1994

Life History Responses to Fire Season in a Clonal Herb, Pityopsis Graminifolia (Asteraceae).

John Stephen Brewer
Louisiana State University and Agricultural & Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_disstheses

Recommended Citation
https://digitalcommons.lsu.edu/gradschool_disstheses/5689

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Historical Dissertations and Theses by an authorized administrator of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.
INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.
Life history responses to fire season in a clonal herb, *Pityopsis graminifolia* (Asteraceae)

Brewer, John Stephen, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1994
LIFE HISTORY RESPONSES TO FIRE SEASON IN A CLONAL HERB, PITYOPSIS GRAMINIFOLIA (ASTERACEAE)

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

The Department of Botany

by

John Stephen Brewer
B.A., Hendrix College, 1986
M.S., Louisiana State University, 1989
May 1994
ACKNOWLEDGMENTS

I thank Drs. Jeff Glitzenstein and Donna Streng for their helpful comments and for graciously providing housing during a portion of the study. Graduate committee members Drs. William J. Platt, Christopher Clark, James B. Grace, E. Barry Moser, Shirley C. Tucker, and G. Bruce Williamson made suggestions for improving this research. Dr. Moser also gave much needed statistical advice. I gratefully acknowledge the cooperation of St. Mark's Wildlife Refuge, which has fostered the study of fire season effects on vegetation in longleaf pine ecosystems. I am especially indebted to Doug Scott and the rest of the Refuge staff for administering the experimental burns in a timely and highly competent manner. Tall Timbers Research provided housing for a portion of the study, and I thank Dr. Sharon Hermann for her help in this regard. A special word of thanks goes to Ashley Brewer for assistance in the field and with the dissertation. Support for the long term fire season study was provided by National Science Foundation grants BSR-8012090 and BSR-8605318 (W.J. Platt, P.I.), the Florida Fish and Game Commission grants GFC-84-014 (W.J. Platt, P.I.) and GFC-90-014 (J.S. Glitzenstein and W.J. Platt, co-P.I.s). The short term demographic study of Pityopsis graminifolia was funded by a Doctoral Dissertation Improvement Grant (BSR-9101171) from the National Science Foundation awarded to William J. Platt and J. Stephen Brewer.
TABLE OF CONTENTS

Acknowledgments..................................................................ii
List of Tables.......................................................................vi
List of Figures.......................................................................viii
Abstract...............................................................................x

Chapter
1  Introduction.........................................................1

2  Effects of Fire Season and Herbivory on
    Reproductive Success..............................................7
    Introduction.........................................................8
    The Reproductive Biology of *Pityopsis graminifolia*........11
    Study Area..........................................................13
    Methods...............................................................14
    Experimental Design of
    Fire Experiments.................................................14
    Sampling and Censusing
    of *Pityopsis graminifolia*......................................15
    Statistical Analysis of
    Fire Experiments................................................18
    Experimental Design and Analysis
    of Clipping Experiments........................................21

Results............................................................................24
    Effects of Fire vs. No Fire
    on Bolting Dynamics..........................................24
    Effects of Fire Season
    on Bolting Dynamics..........................................28
    Response of Bolting Dynamics to Fires
    in Different Years...............................................31
    Effects of Fire Season and Spatial
    Patterns of Bolting on Bud and
    Branch Herbivory................................................32
    Effects of Fire Season on Achene Set
    and Shoot and Clone Fecundity............................35
    Effects of Fire on
    Seedling Dynamics...............................................40

Discussion..........................................................................42
    Proximate Causes of Fire Effects
    on Floral Induction.............................................42
    Fire Season and Herbivory......................................43
    Fire Season and Herbivory Effects
    on Clone Fecundity and
    Seedling Survival...............................................44
    The Evolution of Mass Reproduction
    in Clonal Perennial Herbs....................................47

iii
LIST OF TABLES

2.1. Mean number of live shoots/plot observed in December 1990 and December 1992 .................17

2.2. ANOVA table for RBD with 2x2 factorial arrangement of treatments testing the effect of blocks, season of clipping, and fertilization on ranks of proportions of shoots that bolted .........................27

2.3. Split-plot ANOVA table of the effects of fire season and year of fire on logistic transformations of proportions of shoots that bolted ...........................................29

2.4. ANOVA table of Randomized Block Design testing the effect of season of clipping + fertilization on ranked cumulative proportional bud herbivory in 1992 .........................36

3.1. Split-split-plot ANOVA table of the effects of blocks, season, clipping, and census on shoot density .................................................................69

3.2. Split-plot ANOVA table of the effect of fire season on per shoot rates of increase in shoot density \( \log \frac{N_t}{N_0} \) during the first two censuses after fire in 1992 .........................70

3.3. Split-plot ANOVA table of the effects of blocks, season of clipping, fertilization, and census (initial and final) on shoot density in 1992 .............................75

3.4. Sub-divided contingency table of the number of shoots/subplot/plot ........................................81

3.5. Sub-divided contingency table of the number of rhizomes/subplot/plot .................................83

3.6. Analysis of the effect of fire season on mean number of shoots/clone/subplot, mean number of rhizomes/clone/subplot, mean shoot weight/subplot, mean ramet weight/subplot, and mean clone weight/subplot using Multi-Response Permutation Procedures (MRPP) .... 85
4.1. The mean number of live shoots/plot observed in December 1990 and December 1992 following January and May fires.................102

4.2. Numbers of excavated mother and daughter shoots derived from reproductive ramets (R) and non-reproductive (N) ramets in early 1991 and early 1993.....................112

4.3a-e. Matrices of transitions between R shoots and N shoots for each fire season plot...........113

4.4. Reproductive values and overall per shoot rates of change in shoot population size for May- and January-burned shoots..............117
LIST OF FIGURES

2.1. Mean number of bolting shoots/m²/plot ± SE from December 1990 to December 1992.........25

2.2. The effects of season of clipping and fertilization on mean proportions of shoots that bolted/clipped plot...................26

2.3. The effect of fire season on mean proportions of shoots that bolted/plot in December 1990 and December 1992................30

2.4. (a) The effect of fire season on mean proportions of branches damaged by herbivores in December 1990. (b) The effect of fire season on mean cumulative proportions of buds eaten by December 1992....33

2.5. Seasonal patterns of mean cumulative total bud abundance ± SE and mean cumulative total herbivory ± SE in plots burned in January 1992................34

2.6. The effect of fire season on the number of achenes per bolting shoot and bolting shoot height..............................38

2.7. The effect of fire season on clone fecundity and the number of reproductive shoots/clone.....39

2.8. The number of seedlings/m²/plot ± SE from March 1991 to December 1992...................41

3.1. Diagram of two connected ramets of Pityopsis graminifolia.......................................55

3.2. Mean shoot density/m²/plot ± SE from December 1990 to December 1992...............67

3.3. The effect of fire season on log (per shoot increase in shoot density) during two census intervals following fire in 1992........72

3.4. The effects of season of clipping (May, August) and fertilization on mean increases in shoot density/plot..........................74

3.5. The effect of fire season on mean shoot natality/plot ± SE.................................76
3.6. The effect of fire season on mean shoot mortality/plot ± SE.........................78

3.7. Age-class frequency distribution of mean percent shoots/plot in 1993 in relation to fire season..........................79

3.8. Age-class frequency distribution of mean percent rhizomes/plot in 1993 in relation to fire season..............................82

3.9. Biplot ordination diagram of variables associated with clone structure and centroids of subplots burned in three different seasons (January, May, and August) using canonical discriminant analysis..............86

4.1a-c. Plots of simple correlations of subplot means of a) shoot number/clone, b) shoot weight, and c) clone weight with the first canonical axis derived from canonical discriminant analysis..................105

4.2. Mean shoot density/m²/plot ± SE from March 1991 to December 1992.................................107

4.3. Mean number of bolting shoots/m²/plot ± SE from March 1991 to December 1992......................108

4.4. Flow diagram of transitions of shoots between early (Jan-Mar) 1991 to early (Jan-Feb) 1993..............................111
ABSTRACT

The effects of three fire seasons (May, August, and January) on reproductive success and clonal growth of a golden aster (*Pityopsis graminifolia*) were examined within experimental burn plots in a longleaf pine savanna in north Florida. Several factors influenced reproductive success in this species, including rates of floral induction and bud herbivory, clone fecundity, and seedling dynamics. Flowering was induced by fire, especially when it occurred in May or August. Fire season affected rates of floral induction and bud herbivory by as much as one to two orders of magnitude. Sizes of bolting shoots were also affected by fire season. Survival of 1991 cohorts of seedlings through December 1992 was highest in May-burned plots, intermediate in August-burned plots, and lowest in January-burned plots.

Fire season also influenced patterns of clonal growth in this species. May fires caused higher short-term per shoot rates of increase in shoot density than did either January or August fires. May fires also resulted in greater numbers of shoots/clone than did either January or August fires. January-burned plots contained clones with larger (but fewer) shoots than did May-burned or August-burned plots. Such variation in clone structure may indicate a greater capacity of clones to locate soil resources following May fires than following January or August fires.
The reproductive and clonal responses of this species to fire season indicate that plants perform best following fires in May, the season in which lightning fires are most likely to occur.

Models of resource allocation and clonal growth dynamics revealed that widespread but short-lived increases in rates of vegetative spread following May fires corresponded to a hypothesized shift in competition from aboveground to belowground. In contrast, prolonged increases in rates of vegetative spread occurring at smaller scales (e.g. within gaps) might have resulted from increased growth rates or larger sizes of clones.
CHAPTER 1 - INTRODUCTION
Conservation of longleaf pine ecosystems requires knowledge of the ecological and evolutionary significance of fire. Since the 1940s, prescribed fire has been used as a management tool in longleaf pine communities with little knowledge of what represented a natural fire regime. A scientific basis for deciding the appropriate burning schedule should include knowledge of the ecological responses of native plants to variation in the fire regime. There have been few properly designed experiments, however, that have adequately addressed the significance of responses of vegetation to variation in the fire regime (Robbins and Myers 1992, Streng et al. 1993). Thus, the ecological and evolutionary significance of fire in longleaf pine communities is still poorly understood.

Assessing the evolutionary importance of a particular fire regime to native plants involves examining those traits that affect fitness. These include the incidence of sexual reproduction, adult and juvenile mortality, and growth (Gill 1981). Some fire ecologists believe that native plants should perform best in response to fire regimes important in their evolutionary history (Komarek 1965, Robbins and Myers 1992). The application of optimality techniques to reconstructing the natural fire regime requires intensive study of the population dynamics of individual species. Such an approach limits the number of species that can be studied at one time. In deciding which species to study, I believed
it was appropriate to choose a species with a life history that was representative of many of the dominant groundcover species of longleaf pine savannas.

The groundcover communities of longleaf pine savannas are dominated by long-lived, clonal perennial herbs, capable of rapid regrowth following growing-season fire. Increased flowering in several perennial herbs following growing-season fire has been cited as evidence of an optimal trait in pyrogenic habitats (Gill 1981). However, the effects that variation in the fire regime has on fitness in long-lived perennial herbs has not been well studied. Thus, in this dissertation, I chose to examine the population dynamics of a native clonal perennial herb that exhibits increased flowering following fire, *Pityopsis graminifolia*.

Understanding the effect of variation in the fire regime on fitness requires experimental manipulation of the fire regime. There have been few attempts to examine the responses of populations of perennial herbs to variation in the fire regime. In this dissertation, I experimentally manipulated fire season and examined reproductive and clonal growth responses of *P. graminifolia*. It is assumed that different seasons of fire vary with respect to their historical importance in longleaf pine savannas. By examining the effects of fire season, I was able to determine the relationship between the expected frequency of lightning fires occurring at different times of the year and
the performance of *P. graminifolia*. Overall, this project was designed to examine the effects of three different seasons of burn (hereafter referred to as fire seasons): January, May, and August.

One component of fitness in *P. graminifolia* that is potentially influenced by fire season is reproductive success. The effect of fire season on reproductive success likely depends to a degree on flowering responses to fire season. Previous studies have shown a significant effect of fire season on flowering responses of many groundcover species in longleaf pine savannas (Platt et al. 1988a, Platt et al. 1991, Streng et al. 1993). Prescribed fires during the growing season (April-September) stimulate the flowering of *Pityopsis graminifolia* and reduce overlap in its peak flowering time with that of other species (Streng et al. 1993, Platt et al. 1988a). In contrast, fires prescribed between growing seasons (Oct-Mar) only modestly stimulate flowering in *P. graminifolia* and maintain significant overlap with the peak flowering times of other species (Streng et al. 1993, Platt et al. 1988a). These data suggest that the fitness of *P. graminifolia* may be greater when frequently burned during the growing season. However, the effects of fire season on seed set, clone fecundity, and seedling establishment have not been studied. Therefore, the effects of fire season on reproductive success in this species are still unknown. Furthermore, no one has examined
the life history conditions and phenological constraints that may influence the evolution of fire-stimulated flowering. Thus, the evolutionary significance of fire-stimulated flowering is still poorly understood.

Another component of fitness in *P. graminifolia* that is potentially influenced by fire season is clonal growth. In a central Florida population of *P. graminifolia*, Hartnett (1987) found that frequent May fires promoted module survival within clones. The evidence for this statement was based on data showing that frequently-burned plots contained clones with numerous small modules, while an unreplicated, unburned "control" plot contained clones with few large modules. Several researchers have suggested that trade-offs between numbers of modules within clones and module size may indicate phenotypic plasticity in patterns of proportional allocation to mother and daughter modules (Cook 1983, 1985, Coughenour et al. 1985b, Milchunas et al. 1988, Grace 1989). Furthermore, Milchunas et al. (1988) proposed that in grazophilic species, proportional allocation to daughter modules should increase in response to shifts in competition from aboveground to belowground associated with chronic, sublethal aboveground disturbances such as grazing. In this dissertation, I tested whether or not this theory applied to another form of chronic, sublethal disturbance, fire, by examining the effect of fire season on patterns of proportional allocation within clones of *P. graminifolia*. In
addition, I partitioned the effects of fire from other sources of phenotypic variation in clonal growth patterns using a spatial model of the dynamics of vegetative spread.

