 1991 around the time of emergence of seedlings produced by the 1990 fires. Hence, the 6% establishment rate in 1992 could have been atypically high for this species. However, seedling survivorship in the current study was not significantly lower than that of the 1991 cohort. Regardless, short-term shoot population dynamics in this species were regulated more by shoot survival and clonal growth than by the effects of fire season or year-to-year variation on seedling establishment in this species.

If seedling establishment has very little effect on population sizes, then of what benefit is fire-induced flowering to this species? I offer two possible answers. First, fire-induced flowering and seedling establishment may allow plants to produce more genetically variable offspring than plants that rely almost exclusively on vegetative reproduction. If such differences between May- and January-burned treatments are significant, then May-burned genotypes could have a selective advantage over January-burned genotypes in a changing or variable environment. Second, the benefit

of fire-induced flowering likely has more to do with increasing survival (and therefore residual reproductive effort) in established adults than with increasing rates of seedling establishment in years with fire (i.e., current reproductive effort). Instead of asking why *Pityopsis graminifolia* increases flowering after a fire, perhaps we should ask why this species suppresses flowering in years without fire. One might expect flowering to be costly, especially when resources are limiting or when competition is intense (Brewer 1995, Gowe and Brewer 2005). Suppressing flowering until shortly after a fire reduces the cost of reproduction, the risk of losing costly reproductive structures to fire, and the risk of shoot mortality (Brewer 1995), which in turn could increase future reproduction. Of course, very frequent lightning-season burning could undermine the effectiveness of such a life-history strategy. The lack of replacement of bolting shoots by axillary shoots in 2004 indicates that frequent lightning-season burning can in some years increase costs associated with flowering. Therefore, all else being equal, this species should benefit from modest variability in fire frequency or fire season.

As expected, May fires were consistently more effective at stimulating flowering in this species than were January fires. This response applies to most fall-flowering grasses and composites that are induced to flower by fire (Streng et al. 1993; S.E. Hinman and J.S. Brewer, unpubl. data). Many fall-flowering grasses and composites are "long-day" plants. This might explain why fires during long photoperiods (e.g., late May through early July) are more effective at stimulating flowering in these species than fires at other times of the year (Streng et al. 1993, Brewer and Platt 1994a). This might also explain why fire-dependent species that typically flower earlier in the year [e.g., *Schwalbea americana* L. (American Chaffseed), Eriogonum *longifolium* Nutt. var. *gnaphalifolium* Gand. (Scrub Buckwheat)] show similar flowering responses to dormant-season and lightning-season fires (Kirkman et al. 1998, McConnell and Menges 2002). Interestingly, there do not appear to be many examples of species for which dormant-season or early-spring fires are more effective at inducing flowering

than lightning-season fires, even though numerous pine savanna species flower from mid-spring to early summer (Streng et al. 1993; S.E. Hinman and J.S. Brewer, unpubl. data). One could, therefore, argue that most fire-dependent plants present in longleaf pine systems today evolved with lightning-season fires (Gowe and Brewer 2005) or perhaps a mixture of fire seasons but, as this study indicates, fire-dependent plants tolerate and even benefit from frequent fires outside the lightning season (Kirkman et al. 1998, McConnell and Menges 2002, Glitzenstein et al. 2003). More comparative phylogenetic analyses (such as in Gowe and Brewer 2005), along with analyses of long-term population trends, need to be done, however, to test this hypothesis.

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Stephen Brewer is Associate Professor of Biology at the University of Mississippi. His research focuses on the ecology and evolution of fire-dependent communities and species in the southeastern coastal plain of the United States.

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