The three studies presented in this dissertation were subsets of a long-term ongoing study of the effects of fire season on vegetation dynamics in longleaf pine savannas (Platt et al. 1988a). They were designed to assess the ecological and evolutionary significance of fire season in a clonal pyrophilic perennial forb, *Pityopsis graminifolia*. The objectives of these studies were 1) to determine the effects of fire season on reproductive success and clonal growth in *P. graminifolia*, and 2) to distinguish between the effects of fire and other sources of phenotypic variation in clonal growth dynamics in this species.
CHAPTER 2 - THE EFFECTS OF FIRE SEASON AND HERBIVORY

ON REPRODUCTIVE SUCCESS
INTRODUCTION

Fire-enhanced floral induction has been suggested to be an adaptive trait in pyrogenic grasslands and savannas (Gill 1981, Christensen 1991). Growing-season fires have been shown to result in increased numbers of flowering shoots produced by some perennial herbs of longleaf pine savannas of the southeastern United States (Platt et al. 1991, Streng et al. 1993). Field observations also indicate that, in years without fire, flowering shoots of these species are much less frequent and occur mostly within large clones that occupy discrete gaps in the unburned herbaceous groundcover.

Several ecologists have hypothesized that synchronized, mass reproduction of genets in a population, such as occurs following growing-season fires in longleaf pine savannas (Platt et al. 1988a, Platt et al. 1991, Streng et al. 1993), can both increase the chances of pollination and outcrossing and satiate seed predators (Janzen 1967, Baker 1973, Parrish and Bazzaz 1979, Augspurger 1981, Schmitt 1983).

Fire-enhanced mass reproduction has been shown to result in increased seed set in some grasses (Mark 1965, 1968) and seed predator satiation in an obligate seeding shrub (O'Dowd and Gill 1984) in Australia. However, the effect of fire-enhanced mass reproduction on seed set in rhizomatous forbs is unknown.

Furthermore, little is known about the effect of mass reproduction on herbivory in clonal plants. In contrast to
the effect of seed predation on reproductive success, genets may be able to compensate, at least in part, for the loss of pre-fruiting meristems to herbivores by producing additional reproductive ramets or branches following herbivore-induced release of protected buds from dormancy (Doak 1991).

Even if mass flowering in response to fire were to increase seed set, it would have no effect on the reproductive success of genets/clones unless there were also successful seedling establishment. Seedling establishment of clonal perennials is very low (1-3%) in most grasslands and savannas (Cook 1985) probably because seedlings compete poorly with established adults (Sarukhan and Harper 1973, Hartnett and Bazzaz 1985, Schmid 1985). Fire rarely kills established genets in longleaf pine systems (Streng et al. 1993). While some authors have suggested that seedling establishment may vary in response to variation in the fire regime (Barker and Williamson 1988), others have found no relationship between the fire regime and seedling establishment. (Hartnett 1987, Kaczor and Hartnett 1990). To my knowledge, no studies have demonstrated a positive effect of growing-season fire on seedling establishment of pyrogenic clonal herbs in pine savannas. And yet, such studies are crucial to understanding the evolutionary significance of fire-induced flowering.

In addition to the effects of fire-induced flowering on reproductive success, the proximate cues involved require
further study. Several studies have shown canopy/litter removal, and in some cases, mineral nutrient addition to be the most important cues for fire-induced flowering (Old 1969, Hulbert 1988, see references in Gill 1981). However, very little is known about how the inductive effects of canopy/litter removal and nutrients change seasonally. In longleaf pine savannas of north Florida, fire season has been shown to influence the amount and timing of flowering of numerous grasses (e.g. *Aristida beyrichiana* Trin. and Rupr., *Andropogon arctatus* Chapm.) and some forbs (e.g. *Pityopsis graminifolia* (Michx.) Nutt., *Liatris* spp.) (Clewell 1985, Platt et al. 1988a, Streng et al. 1993).

Flowering responses are typically greatest following fires occurring during the warm growing-season months, when the frequency of thunderstorms and lightning strikes is highest (Streng et al. 1993). However, little is known about how "precisely correlated" floral inductive cues are to seasonal changes in the likelihood that areas will be burned by lightning fires. While the frequency of lightning strikes is high during both May and August in Florida, the greatest amount of area burned by lightning fires occurs during May and June (Komarek 1964) because of the combination of a moderately high frequency of thunderstorms and low rainfall at this time of the year (Chen and Gerber 1990). Thus, a comparison among January, May, and August fires provides an opportunity to assess the precision and reliability of
inductive cues in reflecting seasonal variation in the expected likelihood that plants will be burned by lightning fires.

In this study, I experimentally manipulated fire season and, hence, the amount and timing of floral induction in \textit{Pityopsis graminifolia}. In addition, I examined floral induction responses to a factorial arrangement of season of clipping and fertilization treatments. The clipping experiment was designed to examine the importance of canopy and litter removal effects of fire and how they interact with seasonal rhythms and nutrient availability. These experiments were conducted in a longleaf pine sandhill community in northern Florida, USA. Four questions were addressed. First, how does fire season influence rates of floral induction and bud herbivory by white-tailed deer? Second, what are the underlying causes of observed floral induction responses to fire and fire season? Third, what is the overall effect of fire season on clone fecundity? Fourth, what is the effect of fire season on seedling survival and establishment?

\textbf{THE REPRODUCTIVE BIOLOGY OF PITYOPSIS GRAMINIFOLIA}

\textit{Pityopsis graminifolia} (Michx.) Nutt. is a perennial, fall-flowering composite, common throughout the coastal plain of the southeastern United States (Semple and Bowers 1985). In north Florida, during the winter and early spring,
shoots occur as basal arrangements of linear leaves (cataphylls), emerging either from the terminal end of rhizomes or from axillary buds on older portions of perennial rhizomes. Apical shoot buds are at or below the soil surface, well protected from fire, until shortly after fire. In flowering shoots, anthesis occurs from late summer to late fall, and seed set occurs from late fall to early winter. The exact timing of each of these stages depends on fire season.

*P. graminifolia* has yellow ray and disc flowers and is predominantly visited by bumblebees and a large assortment of lepidopterans (Brewer, pers. obs.). Its breeding system is typical of many golden asters and goldenrods in that pollen is presented secondarily on the outer surfaces of the style of disc flowers. The style branches are oppressed prior to the stigmatic surface spreading and becoming receptive. Thus, each disc flower is protandrous, and any selfing in this species is likely the result of geitonogamy. Capitula are protogynous and gynodioecious as a result of the centripetal development of female ray and perfect disc flowers. Total numbers of flowers per capitulum range from 20-70, but do not vary with the fire regime.

Fruits of this species are wind-dispersed achenes. Mature achenes are easily distinguishable from those that fail to develop by color and size. Controlled germination tests with seeds collected in the field revealed that more
than 80% of the seeds from developed achenes germinate within the first four months after collection regardless of the fire regime.

STUDY AREA

This study was conducted in a second growth sandhill community in the St. Marks Wildlife Refuge, Wakulla County, Florida. Sandhills are open, xeric pine forests that overlie deep Plio-Pleistocene-age sands (Platt et al. 1988a, Myers 1990). The overstory is dominated by longleaf pine, Pinus palustris Mill. The understory contains a diverse mixture of perennial grasses (e.g., wiregrass, Aristida beyrichiana Trin. and Rupr., little bluestem, Schizachyrium scoparium (Michx.) Nash, beardgrasses, Andropogon spp., and Dicanthelium spp.), forbs (e.g. grass-leaf goldenaster, Pityopsis graminifolia (Michx.) Nutt., blazing star, Liatris tenuifolia Nutt., milk-pea, Galactia floridana T. and G., and elephant's foot, Elephantopus elatus Bertol.), and shrubs and small trees (e.g. shiny blueberry, Vaccinium myrsinites Lam., dwarf-live oak, Quercus minima (Sarg.) Small, turkey oak, Q. laevis Walt., and blue-jack oak, Q. incana Bartr.) in a low groundcover (Streng et al. 1993). All nomenclature follows Clewell (1985) except Aristida beyrichiana, which follows Peet (1993), but is synonymous with Aristida stricta Michx. in Clewell (1985).
Sandhill communities depend upon frequent (every 1-5 yr), low-intensity surface fires that prevent the growth of hardwood trees into the canopy (Chapman 1932a,b, Christensen 1981, Platt et al. 1988b, 1991). In addition, while these fires typically kill aboveground, but not belowground parts of herbaceous perennials, survival and resprouting is extensive (Platt et al. 1988a). Lightning-started fires typically occurred during the growing season (April to October) prior to European settlement (Chapman 1932a,b, Platt et al. 1991). Settlers altered the natural fire regime by burning pine forests during the winter, between growing seasons (Platt et al. 1988a). Over the past 35 years, prescribed burning by the refuge staff has occurred 2-3 times a decade, mostly during the winter (Platt et al. 1988a).

METHODS

Experimental Design of Fire Experiments

The fire experiments for the current study are subsets of a larger long-term study of the effects of fire season on vegetation dynamics in longleaf pine savannas initiated in 1980 by W.J. Platt. The design of the long-term study (Platt et al. 1988a) consists of two replicate plots of eight different seasons of burn within both sandhill and flatwoods habitats. Replicate plots are 2-5 hectares each and were selected based on similar densities of longleaf pine,
wiregrass, and *Quercus* sp. (Platt et al. 1988a). Large oaks that had entered the overstory as a result of fire suppression after logging earlier in the century were cut at the base of the tree during the winter of 1980-1981. Most trees resprouted, forming shrubs in the ground cover. A pretreatment burn was applied to all plots in the winter of 1980-1981 to establish similar times since the last burn. Season of burn treatments were randomly assigned to plots.

All plots are burned biennially.

**Sampling and Censusing of *Pityopsis graminifolia***

The current study is based on data collected between December 1990 and February 1993 from six plots within the sandhills. These plots included two replicates burned during two-week intervals in early January, late May, and late August of 1990 and 1992. Both replicate plots of each treatment were burned on the first day suitable for the combined use of strip headfires and a single backfire.

In mid-December of 1990, twenty-five points were randomly located within the central one-hectare area of each replicate plot. At each point, I located the closest shoot of *P. graminifolia*. If no shoots were visible nearby, I moved in a randomly-determined direction away from the point until the closest shoot was located. This shoot was designated as the center of a 0.125 m² circular subplot (diameter of 40 cm). All shoots within the subplot were permanently marked using numbered aluminum tags. Note that
this sampling method was used to obtain an unbiased and representative sample of the types of shoots present (e.g. bolting, rosettes, large, small, etc.), not to provide an accurate initial estimate of shoot density. Initial (Dec. 1990) average numbers of shoots/plot marked in May-burned, August-burned and January-burned plots were 240.5, 230.5, and 213.5, respectively (Table 2.1). These numbers changed over the course of the study, and thus sample sizes varied with time (Table 2.1).

Each subplot was censused once every 9 weeks from December 1990 to December 1992. At each census, the reproductive status of each shoot was determined using the categories: non-bolting, bolting, height, and the number of branches, buds, and achene heads/shoot. In December 1990, bud herbivory by white-tailed deer, *Odocoileus virginianus*, was assessed indirectly by counting the number of damaged branches of bolting shoots/plot. Following the 1992 fires, bud herbivory was monitored throughout the year, and thus, I was able to count directly the number of buds eaten on all bolting shoots in each plot.

Seed dispersal was first observed in December 1990. Seed germination occurred between December 1990 and March 1991, prior to the dry period in the spring. In March 1991, the number of seedlings (shoots with cotyledons) in each subplot was counted. Beginning in May 1991, all surviving seedlings were permanently marked with numbered aluminum tags and censused thereafter every 9 weeks until December
Table 2.1. The mean number of live shoots/plot observed in December 1990 and December 1992. Fires occurred in January, May, and August of 1990 and 1992. The numbers of shoots observed in December 1992 included both surviving shoots initially observed in December 1990 and all surviving shoots derived from buds since December 1990.

<table>
<thead>
<tr>
<th>Fire Season</th>
<th>December 1990</th>
<th>December 1992</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>213.5</td>
<td>352.0</td>
</tr>
<tr>
<td>May</td>
<td>240.5</td>
<td>647.0</td>
</tr>
<tr>
<td>August</td>
<td>230.5</td>
<td>432.5</td>
</tr>
</tbody>
</table>
In January and February 1993, all shoots (seed- and bud derived) that were first tagged in May 1991 were excavated and examined to insure that no bud-derived shoots had been misidentified as seedlings. In December 1992, I determined the proportion of surviving seedlings that bolted in each plot.

In December 1992, a single achene head was haphazardly sampled from an area adjacent to twenty of the twenty-five subplots in each replicate plot. The number of mature and undeveloped achenes in each achene head was counted. The average number of mature achenes/head was multiplied by the number of heads/bolting shoot to estimate shoot fecundity.

In January and February, 1993, at the end of the study, five subplots in each replicate plot were completely excavated to a depth of 15 cm to uncover underground connections among shoots. A clone was defined as the set of all physically interconnected shoots and as such represented minimum genet size. The average numbers of reproductive shoots/clone/subplot, and mature achenes/clone/subplot were determined for each replicate plot. The average number of mature achenes/head (see above) was multiplied by the number of heads/clone to estimate clone fecundity.

Statistical Analysis of Fire experiments

The effects of year (1990, 1992) and season of fire (January, May, and August fires) on per shoot bolting were analyzed using ANOVA with a split-plot arrangement of
treatments. Analyses were performed on logistic transformations of proportions of shoots that bolted (see Bessin et al. 1990). The whole plot effect was fire season and the split plot effect was year of fire. For whole plot effects, two planned a priori orthogonal contrasts included May vs. August burns and January vs. May + August burns. These effects were tested using the whole plot error term. For split plot effects, three a priori orthogonal contrasts included May 1990 vs. August 1990 burns, May 1992 vs. August 1992 burns, and the year x dormant-season vs. growing-season fire interaction. These effects were tested using the split plot error term. All the above contrasts had a critical type I error rate of 0.05.

The effects of fire season on herbivory of branches in 1990 and proportional herbivory of buds in 1992 were analyzed separately using one-way ANOVA. Data used were logistic transformations of proportions of branches or buds eaten. The effects of fire season on achene set were examined using one-way ANOVA. In this case, data used were ranks of proportions of achenes set per head, because the logistic transformation did not adequately reduce error heterogeneity. Replicate and sampling errors were pooled when justified by the criteria outlined by Bancroft and Han (1983). The effect of fire season on the number of achenes/bolting shoot and bolting shoot height were analyzed separately using one-way ANOVA. No transformations were
necessary in this case. The effect of fire season on log
(clone fecundity/subplot + 1) was examined with one-way
ANOVA using pooled replicate and sampling error terms with a
pooled df of 27. Because of substantial variation among
replicate plots (relative to subplot variation), error terms
could not be pooled when testing the effect of fire season
on the ranked number of reproductive shoots/clone/subplot.
on. Comparisons of means following significant one-way
ANOVARs were done with Scheffe's tests using the appropriate
term and with a critical type I error rate of 0.05. In
comparing mean ranked proportional seed set among
treatments, least significant difference tests (lsd's) were
done in addition to Scheffe's comparisons that showed no
significant difference, since lsd tests are less
conservative. Lsd tests were done using the means statement
and lsd option in PC SAS (SAS Institute Inc., Cary NC, USA,
1985). All other statistical analyses were done with
STATISTIX 1.0 (Analytical Software, St. Paul, MN, 1985) or
PC SAS when the number of levels/error term exceeded 20.

I examined short-term effects of May fires on seedling
survival. Densities of 1-1.5 year-old seedlings in burned
and unburned plots were compared before and 8 weeks after
fires in May 1992 fires using split-plot ANOVA. In this
analysis, the August-burned plots were used as an unburned
control because fires had not yet occurred. The presence of
fire in May represented the whole plot effect, and the pre
and post-fire censuses represented the two levels of the
split-plot effect. A significant fire x census interaction
was considered to indicate a significant short-term effect
of fire on seedling survival. Variability among fire plots
was too great to pool error terms; therefore, the fire x
census interaction was tested with the replicate error term.

I also examined the immediate effects of May fires vs.
August fires on seedling density using a separate split-plot
ANOVA. Seedling densities in May-burned plots before and
after May 1992 fires were compared to seedling densities in
August-burned plots before and after August 1992 fires. A
significant fire season x census interaction was considered
to indicate a significant short-term effect of fire season
on seedling survival. Again, variability among fire plots
was too great to pool error terms; therefore, the fire
season x census interaction was tested using the replicate
error term.

The association of fire season with bolting of
seedlings that survived until December 1992 was also
examined. A chi-square test of independence was run on the
number of seedlings in each treatment that had bolted by

**Experimental Design and Analysis of Clipping Experiments**

In late May 1992, I established four parallel 35 m
transects, containing 7 equidistant points haphazardly
located within the central one-hectare portion of two 2-3
hectare plots last burned in October 1990. At each point, the nearest shoot was designated as the center of a 0.25 m² clipping plot. Some plots were moved to avoid sampling points from other experiments. The set of all clipping plots within each large burn plot represented a block. Seven samples of each season of clipping (late May, mid August) x fertilization (water, aqueous plant growth solution) combination (7x2x2=28) were randomly assigned to clipping plots in each block. Thus, the design for this experiment was a randomized block design with a 2x2 factorial arrangement of treatments containing 56 experimental clipping plots. An unclipped, unfertilized control plot was established 2m from each unfertilized experimental plot.

All herbs and shrubs in each clipping plot were clipped to the ground using a combination of pruning and grass shears. All clippings and surface litter were removed. Clipping and litter removal were done to simulate the effects of canopy and litter removal by fire. Fertilized plots received 2 liters of aqueous (19 g/L) Miracle Gro plant growth solution containing an 18:24:16 ratio of N:P:K, along with trace amounts of various micronutrients (e.g. Fe, Cu, Mn, and Zn). Studies of the effects of fire on soil nutrients in slash pine forests have shown that fire most notably increased concentrations of phosphorus in the soil (Gholz and Fisher 1984, Gholz et al. 1985). In addition, Brewer and Platt (unpublished data) have found increased
tissue concentrations of potassium in *P. graminifolia* following fire. Therefore, a nutrient solution containing relatively high amounts of phosphorus and potassium was chosen for the current study. The unfertilized and control plots received 2 liters of water at the time of the clipping. An application of nutrient solution and water was repeated two weeks later.

Each clipping plot was censused three times over a seven week period. The proportion of bolting shoots within the central 0.125 m$^2$ portion of each 0.25 m$^2$ clipping plot was determined at each census. The effects of blocks, season of clipping, fertilization, and their interactions on ranked proportions at the final census were analyzed using three way ANOVA. In addition to measuring bolting proportions, the cumulative proportion of eaten buds was determined for each replicate plot that was clipped and fertilized. This was done to determine whether or not the timing of bolting could affect herbivory in years with little bolting overall (i.e. in fire free years). (The "clipping only" plots were excluded in this comparison due to the large number of plots in which no plant bolted). The effects of blocks, season of clipping + fertilization, and their interaction on ranked proportional bud herbivory at the final census were analyzed using two-way ANOVA. All analyses were done with STATISTIX 1.0.
RESULTS

Effects of Fire vs. No Fire on Bolting Dynamics

Flowering was induced by fire in *P. graminifolia*. Numbers of bolting shoots/m²/plot at each census from December 1990 to December 1992 are presented in Figure 2.1. Numbers of bolting shoots were greater in 1990 and 1992, years with fire, than in 1991, a year with no fire. In addition, during 1992, no significant changes in numbers of bolting shoots were observed in the May- and August-burned plots until the first census following fires in the plots. In January-burned plots, no significant changes in numbers of bolting shoots were observed until the second census following the fires.

Results from the clipping experiments showed that the removal of canopy and litter stimulated bolting in this species (Figure 2.2). No unclipped shoots bolted in this study, while 8 - 50% of the clipped shoots bolted. Floral induction of clipped shoots was stimulated further by the addition of mineral nutrients (Figure 2.2). Shoots that were clipped and fertilized were more likely to bolt than shoots that were clipped but unfertilized (43.34% vs. 18.62%, respectively). As a result, the main effect of fertilization on floral induction of clipped shoots was highly significant (p<0.0001, Table 2.2).
Figure 2.1. Mean number of bolting shoots/m²/plot ± SE from December 1990 to December 1992. Triangles below the abscissa represent the timing of January, May, and August fires in 1992.
Figure 2.2. The effects of season of clipping and fertilization on mean proportions of shoots that bolted/clipping plot. May-clipped plots were clipped and fertilized in late (24-26) May 1992 and finally censused in mid (13-14) July 1992. August-clipped plots were clipped and fertilized in mid (12-13) August 1992 and finally censused in early (2-3) October 1992. Unclipped plots were unfertilized an were censused from May to July and August to October. Statistical analyses were performed on ranked proportions.
Table 2.2. ANOVA table for RBD with 2x2 factorial arrangement of treatments testing the effects of blocks, season of clipping, and fertilization on ranks of proportions of shoots that bolted. Block interactions were not significant and were pooled with sampling error. Ranks were used because other transformations (e.g. logistic) failed to sufficiently reduce error heterogeneity. Asterisks (*) denote statistical significance.

Dependent Variable: Ranked Proportional Bolting

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block-B</td>
<td>1</td>
<td>412.57</td>
<td>2.59</td>
<td>0.1137</td>
</tr>
<tr>
<td>Season of Clipping-C</td>
<td>1</td>
<td>2418.30</td>
<td>15.18</td>
<td>0.0003 *</td>
</tr>
<tr>
<td>Fertilization-F</td>
<td>1</td>
<td>3301.80</td>
<td>20.73</td>
<td>&lt;0.0001 *</td>
</tr>
<tr>
<td>C x F</td>
<td>1</td>
<td>108.64</td>
<td>0.68</td>
<td>0.4128</td>
</tr>
<tr>
<td>Error</td>
<td>51</td>
<td>159.31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>55</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Effects of Fire Season on Bolting Dynamics

Fire season influenced the density and proportion of shoots that bolted. In December 1992, the number of bolting shoots was greatest in May-burned plots \([72.48 \pm 9.44\text{ (SE)/m}^2]\), intermediate in August-burned plots \([22.56 \pm 2.08\text{ (SE)/m}^2]\), and lowest in January plots \([3.36 \pm 0.48\text{ (SE)/m}^2]\) (Figure 2.1). Fire season influenced the proportions of shoots that bolted during this study, resulting in a significant whole plot effect of fire season \((p=0.031; \text{ Table 2.3a})\). The mean logistically-transformed proportion of shoots that bolted following growing-season fires (May and August fires) was greater than that following January fires \((0.32 \text{ vs. } 0.07, \text{ respectively}; \text{ contrast SS}=10.18, F_{1,3}=23.58, p=0.0146, \text{ Figure 2.3})\). The whole plot contrast of May vs. August fires on the proportion of shoots that bolted was not significant \((\text{means }= 0.38 \text{ vs. } 0.25, \text{ respectively}; \text{ contrast SS}=0.8339, F_{1,3}=1.93, p=0.2891, \text{ Figure 2.3})\).

The effectiveness of removal of canopy and litter as an inductive cue depended on the time of year that it occurred (Figure 2.2). The mean proportions of shoots that bolted following May and August clippings were 0.40 and 0.22, respectively. The main effect of season of clipping on ranks of proportions of shoots that bolted was highly significant \((p=0.0003; \text{ Table 2.2})\). There were no significant interactions between season of clipping and fertilization on floral induction \((p=0.4128; \text{ Table 2.2})\).
Table 2.3. Split-plot ANOVA table of the effects of fire season and year of fire on logistic transformations of proportions of shoots that bolted.

Dependent Variable: Logistically-Transformed Proportion of Bolting Shoots

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Fire Season</td>
<td>2</td>
<td>5.5091</td>
<td>25.51</td>
<td>0.0131</td>
</tr>
<tr>
<td>Rep(Fire season)</td>
<td>3</td>
<td>0.2160</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Year</td>
<td>1</td>
<td>2.3991</td>
<td>57.57</td>
<td>0.0047</td>
</tr>
<tr>
<td>Fire Season x Year</td>
<td>2</td>
<td>0.3403</td>
<td>8.17</td>
<td>0.0611</td>
</tr>
<tr>
<td>Rep x Year(Fire Season)</td>
<td>3</td>
<td>0.0417</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.3. The effect of fire season on mean proportions of shoots that bolted/plot in December 1990 and December 1992. Fires were prescribed during 1990 and 1992. Different upper case and lower case letters represent mean differences in 1990 and 1992, respectively. Statistics were performed on logistically-transformed proportions.
Response of Bolting Dynamics to Fires in Different Years

The effects of fire on floral induction differed between years. Despite the fact that the absolute number of bolting shoots was greater in 1992 than in 1990 (Figure 2.1), the proportion of shoots that bolted was significantly greater in 1990 than in 1992 (p=0.0047; Table 2.3a, Figure 2.3). The total number of shoots was about 1.5-3 times greater in December 1992 than in December 1990 (Table 2.1).

The effects of fire season on floral induction differed between years. The interaction between fire season and year of fire on logistically-transformed proportions of shoots that bolted approached statistical significance (p=0.0611; Table 2.3b), but the power of the test was low. Differences in the proportions of shoots that bolted following May vs. August fires were not significant in 1990 (contrast SS=0.0828, F_1,3=1.99, p=0.253, Figure 2.3), but were significant in 1992 (contrast SS=1.107, F_1,3=24.17, p=0.016, Figure 2.3). The differences among years in the effect of season of fire was largely the result of between-year variation in the proportion of shoots that bolted following August fires (Figure 2.3). The interaction between year and dormant vs. growing-season fire was significant (contrast SS=0.4242, F_1,3=10.18, p=0.050, Figure 2.3). Growing-season fires (particularly August fires) exhibited greater year to year variation in bolting than did dormant-season fires.
Effects of Fire Season and Spatial Patterns of Bolting on Bud and Branch Herbivory

Herbivory by deer was strongly influenced by fire season. Plants burned in late May and late August experienced much lower rates of herbivory than plants burned in January, and this result was consistent across fire years (Figure 2.4). Rates of branch herbivory/plot in December 1990 and cumulative bud herbivory/plot in December 1992 differed with respect to fire season ($F_{2,3}=21.42$, $F_{2,3}=56.85$, $p=0.0167$ and $0.0041$; Figure 2.4). Differences in herbivory following May vs. August fires were not significant in either year (Figure 2.4).

The absolute frequency of bud herbivory in January 1992-burned plots increased between May and October and declined after October (Figure 2.5). The relative rate of bud herbivory (i.e. the proportion of buds eaten) was greatest between May and August and declined between August and October. This resulted from rates of bud production between August and October that were greater than absolute rates of bud herbivory between August and October (Figure 2.5).

The incidence of bud herbivory was related to the density and/or spatial pattern of bolting shoots in *P. graminifolia*. Clipping and fire experiments had similar effects on the timing of bolting but different effects on the density and/or spatial pattern of bolting shoots. Seven
Figure 2.4. (a) The effect of fire season on mean proportions of branches damaged by herbivores in December 1990. (b) The effect of fire season on mean cumulative proportions of buds eaten by December 1992. Different letters represent significant mean differences. ANOVAs and means comparisons were done on logistically-transformed proportions.
Figure 2.5. Seasonal patterns of mean cumulative total bud abundance ± SE and mean cumulative total bud herbivory ± SE in plots burned in January 1992.
weeks after fire and clipping, herbivory was much greater in small (0.25 m²) plots that were clipped and fertilized in May and August, but embedded in a matrix of largely non-bolting shoots (mean proportions = 0.272 and 0.088 for May and August clippings, respectively) than in large (2-3 ha) plots burned in May and August (mean proportion for both fires = 0.004) \( (t_{df=2}=6.01, p=0.026 \text{ for May}; t_{df=2}=9.33, p=0.011 \text{ for August}). \) In addition, the pattern of bolting in clipped plots interacted with the seasonal timing of bud production to influence herbivory. In contrast to the effects of May and August fires (Figure 2.4b), the mean proportion of buds eaten per clipped plot was significantly greater following clipping + fertilization in May (0.272) than following the same treatment in August (0.088) \( (p=0.0477, \text{ Table 2.4}). \)

**Effects of Fire Season on Achene Set and Shoot and Clone Fecundity**

Fire season had a small, but statistically significant, effect on achene set as measured by the ranked proportion of achenes set/head \( (p=0.033, F_{2,117}=3.51). \) August fires resulted in significantly greater proportions of achenes set/head than did either May fires or January fires using least significant difference tests (0.44 vs. 0.38 vs. 0.38). There was no significant difference between the effects of January and May fires on proportions of achenes set (0.38 vs. 0.38). Absolute numbers of achenes set/head were
Table 2.4. ANOVA table of Randomized Block Design testing the effect of season of clipping + fertilization on ranked cumulative proportional bud herbivory in 1992. The B x S interaction was not significant and was pooled with sampling error. Asterisk denotes statistical significance.

Dependent Variable: Ranked Cumulative Proportional Bud Herbivory

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block-B</td>
<td>1</td>
<td>86.71</td>
<td>2.07</td>
<td>0.1641</td>
</tr>
<tr>
<td>Season of Clip + Fert-S</td>
<td>1</td>
<td>183.74</td>
<td>4.38</td>
<td>0.0477 *</td>
</tr>
<tr>
<td>Error</td>
<td>23</td>
<td>41.98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Missing Values</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
15.83±0.19(SE), 16.7±0.11(SE), and 18.45±0.06(SE) following January, May, and August fires, respectively.

Shoot fecundity (measured as the number of achenes/bolting shoot) mostly reflected the number of achene heads/bolting shoot. The number of achene heads/bolting shoot was a function of both shoot height and herbivory of buds on bolting shoots. As a result, the number of achenes/bolting shoot was a function of both shoot height and herbivory of buds on bolting shoots (Figure 2.6). Fire season had statistically significant effects on bolting shoot fecundity ($F_{2,3}=18.31$, $p=0.02$, Figure 2.6). Bolting shoot height was significantly affected by fire season ($F_{2,3}=14.43$, $p=0.029$, Figure 2.6). Bolting shoots following May fires had higher fecundity than those following August fires because of significant differences in bolting shoot height (Figure 2.6). In contrast, May-burned shoots were not significantly taller than January-burned shoots but still were more fecund because of differences in herbivory (Figure 2.6, Figure 2.4b).

Clone fecundity largely reflected shoot fecundity and, to a lesser extent, the number of bolting shoots/clone (Figures 2.6 and 2.7). Fire season had statistically significant effects on log-transformed clone fecundity ($F_{2,27}=16.62$, $p<0.0001$, Figure 2.7). Fire season also influenced the number of bolting shoots/clone, but sample size was small, and the effect of fire season on the ranked
Figure 2.6. The effect of fire season on the number of achenes per bolting shoot and bolting shoot height. There are two observations per treatment. Different upper case letters represent significant mean differences in shoot fecundity. Different lower case letters represent significant mean differences in shoot height.
Figure 2.7. The effect of fire season on clone fecundity and the number of reproductive shoots/clone. The effect of fire regime on the log (achenes/clone subplot + 1) has 10 observations/treatment as a result of pooling. Different letters represent significant mean differences. The effect of fire regime on the ranked number of reproductive shoots/clone has 2 observations per treatment. It was not significant, so contrasts were not done.
number of bolting shoots/clone was not statistically significant ($F_{2,3}=3.72$, $p=0.1754$).

**Effects of Fire on Seedling Dynamics**

Most seedling mortality occurred between the initial census in March 1991 and August 1991 (Figure 2.8). Initial seedling density was highest in May-burned plots [$97.28\pm3.84$(SE)/m$^2$], intermediate in August-burned plots [$56.64\pm15.04$(SE)/m$^2$], and lowest in January-burned plots [$4.80\pm2.77$(SE)/m$^2$] (Figure 2.8). All seedlings in the January-burned plots died before January 1992 fires. Final seedling densities were about four times higher in the May-burned plots than in the August-burned plots [$5.92\pm1.54$(SE)/m$^2$ vs. $1.28\pm0.32$(SE)/m$^2$, respectively] (Figure 2.8). The proportion of seedling cohorts that had survived till December 1992 (final seedling density/initial seedling density) was 0 for January-burned plots, 0.0227 for August-burned plots, and 0.0605 for May-burned plots.

Fire season appeared to have little immediate effect on seedling mortality in 1992. The difference in seedling density before and after May 1992 fires was not significantly different from that in the unburned plots (i.e. there was no significant fire x census interaction). Sample sizes were small, however, because replicate and sample error terms could not be pooled ($F_{2,2}=7.11$, $p=0.1233$). The difference in seedling density before and after May 1992 fires was also not significantly different
Figure 2.8. The number of seedlings/m²/plot ± SE from March 1991 to December 1992. Vertical dashed lines represent the timing of fires in 1992.
from that before and after August 1992 fires (i.e. there was no significant fire season x census interaction, $F_{2,2}=3.76, p=0.21$). Altogether, only 39 of the 992 seedlings initially censused in March 1991 survived until December 1992. Of these 39 survivors, six bolted, all of which were located in May-burned plots. Because of high seedling mortality, sample sizes were likely too small for a chi-square test of independence of fire season and bolting to result in significance ($X^2_{df=1}=1.83$).

**DISCUSSION**

**Proximate Causes of Fire Effects on Floral Induction**

Removal of canopy and litter induced flowering in *P. graminifolia*. Previous studies also have found significant effects of canopy and litter removal on flowering in other pyrogenic habitats (Old 1969, Hulbert 1988, see ref. in Gill 1981). The effectiveness of canopy and litter removal as an inducer of flowering in *P. graminifolia* depended on the season during which it occurred. I suggest that fire might interact with seasonal rhythms and/or soil fertility to influence floral induction in this species. In 1990 and 1992, floral induction was greater following fires occurring during the spring and summer (e.g. May and August), when days were longer. Furthermore, in 1992, floral induction was greater following May fires and clippings than August fires and clippings. Daylengths are slightly greater
in late May than in late August. However, two lines of evidence suggest that other factors (e.g. soil fertility) may occasionally obscure subtle effects of photoperiodism on floral induction. First, May fires did not stimulate greater floral induction than did August fires in 1990. Second, floral induction was equally limited by soil fertility following removal of canopy and litter in both May and August in 1992. Further research is needed to determine how fire season influences soil fertility and how fertility varies among years.

**Fire Season and Herbivory**

The experimental results presented here on bud/branch herbivory show that the occurrence of fires in May and August, but not January, reduced the rates of herbivory in *P. graminifolia*. This result was consistent among years of fire. In addition, there was no evidence of effective compensation for buds lost to herbivores in January-burned plots, although buds initiated later in the growing season in both January-burned and unburned plots were more likely to escape herbivory. Thus, the occurrence of fire and the season in which fire occurs interacted strongly with the feeding behavior of large mobile herbivores (white-tailed deer). I hypothesize that the greater abundance of buds within plots burned in May and August may have satiated deer (see also Janzen 1978, Augspurger 1981, O'Dowd and Gill 1984, Whelan 1986); however, alternative hypotheses, such as
the greater availability of alternative food sources following May and August fires, cannot be excluded.

Fire Season and Herbivory Effects on Clone Fecundity and Seedling Survival

Fire season affected clone fecundities in this north Florida population of *P. graminifolia* primarily by influencing shoot growth, bud herbivory, and floral induction. At the end of the 1992 growing season, clones burned in May had the highest fecundities because of low herbivory rates, the production of tall bolting stems, and high rates of floral induction. Although clones burned in August also had low rates of herbivory, slightly higher rates of achene set, and the shortest duration of flowering, which might have reduced pollinator limitation of achene set (see Augspurger 1981), clone fecundities were much lower than those following May fires. The decreased length of time between August fires and the end of the growing season probably constrained the heights of bolting shoots. January-burned clones had even lower fecundities than August-burned clones because of high rates of herbivory and low rates of floral induction.

The effects of fire on clone fecundity in this north Florida population contrast sharply with those in central and south Florida populations of this species (Hartnett 1987, E. Menges, pers. comm.). In a central Florida population of *P. graminifolia*, floral induction was not
dependent upon fire (Hartnett pers. comm.). May fires reduced shoot size but increased ramet survival within clones, and thus had little net effect on clone fecundity (Hartnett 1987). The cause of such geographic variation in response to fire is unknown but could be related to habitat differences (e.g. soil fertility) among sites (Brewer and Platt, unpublished data).

To my knowledge, no studies have demonstrated a positive effect of growing-season fires on seedling establishment of pyrogenic clonal herbs in pine savannas. And yet, such studies are crucial to any putative evolutionary significance of fire-induced flowering. Low rates of seedling survival and establishment of *P. graminifolia* in other sandhill communities (Hartnett 1987, Kaczor and Hartnett 1990) have resulted in seedling establishment of *P. graminifolia* being hypothesized to require small scale disturbances such as the burrowing mounds of gopher tortoises. Variation in the fire regime was hypothesized to have little influence on seedling establishment and survival (Hartnett 1987, Kaczor and Hartnett 1990). Results from my study do not support the latter hypothesis. Fire season influenced initial seedling densities. Although seedling mortality was 70 - 80% five months after emergence in all fire treatment plots, seedling dynamics varied in response to fire season at the north Florida site. Differences among fire treatments in the
density of two-year-old genets largely reflected the initial differences in seedling density. Growing-season-burned plots had the highest rates of seedling emergence, and only those seedlings in growing-season-burned plots survived to two years of age. Further, only seedlings in the May-burned plots reached reproductive maturity following 1992 fires. It would appear that mass reproduction and subsequent massive seedling emergence overrode, to a small extent, the inherent environmental vagaries associated with seedling establishment during the course of my study in north Florida.

In addition to fire-related massive seedling emergence, there are two observations that indicate an important role for fire in promoting seedling establishment at my study site. First, most seedlings did not appear to increase substantially in size (aboveground at least) between the time of their emergence and the occurrence of 1992 fires. Yet, some juveniles that were alive at the time of the 1992 fires not only survived the fires, but grew substantially and even flowered during the growing season after May fires. Thus, May fires may stimulate growth and reproduction of juvenile recruits of _P. graminifolia_, thereby promoting successful establishment of new genets. Second, while fire generally does not alter the seedbed in longleaf pine savannas to the extent that it does in some other pyrogenic habitats (e.g. Australian sclerophyll vegetation; see O'Dowd
and Gill 1984), it may alter small areas of the seedbed significantly by killing established plants in a few localized "hot spots" associated with downed trees and areas of dense needle cast (Platt et al. 1991, Streng et al. 1993). In this north Florida population of P. graminifolia, small disturbed areas resulting from hot spots in normally low-intensity fires may provide more reliable areas of seedling establishment than mounds adjacent to occupied gopher tortoise burrows because seedlings around burrows would likely be buried by the repeated burrowing of the tortoises.

The Evolution of Mass Reproduction in Clonal Perennial Herbs

More attention has been given to the phenomenon of mass reproduction in trees (Harper and White 1974, Janzen 1978, Augspurger 1981, Waller 1979, Silvertown 1980) than in perennial herbs. A demographic model of periodic, mass reproduction that employs a cost-benefit analysis of the effect periodic and annual reproduction have on the intrinsic rate of population increase was developed by Waller (1979). According to the model, mass reproduction should be favored when the benefit of periodic reproduction exceeds both direct and indirect costs of foregoing reproduction between years of mass reproduction. Waller therefore predicted that mass reproduction should evolve in life history types with characteristically high adult survival and low population growth rates (e.g. many long
lived trees). These predictions may apply equally well to many long-lived clonal perennial herbs. Clonal growth can result in extreme longevity in perennial herbs (Cook 1985), and low survival rates of juveniles may result in slow rates of population growth (Cook 1985). Therefore, periodic, mass reproduction might well also evolve in long lived, clonal perennial herbs.

I believe that *P. graminifolia* exhibits a life history and phenology required for the evolution of fire-stimulated mass reproduction. It is a clonal perennial with low adult and high juvenile mortality rates. By foregoing reproduction until immediately following a lightning fire (a predictable cue that shading and perhaps nutrient stresses are reduced), it may reduce the energetic and nutrient costs of sexual reproduction and thus reduce the risk of adult mortality even further. In addition, I have demonstrated that May fires result in mass reproduction, reduced bud herbivory, and increased clone fecundity. This results in the production of a large number of seedlings, a small fraction of which survive to reproductive maturity. I suggest that the various risks associated with sexual reproduction (e.g. resource costs, herbivory, seedling mortality) could be additive selection pressures on flowering behavior in *P. graminifolia* (see Augspurger 1981). I hypothesize that fire during the peak lightning-fire season (i.e. May-June) may play an important role in the life history evolution of *P.*
graminifolia by reducing the costs of sexual reproduction and by increasing the likelihood of successful establishment of new genets.
CHAPTER 3 - EFFECTS OF FIRE SEASON AND SOIL FERTILITY
ON CLONAL GROWTH
INTRODUCTION

The study of clonal growth is crucial to understanding the responses of many perennial herbs to chronic, sub-lethal disturbances. Over the past decade, studies have examined the effects of defoliation by fire (Hartnett 1987) and by herbivores (McNaughton et al. 1983, McNaughton 1984, Coughenour et al. 1985a,b, Jeffries 1988, Hartnett 1989, Doak 1991) on clonal growth in a variety of perennial herbs. Following defoliation of clonal plants by fire or grazers, regrowth of genets is influenced both by regrowth of defoliated ramets and/or by rates of tillering and vegetative spread. Results from grazing and clipping studies have shown that the direction of regrowth of genets following defoliation (i.e. regrowth of defoliated ramets vs. initiation of new ramets) is important, because it may reveal the nature of competitive interactions (i.e. aboveground vs. belowground) (Coughenour et al. 1985b, Milchunas et al. 1988; Turkington et al. 1993). However, effects of chronic, low-intensity fire on the direction of regrowth of genets have not been extensively studied.

Effects of various post-fire environmental conditions on rates of tillering and vegetative spread need to be examined to understand clonal growth responses to fire. Such conditions may include altered light levels (Deregibus et al. 1985), removal of allelopathic compounds bound in litter (Christensen 1977) and changes in soil fertility (Coughenour
et al. 1985b). In pyrogenic grasslands and savannas, fire removes the herbaceous canopy and litter, and in some cases, increases soil fertility (Old 1969, Hulbert 1988). While nutrient addition and the removal of canopy and litter have been shown to increase net primary productivity in pyrogenic grasslands and savannas (Old 1969, Christensen 1977, Hulbert 1988), little is known about how they affect rates of tillering and vegetative spread in individual genets.

The responses of clonal plants to fire may also correspond to the likelihood of being burned by lightning fires at different times of the year. The frequency of lightning strikes in longleaf pine savannas is high from April to September (Chen and Gerber 1990). Fires also occur frequently in pine savannas from October to March, but are generally started by man, and are a more recent phenomenon than lightning fires (Platt et al. 1988a, Frost 1993). Consequently, the likelihood that plants will be burned by lightning fires is greater from April-September than from October-March. The likelihood that plants will be burned by lightning fires is influenced not only by the frequency of lightning strikes but by rainfall amounts (Chen and Gerber 1990). Longleaf pine savannas are more likely to burn in May than in August (Komarek 1964) as a result of lower rainfall amounts in May (Chen and Gerber 1990) and hence larger areas being burned by single fires. The extent to which rates of tillering and vegetative spread by groundcover herbs
correspond to seasonal variation in expected fire frequency is not known.

In this study I experimentally manipulated two factors that potentially limit post-fire clonal growth of a dominant forb, *Pityopsis graminifolia*, in longleaf pine sandhills in north Florida. These factors included fire season and the addition of mineral nutrients following the removal of canopy and litter. The objectives of this study were 1) to determine the effects of fire season on the direction of regrowth of clones by examining the size and demography of shoots and ramets and the size and structure of clones, and 2) to examine shoot density responses to canopy/litter removal and fertilization and the season during which this treatment occurred.

**CLONAL MORPHOLOGY OF *PITYOPSIS GRAMINIFOLIA***

*Pityopsis graminifolia* (Michx.) Nutt. is a rhizomatous, perennial composite, common throughout the coastal plain of the southeastern United States (Semple and Bowers 1985). Its clonal morphology is analogous to that of many rhizomatous grasses (e.g. little bluestem, *Schizachyrium scoparium*; Brewer, pers. obs.). A clone of *P. graminifolia* was defined as the set of all physically interconnected ramets and as such represented minimum genet size. A ramet (Figure 3.1) was considered equivalent to a "crown" in rhizomatous grasses, that is, a single rhizome plus all shoots derived
from buds on that rhizome (also see Coughenour et al. 1985b). Shoots were defined as branches produced either on the terminal end of rhizomes or emerging from axillary buds on older portions of perennial rhizomes (Figure 3.1).

Prior to bolting, the apical shoot bud is at or below the soil surface, well protected from fire by a compact basal arrangement of grass-like leaves. Bolting occurs most frequently following fires during the peak lightning fire season (Streng et al., 1993, Chapter 2). Following seed set, bolting shoots die. But before dying, one to several basal offshoots may arise from axillary buds on the same rhizome (Figure 3.1). Thus, while shoots are monocarpic, ramets are polycarpic.

STUDY AREA

This study was conducted in a second growth sandhill community in the St. Marks Wildlife Refuge, Wakulla County, Florida. Sandhills are open, xeric pine forests that overlie deep Plio-Pleistocene-era sands (Platt et al. 1988a, Myers 1990). The overstory is dominated by longleaf pine, Pinus palustris. The understory contains a diverse mixture of perennial grasses (e.g., Aristida beyrichiana, Schizachyrium scoparium, Andropogon spp., and Dicanthelium spp.), forbs (e.g. Pityopsis graminifolia, Liatris tenuifolius, Galactia floridana, and Elephantopus elatus), and shrubs (e.g.
Figure 3.1. Diagram of two connected ramets of *Pityopsis graminifolia*. (P) - Parent ramet, (D) - Daughter ramet, (R) - Rhizome (part of daughter ramet), (Tp) - Shoot (bolted) derived from terminal bud of the parental ramet, (Ap) - Shoot (rosette) derived from an axillary bud at the base of Tp on the parental ramet.
Vaccinium myrsinites, Quercus minima, Q. laevis, and Q. incana) in a low groundcover (Streng et al. 1993).

Sandhill communities depend upon frequent (every 1-5 yr), low-intensity surface fires that prevent the growth of hardwood trees into the canopy (Chapman 1932a,b, Christensen 1981, Platt et al. 1988b, Platt et al. 1991). In addition, while these fires typically kill aboveground parts of herbaceous perennials, survival and resprouting is extensive (Platt et al. 1988a). Lightning-started fires typically occurred during the growing season (April to October) prior to European settlement (Chapman 1932a,b, Platt et al. 1991). European settlers altered the natural fire regime by burning pine forests during the winter, between growing seasons (Platt et al. 1988a). Over the past 35 years, prescribed burning by the refuge staff has occurred 2-3 times a decade, mostly during the winter (Platt et al. 1988a).

METHODS

Experimental Design of Fire Experiments

Fire experiments for the current study were subsets of a larger long-term study of the effects of fire season on vegetation dynamics in longleaf pine savannas initiated in 1980 by W.J. Platt. The design of the long-term study (Platt et al. 1988a) consisted of two replicate plots of eight different seasons of burn within both sandhill and flatwoods habitats. Replicate plots, 2-5 hectares each, were selected
based on similar densities of longleaf pine, wiregrass, and Quercus sp. (Platt et al. 1988a). Large oaks that had entered the overstory as a result of fire suppression after logging earlier in the century were cut at the base of the tree during the winter of 1980-1981. Most trees resprouted, forming shrubs in the ground cover. A pretreatment burn was applied to all plots in the winter of 1980-1981 to establish similar times since the last burn. The season of burn treatments were randomly assigned to plots. All plots were burned biennially during the course of the current study.

**Sampling and Censusing of Pityopsis graminifolia**

The current study was based on data collected between December 1990 and February 1993 from six plots within the sandhills. These plots included two replicates burned during two-week intervals in early January, late May, and late August of 1990 and 1992. Both replicate plots of each treatment were burned on the first day suitable for the combined use of strip headfires and a single backfire. The general null hypothesis of the fire experiments was that variation in fire season has no effect on clonal dynamics in P. graminifolia.

In mid-December of 1990, twenty-five points were randomly located within the central one-hectare area of each replicate plot. At each point, I located the closest shoot of P. graminifolia. If no shoots were visible nearby, I moved in a randomly-determined direction away from the point
until the closest shoot was located. This shoot was designated as the center of a 0.125 m² circular subplot (diameter of 40 cm). All shoots within the subplot were permanently marked using numbered aluminum tags. Note that this sampling method was used to obtain an unbiased and representative sample of the types of shoots present (e.g. bolting, rosettes, large, small, etc.), not to provide an accurate initial estimate of shoot density. I was interested in how fire season affected shoot demography over the course of two years.

Each subplot was censused once every 9 weeks from December 1990 to December 1992. At each census, new shoots were permanently tagged. When senescent shoots gave rise to new daughter shoots derived from basal axillary buds, tags of parent senescent shoots were moved to the new daughter shoots. Otherwise, tags of senescent shoots were kept in place throughout. Dynamics of seedlings that emerged during this study have been described in Chapter 1 and are not included in the present study.

In January and February, 1993, five subplots in each replicate plot were completely excavated to a depth of 15 cm to uncover underground connections among shoots and ramets within clones. Tag identification combined with excavation of clones enabled us to age all shoots and rhizomes initiated between December 1990 and January-February 1993 in all plots. All shoots and rhizomes in each excavated subplot
were assigned to one of four cohorts based on year of initiation: prior to 1991, during 1991, during 1992, and during 1993. The average numbers of shoots/clone, rhizomes/clone, and shoots/rhizome were determined for each excavated subplot. All clones were separated into their constituent shoots and oven-dried at 40°C to a constant weight. Average shoot weight, average ramet weight, and average clone weight were determined for each excavated subplot.

Statistical Analysis of Fire Experiments

The effect of fire season on per shoot rate of increase in shoot density during two consecutive time intervals following fire in 1992 was tested using split-plot ANOVA. The whole plot effect was fire season, and the split plot effect was interval. Interval 1 was from 1-2 weeks before to 6-7 weeks after the fire and interval 2 was from 6-7 weeks after the fire to 15-16 weeks after the fire. Data used were log transforms of $N_1/N_0$ for each interval, where $N_0$ is the number of shoots/subplot counted during the initial census of the interval, and $N_1$ is the density of shoots/subplot counted during the subsequent census of the interval.

Replicate and sampling error terms were pooled based on criteria outlined by Bancroft and Han (1983). I tested replicate error terms against sampling error terms for both the whole plot and split plot. The probability of a greater
F was 0.48 for the whole plot test and 0.47 for the split plot test. Accordingly, all subplots within both replicate burn plots/fire season were treated as originating from the same population. As a result, I used the pooled error nested within fire season with 147 df to test the whole plot effect of fire season. The split plot error term was the pooled error x interval interaction nested within fire season with 147 df.

The whole plot null hypothesis was that fire season had no effect on the per shoot rate of increase in shoot density during two census intervals following fire. Two planned orthogonal linear contrasts included January vs. May and August fires and May vs. August fires.

The null hypothesis tested in the split plot was that the effect of fire season on per shoot rate of increase in shoot density did not change between the two census intervals. A significant fire season x interval interaction was considered a rejection of the null hypothesis. In addition, two planned orthogonal contrasts included January vs. May + August fires for interval 1 and May vs. August fires for interval 1. The purpose of these contrasts was to determine whether fire season had an immediate (during interval 1) effect on the per shoot rate of increase in density. The contrasts were tested using the split plot error term. Statistical analyses were done using the ANOVA procedure in PC SAS (SAS Institute, Cary, NC, USA, 1985).
Contrasts were done by hand. Probabilities of greater than or equal F values associated with contrasts were calculated by STATISTIX 1.0 (Analytical Software, St. Paul, MN, 1985).

The association between fire season and the age structure of shoots and rhizomes was examined with subdivided log-likelihood ratio (G) tests of independence. Log-likelihood ratios were subdivided to compare the relative contributions of between vs. within fire season effects to the total log-likelihood ratio. Large between relative to within-fire season G values indicate a substantial interaction between fire season and age structure. These tests were performed by hand as described by Sokal and Rohlf (1981) using a QUATTRO spreadsheet (Borland International, Scotts Valley, CA, 1987). Probabilities of greater or equal 2G (Chi-square) values were calculated by STATISTIX.

To analyze the effects of fire season on clone structure, I used a non-parametric multivariate multi-sample comparison test – MRPP (Multi-Response Permutation Procedures, see Mielke, Berry, and Johnson, 1976; Zimmerman, Goetz, and Mielke, 1985; Biondini, Mielke, and Berry, 1988). Significant heterogeneity of variance-covariance matrices among treatments (as determined by a chi-square approximation test using the DISCRIM procedure in PC SAS) precluded the use of one-way MANOVA. Because of the small number of replicates, it was desirable to pool replicate and
sample error terms, if possible, based on criteria outlined in Bancroft and Han (1983). Therefore, before running MRPP, univariate parametric tests of replicate errors were run for each dependent variable using nested ANOVA. Data used were ranks of the following dependent variables: mean number of shoots/clone/subplot, mean number of rhizomes/clone/subplot, mean number of shoots/rhizome/subplot, mean shoot weight/subplot, mean ramet weight/subplot, and mean clone weight/subplot. Variances were homogeneous among fire seasons in each univariate case. Furthermore, with the exception of mean number of shoots/rhizome/subplot, replicate errors and sampling errors could be pooled. Thus, MRPP was run using untransformed data with 5 dependent variables, 3 treatment groups and 10 observations per treatment group. In this case, MRPP was analogous to a one way MANOVA using pooled replicate and sampling error terms to test the overall effect of fire season on clone structure.

MRPP calculates average Euclidean distances among observations within each group (fire season). It then calculates an observed weighted average (Delta) of the mean euclidean distances for all groups. A small value of Delta indicates a tendency for clustering of observations within groups. Multiple random permutations are then calculated to determine whether Delta is unusually small (Biondini et al. 1988).
To present the relationship between fire season and clone structure graphically, an ordination of results obtained from canonical discriminant analysis (CANDISC procedure in PC SAS) was done. However, statements of statistical significance associated with the model were not included because of non-homogeneous variance-covariance matrices among fire season treatments. Results from canonical discriminant analysis were based on untransformed values of all dependent variables except mean number of shoots/rhizome/subplot in each of the three fire seasons. The ordination was based on the first two canonical axes. Ordination scores for each dependent variable were calculated as follows:

\[
    s_{ij} = r_{ij}x_j
\]

where, \( s_{ij} \) is the ordination score of dependent variable \( i \) for canonical axis \( j \); \( r_{ij} \) is the Pearson correlation coefficient for the linear relationship between dependent variable \( i \) and canonical axis \( j \); and \( x_j \) is the characteristic root or eigenvalue for canonical axis (eigenvector) \( j \). Although not part of the analysis, a score for mean number of shoots/rhizome/subplot was calculated and superimposed upon the ordination diagram by running a separate simple correlation of this variable with each canonical axis and then multiplying it by \( x_j \). In addition,
centroids of subplots burned in May, August, and January were superimposed upon the ordination of dependent variables.

Interpretation of such an ordination diagram requires recognition of several features. First, an acute angle between two vectors indicates that the two corresponding variables are responding similarly to fire season, whereas an obtuse angle indicates that the two variables are responding to fire season in opposite ways. A right angle indicates that the two variables are responding to fire season independently. Second, the length of each vector is proportional to the total amount of canonical variation associated with its corresponding variable. Third, the direction of each vector in relation to the location of each fire season centroid indicates the degree of association between the corresponding variable and that particular fire season.

**Experimental Design and Analysis of Clipping Experiments**

In late May 1992, I established four parallel haphazardly located 35 m transects within the central 1-ha portion of two 2-3 ha plots last burned in October 1990. Each transect contained 7 equidistant points. At each point, the nearest shoot was designated as the center of a $0.25 \text{ m}^2$ clipping plot. Some plots were moved to avoid sampling points of other experiments. The set of all clipping plots within each large plot represented a block. Seven samples of
each season of clipping (late May, mid August) x fertilization (water, aqueous plant growth solution) combination (7x2x2=28) were randomly assigned to clipping plots in each block. Thus, the design for this experiment was a randomized block design with a 2x2 factorial arrangement of treatments containing 56 experimental clipping plots. An unclipped, unfertilized control plot was established 2m from each unfertilized experimental clipping plot.

All herbs and shrubs in each clipping plot were clipped to the ground using a combination of pruning and grass shears. All clippings and litter were removed. Clipping and litter removal were done to simulate the effect of canopy and litter removal by fire. Fertilized plots received 2 L of aqueous (19 g/L) Miracle Gro plant growth solution containing an 18:24:16 ratio of N:P:K, along with trace amounts of various micronutrients (e.g. Fe, Cu, Mn, and Zn). Studies of the effects of fire on soil nutrients in slash pine forests have shown that fire most notably increased concentrations of phosphorus in the soil (Gholz and Fisher 1984, Gholz et al. 1985). In addition, Brewer and Platt (unpublished data) have found increased tissue concentrations of potassium in *P. graminifolia* following fire. Therefore, a nutrient solution containing relatively high amounts of phosphorus and potassium was chosen for the current study. The unfertilized and control plots received 2
liters of water at the time of the clipping. An application
of nutrient solution and water was repeated two weeks later.

Each clipping plot was censused three times over a
seven week period. The number of shoots within the central
0.125 m² portion of each 0.25 m² clipping plot was
determined at each census. The experimental design allowed
two separate analyses of treatment effects on shoot density.
First, the effect of blocks on shoot density and the effects
of season, clipping, and their interactions on initial and
final shoot density were analyzed using split-split-plot
ANOVA. The effects of interest were the split-split plot
interactions of clipping x census, and season x clipping x
census. Fertilized plots were excluded from this analysis.
Second, to examine the interaction between season of
clipping and fertilization, the effects of blocks, season of
clipping, fertilization, and their interactions on initial
and final shoot density were analyzed using split-plot three
way ANOVA. The effects of interest were the split-plot
interactions of season of clipping x census, fertilization x
census, and season of clipping x fertilization x census. All
analyses were done with STATISTIX.

RESULTS

Fire and Fire Season Effects on Shoot Density

Shoot densities, initially the same in all plots,
increased in all plots throughout this study (Figure 3.2).
Figure 3.2. Mean shoot density/m²/plot ± SE from December 1990 to December 1992. Triangles below the abscissa represent the timing of January, May, and August fires in 1992.
Patterns of shoot density changed between years as a result of fire (Figure 3.2). Shoot density increased at a lower rate in 1991 (a year without fire) than in 1992 (a year with fire). The greatest increase in shoot density occurred after May 1992, especially in May-burned plots (Figure 3.2).

Results from the clipping experiment showed that the short-term increases in shoot density following fires were not the result of canopy and litter removal alone. As a result, the clipping x census interaction was not statistically significant (p=0.6039; Table 3.1).

Fire season influenced the rate of increase in shoot density (Figure 3.2). While initial shoot densities were similar among fire season treatments, there were significant differences in shoot density among fire season treatments in December 1992. These differences were largely due to the immediate effects (less than 6 weeks after fire) of different seasons of fire on shoot density. Fire season affected the rate of increase in shoot density during the first two census intervals following 1992 fires. There was a significant whole plot effect of fire season (p<0.0001; Table 3.2). May fires in 1992 caused a significantly higher per shoot rate of increase in shoot density during the first two census intervals after fire than did August fires (contrast SS=0.882, \( F_{1,147} = 16.83, \) p<0.001). While May fires caused a higher log per shoot rate of increase in shoot density than did January fires (0.221±0.021 SE vs. 0.197±0.021 SE).
Table 3.1. Split-split-plot ANOVA table of the effects of blocks, season, clipping, and census on shoot density. Block interactions were pooled with sampling errors to produce whole-plot, split-plot, and split-split-plot error terms. The effects of interest were the split-split plot interactions of clipping x census (Cl x Ce), and season x clipping x census (S x Cl x Ce). Fertilized plots were excluded from this analysis.

Dependent variable: Shoot Density.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season-S</td>
<td>1</td>
<td>0.1429</td>
<td>&lt;0.01</td>
<td>0.9513</td>
</tr>
<tr>
<td>Block-B</td>
<td>1</td>
<td>0.3214</td>
<td>0.01</td>
<td>0.9257</td>
</tr>
<tr>
<td>Whole-Plot Error</td>
<td>25</td>
<td>36.2300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clipping-Cl</td>
<td>1</td>
<td>8.0357</td>
<td>0.12</td>
<td>0.7367</td>
</tr>
<tr>
<td>S x Cl</td>
<td>1</td>
<td>1.7500</td>
<td>0.03</td>
<td>0.8752</td>
</tr>
<tr>
<td>Split-Plot Error</td>
<td>26</td>
<td>69.5660</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Census-Ce</td>
<td>1</td>
<td>12.8930</td>
<td>0.41</td>
<td>0.5251</td>
</tr>
<tr>
<td>Cl x Ce</td>
<td>1</td>
<td>9.1428</td>
<td>0.29</td>
<td>0.5923</td>
</tr>
<tr>
<td>S x Ce</td>
<td>1</td>
<td>0.3214</td>
<td>0.01</td>
<td>0.9199</td>
</tr>
<tr>
<td>S x Cl x Ce</td>
<td>1</td>
<td>9.1430</td>
<td>0.29</td>
<td>0.5923</td>
</tr>
<tr>
<td>Split-Split-Plot Error</td>
<td>52</td>
<td>31.4900</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>111</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.2: Split-plot ANOVA table of the effect of fire season on per shoot rates of increase in shoot density (log $N_t/N_0$) during the first two censuses after fire in 1992

**Dependent Variable: log $N_t/N_0$**

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fire Season - S</td>
<td>2</td>
<td>0.5111</td>
<td>9.75</td>
<td>0.0001</td>
</tr>
<tr>
<td>Pooled Variance (S)</td>
<td>147</td>
<td>0.0524</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Census - C</td>
<td>1</td>
<td>0.3665</td>
<td>7.22</td>
<td>0.0081</td>
</tr>
<tr>
<td>S x C</td>
<td>2</td>
<td>0.7930</td>
<td>15.62</td>
<td>0.0001</td>
</tr>
<tr>
<td>Pooled Variance x C (S)</td>
<td>147</td>
<td>0.0508</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Total** 299
0.107±0.023 SE, respectively), there was no significant difference between January and May + August fires (contrast SS=0.140, $F_{1,147}=2.67$, $p=0.100$), because of the small log per shoot rates of increase in August-burned plots (0.088±0.028 SE).

Fire season effects on the per shoot rate of increase in shoot density during census interval 1 (6-7 weeks after fire) were greatly diminished by census interval 2 (15-16 weeks after fire) (Figure 3.3). As a result there was a significant fire season x interval interaction ($p<0.0001$, Table 3.2). The per shoot rate of increase in shoot density during interval 1 was significantly greater following May fires than following August fires (contrast SS=2.41, $F_{1,147}=47.54$, $p<0.001$; Figure 3.3). While the log per shoot rate of increase in shoot density during interval 1 was much greater in May-burned plots than in January-burned plots (0.347±0.029 SE vs. 0.136±0.037 SE, respectively), the per shoot rate of increase in shoot density in January-burned plots was not significantly different from that in May + August-burned plots averaged (contrast SS=0.09, $F_{1,147}=1.84$, $p=0.173$), because of small increases in the log per shoot rate of increase in shoot density in August-burned plots (0.037±0.052 SE). The rate of increase in shoot density in May-burned and January-burned plots decreased in interval 2, whereas the rate of increase in shoot density in August-burned plots increased (Figure 3.3).
Figure 3.3. The effect of fire season on log (per shoot increase in shoot density) during two census intervals following fire in 1992. Interval 1 - from 1-2 weeks before fire to 6-7 weeks after fire. Interval 2 - from 6-7 weeks after fire to 15-16 weeks after the fire.
Results from the clipping experiment indicated that the season during which canopy and litter were removed had little effect on shoot density. The season x clipping x census interaction was not statistically significant (p=0.6039; Table 3.1). However, results from the factorial season of clipping-fertilization experiment showed that the season of canopy and litter removal was important when clipping and litter removal were combined with the addition of fertilizer. Clipping and fertilization in May 1992 caused a short-term increase in shoot density, while clipping and fertilization in August 1992 did not increase shoot density (Figure 3.4). As a result, there was a significant season of clipping x fertilization x census interaction on shoot density (p=0.043; Table 3.3).

**Fire Season Effects on Shoot Demography**

Fire season affected temporal patterns of shoot initiation. Peak increases in percent shoot initiation (i.e. > 15%) were associated with three events. First, a peak in shoot initiation was associated with the emergence of new shoots from axillary buds at the base of senescing reproductive shoots between December 1990 and March 1991 (Figure 3.5). The increase in shoot initiation at the end of the 1990 growing season was greater in plots burned in May and August than in plots burned in January (Figure 3.5). This resulted from larger numbers of reproductive shoots in plots burned during the 1990 growing season. Second, percent
Figure 3.4. The effects of season of clipping (May, August) and fertilization on mean increases in shoot density/plot.
Table 3.3. Split-plot ANOVA table of the effects of blocks, season of clipping, fertilization, and census (initial and final) on shoot density in 1992. Block interactions were not significant and were pooled with sampling error to produce whole-plot and split-plot error terms. The effects of interest were the split-plot interaction of season of clipping x census (S x C) and season of clipping x fertilization x census (S x C x F). Unclipped control plots were excluded from this analysis. Asterisks (*) denote statistical significance.

Dependent Variable: Shoot Density

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block-B</td>
<td>1</td>
<td>12.22</td>
<td>0.10</td>
<td>0.7572</td>
</tr>
<tr>
<td>Season of Clipping-S</td>
<td>1</td>
<td>77.22</td>
<td>0.61</td>
<td>0.4383</td>
</tr>
<tr>
<td>Fertilization-F</td>
<td>1</td>
<td>7.51</td>
<td>0.06</td>
<td>0.8085</td>
</tr>
<tr>
<td>S x F</td>
<td>1</td>
<td>52.94</td>
<td>0.42</td>
<td>0.5207</td>
</tr>
<tr>
<td>Whole-Plot Error</td>
<td>51</td>
<td>126.56</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Censor-C                | 1  | 40.08| 8.66 | 0.0048 * |
| F x C                   | 1  | 6.51 | 1.41 | 0.2410   |
| S x F x C               | 1  | 13.58| 2.93 | 0.0926   |
| Split-Plot Error        | 52 | 4.63 |      |          |

Total                   | 111|      |      |          |
Figure 3.5. The effect of fire season on mean shoot natality/plot ± SE. X-axis labels represent endpoints of census intervals. Triangles below the abscissa represent the timing of January, May, and August fires in 1992.
shoot initiation increased between May and August 1992 (Figure 3.5). This occurred in all fire season plots but was greatest in May-burned plots (Figure 3.2). Third, percent shoot initiation increased during the first census interval following fire in 1992. This was observed in all fire season plots but was greatest in May-burned plots (Figure 3.5). In addition, another peak in shoot initiation was observed in August-burned plots at the second census following August 1992 fires (Figure 3.5).

Fire season also affected temporal patterns of shoot mortality. Peak increases in shoot mortality (i.e. >15%) were associated with two events. First, percent shoot mortality increased between December 1990 and March 1991 following the senescence of monocarpic reproductive shoots. This is represented by the large peak in shoot mortality at the start of the shoot mortality graph in Figure 3.6 (March 1991). Senescence was greater in growing-season-burned plots because there were more reproductive shoots in these plots. Second, increased shoot mortality occurred in January-burned and August-burned plots between fires and the first census following fire in 1992 (Figure 3.6). May fires had little immediate effect on shoot mortality (Figure 3.6).

Fire Season Effects on the Age of Shoots and Rhizomes

Fire season affected age structure of shoot populations (Figure 3.7). The age class distributions of May-, January, and August-burned shoots are shown in Figure 3.7. Larger
Figure 3.6. The effect of fire season on mean shoot mortality/plot ± SE. X-axis labels represent endpoints of census intervals. Triangles below the abscissa represent the timing of January, May, and August fires in 1992.
Figure 3.7. Age-class frequency distribution of mean percent shoots/plot in 1993 in relation to fire season.
percentages of shoots were initiated during 1992 and 1993 in May-burned plots than in January-burned plots (Figure 3.7). A subdivided G-test revealed that more of the total variation among the four plots burned in January and May \((2G_{df}=9=11.70)\) resulted from variation between treatments \((2G_{df}=3=8.65)\) rather than within treatments \((2G_{df}=6=3.05)\) (Table 3.4). Shoot age class distributions were significantly different between May-burned and January burned plots \((p=0.034;\) Table 3.4). This difference largely resulted from greater turnover rates of shoots in May-burned plots than in January-burned plots. The age class distribution of shoots in August-burned plots was intermediate to those in May-burned and January-burned plots. Shoot age class distributions were not significantly different between May-burned and August-burned plots \((p=0.498;\) Table 3.4; Figure 3.7).

Fire season did not affect rhizome turnover rates to the extent that it affected shoot turnover rates (Figure 3.8). While it appears that a larger percentage of rhizomes in May-burned plots were initiated in 1992 compared to January-burned plots \((40.4\% \text{ vs. } 15.07\%;\) Figure 3.8), large percentages of rhizomes had been initiated in both May-burned and January-burned plots prior to 1991 \((35.76\% \text{ and } 65.75\%, \text{ respectively};\) Figure 3.8). Rhizome age class distributions were not significantly different between May-burned and January-burned plots \((p=0.242;\) Table 3.5;
Table 3.4. Sub-divided contingency table of the number of shoots/subplot/plot. $G_{\text{with}}$ was based on the association of year of initiation with the replicate burn plot within fire season treatments. $G_{\text{bet}}$ was based on the association of year of initiation with fire season. $G_{\text{tot}} = G_{\text{with}} + G_{\text{bet}}$.

<table>
<thead>
<tr>
<th>Fire Season of Initiation Row</th>
<th>b91</th>
<th>91</th>
<th>92</th>
<th>93</th>
<th>Total</th>
<th>$2G_{\text{with}}$</th>
<th>$2G_{\text{bet}}$</th>
<th>$2G_{\text{tot}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>January vs. May fires</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>3.6</td>
<td>1.2</td>
<td>2.4</td>
<td>2.2</td>
<td>9.4</td>
<td>0.803</td>
<td>0.034*</td>
<td>0.231</td>
</tr>
<tr>
<td>January</td>
<td>4.6</td>
<td>0.2</td>
<td>3.2</td>
<td>1.8</td>
<td>9.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Jan</td>
<td>8.2</td>
<td>1.4</td>
<td>5.6</td>
<td>4.0</td>
<td>19.2</td>
<td>1.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>3.2</td>
<td>0.8</td>
<td>9.8</td>
<td>8.4</td>
<td>22.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>1.2</td>
<td>2.6</td>
<td>9.2</td>
<td>9.0</td>
<td>22.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total May</td>
<td>4.4</td>
<td>3.4</td>
<td>19.0</td>
<td>17.4</td>
<td>44.2</td>
<td>1.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grand Total</td>
<td>12.6</td>
<td>4.8</td>
<td>24.6</td>
<td>21.4</td>
<td>63.4</td>
<td>3.05</td>
<td>8.65</td>
<td>11.70</td>
</tr>
<tr>
<td>$p &gt; 2G$ df</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August vs. May fires</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>3.4</td>
<td>2.2</td>
<td>4.2</td>
<td>5.4</td>
<td>15.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>1.2</td>
<td>0.8</td>
<td>2.4</td>
<td>3.2</td>
<td>7.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Aug</td>
<td>4.6</td>
<td>3.0</td>
<td>6.6</td>
<td>8.6</td>
<td>22.8</td>
<td>0.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>3.2</td>
<td>0.8</td>
<td>9.8</td>
<td>8.4</td>
<td>22.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>1.2</td>
<td>2.6</td>
<td>9.2</td>
<td>9.0</td>
<td>22.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total May</td>
<td>4.4</td>
<td>3.4</td>
<td>19.0</td>
<td>17.4</td>
<td>44.2</td>
<td>1.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grand Total</td>
<td>9.0</td>
<td>6.4</td>
<td>25.6</td>
<td>26.0</td>
<td>67.0</td>
<td>2.25</td>
<td>2.38</td>
<td>4.63</td>
</tr>
<tr>
<td>$p &gt; 2G$ df</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Asterisk (*) denotes statistical significance.
Figure 3.8. Age-class frequency distribution of mean percent rhizomes/plot in 1993 in relation to fire season.
Table 3.5. Sub-divided contingency table of the number of rhizomes/subplot/plot. $G_{\text{with}}$ was based on the association of year of initiation with the replicate burn plot within fire season treatments. $G_{\text{bet}}$ was based on the association of year of initiation with fire season. $G_{\text{tot}} = G_{\text{with}} + G_{\text{bet}}$.

<table>
<thead>
<tr>
<th>Fire Season of Initiation</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>2G &lt;sub&gt;with&lt;/sub&gt;</th>
<th>2G &lt;sub&gt;bet&lt;/sub&gt;</th>
<th>2G &lt;sub&gt;tot&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b91</td>
<td>91</td>
<td>92</td>
<td>93</td>
<td>Total</td>
<td></td>
<td></td>
</tr>
<tr>
<td>January vs. May fires</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>5.2</td>
<td>0.4</td>
<td>0.8</td>
<td>0.8</td>
<td>7.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>4.4</td>
<td>0.4</td>
<td>1.4</td>
<td>1.2</td>
<td>7.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Jan</td>
<td>9.6</td>
<td>0.8</td>
<td>2.2</td>
<td>2.0</td>
<td>14.6</td>
<td>0.31</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>5.4</td>
<td>0.6</td>
<td>5.8</td>
<td>3.8</td>
<td>15.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>5.4</td>
<td>1.6</td>
<td>6.4</td>
<td>1.2</td>
<td>14.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total May</td>
<td>10.8</td>
<td>2.2</td>
<td>12.2</td>
<td>5.0</td>
<td>30.2</td>
<td>1.89</td>
<td></td>
</tr>
<tr>
<td>Grand Total</td>
<td>20.4</td>
<td>3.0</td>
<td>14.4</td>
<td>7.0</td>
<td>44.8</td>
<td>2.20</td>
<td>4.18</td>
</tr>
<tr>
<td>p &gt;2G df</td>
<td>0.901</td>
<td>0.242</td>
<td>0.701</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>3</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August vs. May fires</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>4.6</td>
<td>0.6</td>
<td>3.0</td>
<td>3.2</td>
<td>11.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>4.2</td>
<td>0.2</td>
<td>1.8</td>
<td>0.8</td>
<td>7.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Aug</td>
<td>8.8</td>
<td>0.8</td>
<td>4.8</td>
<td>4.0</td>
<td>18.4</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>5.4</td>
<td>0.6</td>
<td>5.8</td>
<td>3.8</td>
<td>15.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>5.4</td>
<td>1.6</td>
<td>6.4</td>
<td>1.2</td>
<td>14.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total May</td>
<td>10.8</td>
<td>2.2</td>
<td>12.2</td>
<td>5.0</td>
<td>30.2</td>
<td>1.89</td>
<td></td>
</tr>
<tr>
<td>Grand Total</td>
<td>19.6</td>
<td>3.0</td>
<td>14.3</td>
<td>9.0</td>
<td>48.6</td>
<td>2.90</td>
<td>1.43</td>
</tr>
<tr>
<td>p &gt;2G df</td>
<td>0.821</td>
<td>0.698</td>
<td>0.888</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>3</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.8). Likewise, rhizome age class distributions were not significantly different between May-burned and August-burned plots (p=0.698; Table 3.5; Figure 3.8).

Fire Season Effects on the Size and Structure of Clones

Excavation revealed no mortality of established clones in any of the fire season plots during the course of this study. However, *P. graminifolia* exhibited considerable phenotypic plasticity in clone structure in response to variation in fire season. Results of the MRPP analysis showed a statistically significant effect of fire season on five variables associated with clone structure - shoot size, ramet size, clone size, number of shoots/clone, and number of rhizomes/clone (p=0.027; Table 3.6). An ordination of the first two canonical axes from the canonical discriminant analysis of these five variables is presented in Figure 3.9. A plot of axis scores of these five variables plus the separately calculated axis scores for number of shoots/rhizome are presented with a superimposed plot of three fire season centroids (Figure 3.9). The numbers and sizes of parts within excavated clones (especially shoots) tended to respond to fire season in opposite ways (Figure 3.9). This is indicated by obtuse angles between vectors corresponding to, for example, the number of shoots/clone and shoot size (Figure 3.9). This inverse relationship was associated with differences between the effects of May and January fires. May fires resulted in greater numbers of
Table 3.6. Analysis of the effect of fire season on mean number of shoots/clone/subplot, mean number of rhizomes/clone/subplot, mean shoot weight/subplot, mean ramet weight/subplot, and mean clone weight/subplot using Multi-Response Permutation Procedures (MRPP). The effect of fire season is measured in terms of euclidean distances among subplots.

<table>
<thead>
<tr>
<th>Fire Season</th>
<th>N</th>
<th>Mean Euclidean Distance Among Subplots</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>10</td>
<td>1.3549</td>
</tr>
<tr>
<td>May</td>
<td>10</td>
<td>1.5144</td>
</tr>
<tr>
<td>August</td>
<td>10</td>
<td>1.6547</td>
</tr>
</tbody>
</table>

Test Statistic = -2.447  Delta = 1.508  Pr < Delta = 0.027
Figure 3.9. Biplot ordination diagram of variables associated with clone structure and centroids of subplots burned in three different fire seasons (January, May, and August) using canonical discriminant analysis. Coordinates for the variable, shoots/rhizome, were determined separately and were not included in the canonical discriminant analysis. Points corresponding to subplots were removed for clarity.
shoots/clone than did January fires (Figure 3.9). The greater number of shoots/clone seen in May-burned plots resulted from increased numbers of shoots/rhizome, and to a lesser extent, increased numbers of rhizomes/clone. January burned plots had clones and rhizomes that contained larger (but fewer) shoots than did May-burned plots (Figure 3.9). As a result, sizes of clones were roughly similar in May burned and January-burned plots. August-burned plots contained clones with small shoots and ramets and an intermediate number of shoots/clone. Consequently, clones in August-burned plots were slightly smaller than were clones in May-burned or January-burned plots (Figure 3.9).

DISCUSSION

Results of the current study indicate that fire season has a major effect on shoot demography and clone structure in *P. graminifolia*. When fires occurred in January, shoots had a longer period to grow before the end of the growing season (November–December) than did shoots burned during the growing season (e.g. in May and August). This may partly explain why January-burned shoots were larger than shoots in May-burned or August-burned plots. However, another factor contributing to shoot size was the allocation pattern within clones. Clone sizes were similar in May-burned and January-burned plots at the end of the 1992 growing season, but clone structure was not. May fires caused clones to
shift the allocation of biomass from older, larger shoots to more numerous, smaller shoots emerging from axillary and terminal buds on rhizomes immediately after fire. In contrast, following January and August fires, shoot initiation rates were lower. Therefore, much of the residual biomass was allocated to the replacement of aboveground parts of shoots that survived the fires. Thus, phenotypic plasticity in allocation patterns probably contributed to most of the difference in shoot size between January-burned and May-burned plots. Alternatively, differences between the sizes of January-burned and August-burned shoots and clones were mostly due to differences in the length of time after fire until the end of the 1992 growing season.

The ability of *P. graminifolia* to exhibit plastic allocation responses to fire is, for the most part, positively associated with the likelihood that longleaf pine savannas will burn as a result of lightning fires. Lightning fires have occurred within pine savannas in Florida for thousands of years at least (Frost 1993). The frequency of thunderstorms and thus lightning fires is higher during the growing season (April to September) than during the dormant season (October to March) in Florida (Komarek 1964, Chen and Gerber 1990). Dormant-season fires, while frequent, are typically anthropogenic in origin and as such are a more recent phenomenon in Florida (Frost 1993). In my study allocation to new shoots was greater following May than
January fires. Allocation to new shoots following May fires was also greater than that observed following August fires. This occurred despite the fact that the frequency of lightning strikes is actually slightly higher in August (Chen and Gerber 1990). The likelihood that clones of *P. graminifolia* will be burned by lightning fires is greater in May than in August (Komarek 1964), because of lower rainfall amounts in May (Chen and Gerber 1990) and hence burning of larger areas during single fires. Therefore, the greater efficiency of clones to locate soil resources following May fires than following either January or August fires is positively associated with the likelihood of being burned by fires occurring at different times during the lightning season. The low rates of clonal spread following August fires may also indicate the presence of severe phenological constraints on growth near the end of the growing season.

If these results on clonal foraging responses to fire season were applied to other forms of chronic, sublethal disturbances, such as moderate grazing by generalist herbivores, responses of grazing-adapted species to grazing might also differ in response to differences in season of grazing.

Most discussions of the adaptive significance of allocation patterns within clones following defoliation have dealt with the responses of grasses to herbivores (e.g. McNaughton 1984, Coughenour et al. 1985b, Milchunas et al. ...
The model of plant-grazer interactions presented by Milchunas et al. (1988) predicts that plant species that have coevolved with grazers should be most likely to respond to moderate levels of grazing with increased allocation to new shoots. Increased numbers of shoots or tillers/clone and regrowth of defoliated shoots or tillers have different effects on the subsequent mode of competition (Milchunas et al. 1988). It is suggested that increasing the numbers of shoots/clone following defoliation allows clonal plants to take advantage of windows of relaxed aboveground competition by more efficiently "foraging" for soil resources.

Data from the current study indicate that P. graminifolia responds to May fires in much the same way some grazophilic grasses respond to moderate levels of grazing - with increased numbers of smaller shoots per clone. Such phenotypic plasticity may represent an adaptive response to fire-mediated cyclic variation in the competitive regime experienced by P. graminifolia. The physiognomy of longleaf pine sandhill communities changes with increasing time between fires. As the duration of fire-free intervals increases in fire-frequented habitats, so do the amount of litter (Hartnett 1987) and the height of the vegetation as shrubs increase in size (Waldrop et al. 1992). I predict that allocation to new shoots and rhizomes should be negatively correlated with allocation to existing shoots. Also, I suggest that allocation to new shoots and rhizomes
should decline with increasing time since May fire, while allocation to existing shoots (especially leaves) should increase. Thus, sizes and heights of existing shoots should be positively correlated with litter accumulation and the height of vegetation. I suggest that fires in sandhills shift the mode of competition from canopy resources to soil resources, and that *P. graminifolia* exhibits a plastic allocation strategy that enables it to respond to these changes in the competitive environment.

One factor that apparently limits the ability of fire to cause clones to allocate more resources to new shoots is the availability of nutrients following fire. In the current study, May fires caused an immediate increase in shoot density; however, shoot density was not affected by removal of a dense herbaceous canopy and litter alone. The availability of mineral nutrients (e.g. nitrogen, phosphorus and/or potassium) following May fires limited the release of rhizome and axillary buds from dormancy. When canopy and litter removal in May was combined with fertilization, shoot density increased significantly by six weeks after canopy and litter removal. The effect of May fires on shoot demography differed in the north Florida population I studied and in a central Florida population studied by Hartnett (1987). In the central Florida population, May fires did not stimulate the initiation of new shoots (Hartnett 1987). Perhaps nutrient levels in the central
Florida sandhills do not increase enough following May fires to stimulate shoot initiation in *P. graminifolia*. The importance of mineral nutrient limitation of shoot initiation following fire in *P. graminifolia* is consistent with the findings of Coughenour et al. (1985b) for a grazophilic grass, *Hyparrhenia filipendula*, of the Serengeti plain. In their study, high levels of nitrogen combined with clipping stimulated tillering and the initiation of new crowns. Thus, the morpho-physiological responses of *P. graminifolia* to May fires in this pine savanna in north Florida site appear to be similar to the responses of at least one grazophilic grass to herbivory and nutrient limitation.

In addition to shoot demography, the effect that May fires have on clone structure in *P. graminifolia* may reflect an optimal strategy in the way clones of this species "forage" for nutrients (see Slade and Hutchings 1987). Increased numbers of shoots/clone in *P. graminifolia* following May fires resulted more from increased numbers of shoots/rhizome than from increased numbers of rhizomes/clone. Increased numbers of shoots/rhizome resulted in a more clumped or (phalangeal, sensu Lovett Doust 1981) pattern of shoots within clones than did increased numbers of rhizomes/clone. Previous studies have suggested that, in areas where resources are locally abundant, clumped or compact arrangements of shoots within clones enable clones
to monopolize resources (Lovett Doust 1981, Cook 1985, Slade and Hutchings 1987). By waiting until immediately after May fires to produce numerous shoots per rhizome, a clone of *P. graminifolia* increases the likelihood that it will be able to monopolize nutrients that have become more available immediately following fire. A prerequisite for such a strategy is the existence of different age class distributions of rhizomes and shoots wherein shoots turnover rapidly, but rhizomes are persistent and capable of prolonged energy storage (also see Pitelka and Ashmun 1985, Watkinson and White 1985, Schmid and Bazzaz 1987). This differential age class structure of rhizomes and shoots would enable clones of *P. graminifolia*, as inhabitants of frequently-burned savannas, to forage through time for a temporally variable supply of nutrients.
CHAPTER 4 - MODELING RESOURCE ALLOCATION AND CLONAL GROWTH
INTRODUCTION

Clonal growth, expressed as the iteration of modular units, results in life history traits that differ from those of non-clonal organisms. Such traits include the absence of senescence and the indefinite increase in size and fecundity of genetic individuals (genets) with age (Watkinson and White 1985, Sackville Hamilton et al. 1987). As a result, relative sizes of genets (as determined by the number of modules/genet) are more likely to influence fitness than are age of first reproduction, generation time, and reproductive value (Watkinson and White 1985). Accordingly, modular demographic approaches to clonal growth (White 1979) have been emphasized in the study of clonal perennials, particularly over the past decade (White 1979, McGraw and Antonovics 1983, Fetcher and Shaver 1983, Watkinson and White 1985, Sackville Hamilton et al. 1987).

Modular demographic models have quantified rates of clonal growth by treating genets as populations of modules (e.g. ramets, tillers; for examples, see McGraw and Antonovics 1983, Fetcher and Shaver 1983, Sackville Hamilton et al. 1987). Such populations have been structured on the basis of age or stage classes of modules. Mortality and fecundity schedules of modules have been used to obtain intrinsic rates of increase of module populations as predicted by exponential (e.g. Fetcher and Shaver 1983) or density-dependent (e.g. Sackville Hamilton et al. 1987)
models of population growth. Intrinsic rates of increase have been compared between species or genotypes (e.g. Sarukhan and Gadgil 1974, McGraw and Antonovics 1983) or between module populations of the same species in different habitats (e.g. Fetcher and Shaver 1983). From these comparisons, phenotypic variation in the growth rates of genets has been determined.

The modular demography approach may not always be appropriate for modeling growth rates of genets. A major assumption that underlies modular demographic models is that all modules within a genet are physiologically independent. Genets of many plants, however, fragment into clones containing numerous physiologically integrated modules. Clones are capable of varying patterns of resource allocation among physiologically integrated modules. Cook (1983) demonstrated a negative relationship between the future net growth of a module and the number of daughter modules it produced. Thus, within clones containing physiologically integrated modules, allocation to parent modules may sometimes compete with allocation to daughter modules (Cook 1985). The significance of such a finding is that given a limited supply of resources, the rate of increase in the number of modules a clone contains may be more an indicator of its strategy of resource allocation (i.e. regrowth in the existing location as compared to growth into new locations) than its growth rate. Another
common assumption is that modules of a given age do not vary in size. In many plants, however, clones increase in size not only as a result of net increases in the number of modules they contain, but also as a result of increases in the sizes of individual modules (Law 1983, Coughenour et al. 1985b, Hartnett 1987, Grace 1989, Chapter 3).

In habitats characterized by chronic sublethal disturbance (e.g. low-intensity fire, grazing), the assumption that modules within clones are physiologically independent may not be met. Several studies have demonstrated a negative relationship between module size and module number within clones (Coughenour et al. 1985b, Hartnett 1987, Chapter 3). It has been argued that increased allocation to daughter modules at the expense of parent modules may permit defoliated clones to locate more efficiently soil resources during periods of relaxed aboveground competition. Therefore, there is a need for developing models that incorporate both modular demography and module size within clones growing in chronically disturbed habitats.

While an increasing number of studies have demonstrated significant clonal growth responses to fire and grazing in chronically disturbed habitats (Coughenour et al. 1985b, Jeffries 1988, Chapter 3), little is known about the effects of other factors on clonal growth in these habitats. It is possible that factors unrelated to sublethal disturbance,
such as spatial variation in clone and module density and genetic variation within module populations, also influence rates of vegetative spread in these habitats. It is necessary, therefore, to develop models that distinguish between the effects of sublethal disturbance and other sources of phenotypic variation on rates of clonal growth in module populations.

In the current study, I develop two models to examine the role of physiological integration within clones and multiple sources of phenotypic variation within module populations on rates of vegetative spread in the pyrophilic forb, *Pityopsis graminifolia*. The effect of fire season on clone size, number of shoots (modules) per clone, and shoot size in *Pityopsis graminifolia* was examined using a multivariate model of allocation patterns. Using a spatial model of vegetation dynamics, effects of fire were partitioned from other sources of phenotypic variation in rates of vegetative spread of clones of *Pityopsis graminifolia*. Results of these models were used to address the evolutionary relationship between patterns of clonal growth and fire.

**CLONAL MORPHOLOGY OF PITYOPSIS GRAMINIFOLIA**

*Pityopsis graminifolia* (Michx.) Nutt., a rhizomatous, perennial composite common throughout pine savannas in the coastal plain of the southeastern United States has a clonal
morphology analogous to that of many rhizomatous grasses (Semple and Bowers 1985, Figure 3.1). A clone of *P. graminifolia* was defined as the set of all physically interconnected ramets and as such represented minimum genet size (Chapters 2 and 3). A ramet was considered equivalent to a "crown" in rhizomatous grasses, that is, a single rhizome plus all shoots derived from buds on that rhizome (also see Coughenour et al. 1985). Shoots were defined as aboveground portions of branches located either on the terminal end of rhizomes or emerging from axillary buds on older portions of perennial rhizomes (Chapters 2 and 3; Figure 3.1).

Prior to bolting, the apical shoot bud is at or below the soil surface, well protected from fire by a compact basal arrangement of linear leaves. Bolting occurs most frequently following fires during the peak lightning fire season (Streng et al. 1993, Chapter 2). Following seed set, bolting shoots die. Prior to death, one to several basal offshoots may arise from axillary buds on the same rhizome (Figure 3.1). Thus, while shoots are monocarpic, ramets are polycarpic.

**STUDY AREA**

This study was conducted in a second growth sandhill community in the St. Marks Wildlife Refuge, Wakulla County, Florida. Sandhills are open, xeric pine forests that overlie
deep Plio-Pleistocene-age sands (Platt et al. 1988a, Myers 1990). The overstory is dominated by longleaf pine, *Pinus palustris* Mill. The understory is dominated by perennial grasses (e.g., *Aristida beyrichiana* Trin. and Rupr.), forbs (e.g. *Pityopsis graminifolia*, *Liatris tenuifolia* Nutt.), and shrubs (e.g. *Vaccinium myrsinites* Lam., *Quercus minima* (Sarg.) Small, *Q. laevis* Walt., and *Q. incana* Bartr.) in a low groundcover (Streng et al. 1993).

Sandhill communities depend upon frequent (every 1-5 yr), low-intensity surface fires that prevent the growth of hardwood trees into the canopy (Chapman 1932a,b, Christensen 1981, Platt et al. 1988b, 1991). In addition, while these fires typically kill aboveground, but not belowground parts of herbaceous perennials, survival and resprouting is extensive (Platt et al. 1988a). Lightning-started fires typically occurred during the growing season (April to October) prior to European settlement (Chapman 1932a,b, Platt et al. 1991). European settlers altered the natural fire regime by burning pine forests during the winter, between growing seasons (Platt et al. 1988a). Over the past 35 years, prescribed burning by the refuge staff has occurred 2-3 times a decade, mostly during the winter (Platt et al. 1988a).
SAMPLING AND CENSUSING OF *PITYOPSIS GRAMINIFOLIA*

The current study used four plots and was a subset of an ongoing larger long-term study of the effects of fire season on vegetation dynamics in longleaf pine savannas initiated in 1980 (Platt et al. 1988a). The long-term study consisted of two replicate plots of eight different seasons of burn within both sandhill and flatwoods habitats. Replicate biannually burned plots of 2-5 hectares each were selected based on similar densities of longleaf pine, wiregrass, and *Quercus* sp. (Platt et al. 1988a). The current study is based on data collected between December 1990 and February 1993. The four plots used were located within the sandhills. The two replicates were burned during two-week intervals in early January or late May in both 1990 and 1992. Both replicate plots of each treatment were burned on the first day suitable for the combined use of strip headfires and a single backfire.

In mid-December of 1990, twenty-five 0.125 m$^2$ circular subplots (diameter of 40 cm) containing shoots of *P. graminifolia* were randomly located within the central 1-ha area of each replicate plot. Details of the sampling method used have been described in Chapters 2 and 3. All shoots within each subplot were permanently marked using numbered aluminum tags. Initial (Dec. 1990) average numbers of shoots/plot marked in May-burned, and January-burned plots were 240.5 and 213.5, respectively (Table 4.1). These
Table 4.1. The mean number of live shoots/plot observed in December 1990 and December 1992 following January and May fires. The numbers of shoots observed in December 1992 included both surviving shoots initially observed in December 1990 and all surviving shoots derived from buds since December 1990.

<table>
<thead>
<tr>
<th>Fire Season</th>
<th>December 1990</th>
<th>December 1992</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>213.5</td>
<td>352.0</td>
</tr>
<tr>
<td>May</td>
<td>240.5</td>
<td>647.0</td>
</tr>
</tbody>
</table>
numbers changed over the course of the study, and thus sample sizes varied with time (Table 4.1).

Each subplot was censused once every 9 weeks from December 1990 to December 1992. At each census, the reproductive status of each shoot was determined using bolting and non-bolting categories. When senescent shoots gave rise to new daughter shoots derived from axillary buds, tags of parent senescent shoots were moved to the new daughter shoots. Otherwise, tags of senescent shoots that did not produce axillary daughter shoots were kept in place throughout the study.

In January and February, 1993, five subplots in each replicate plot were completely excavated to a depth of 15 cm to uncover any underground connections among shoots. A clone was defined as the set of all physically interconnected shoots and as such represented minimum genet size. For each clone, I traced the ancestry of all shoots alive at the time of excavation to the shoot initially tagged in December 1990. In addition, the average numbers of shoots/clone were determined for each excavated subplot. I also made a final census of the reproductive status of all excavated shoots. All clones were separated into their constituent shoots and oven-dried at 40°C to a constant weight. Average shoot weight and average clone weight were determined for each excavated subplot.
A MULTIVARIATE MODEL OF FIRE SEASON EFFECTS ON CLONE STRUCTURE IN PITYOPSIS GRAMINIFOLIA

To assess the relationship between fire season and clone structure, canonical discriminant analysis (CANDISC procedure in PC SAS) was performed. Before running CANDISC, univariate parametric tests of replicate errors were run for each dependent variable using nested ANOVA. The dependent variables were mean number of shoots/clone/subplot, mean shoot weight/subplot, and mean clone weight/subplot. All replicate errors and sampling errors could be pooled based upon the criteria of Bancroft and Han (1983). Thus, a canonical discriminant analysis of the effects of fires on clone structure included 2 treatment groups (fire season) and 10 observations (subplots) per treatment group. Since there were only two fire season treatments, only one canonical axis was calculated. Correlations of each dependent variable with this axis were compared with means of canonical scores for each fire season to show the relationship between dependent variables and fire season.

Numbers and sizes of shoots within excavated clones responded to fire season in opposite ways (Figures 4.1a,b). The number of shoots/clone was negatively correlated with the canonical axis \( r = -0.71 \); Figure 4.1a), whereas shoot size was positively correlated with the canonical axis \( r = 0.87 \); Figure 4.1b). This inverse relationship was associated with differences between effects of May and
Figures 4.1a-c. Plots of simple correlations of subplot means of a) shoot number/clone, b) shoot weight, and c) clone weight with first canonical axis derived from canonical discriminant analysis. Symbols correspond to the fire season plot in which a subplot was located.
January fires. This was indicated by a negative mean canonical score for May-burned subplots (-1.37) and a positive mean canonical score for January-burned subplots (1.37). May fires resulted in greater numbers of shoots/clone than did January fires, whereas January-burned subplots had clones that contained larger shoots than did May-burned subplots (Figures 4.1a,b). The opposite changes in these two variables resulted in sizes of clones that were roughly similar in May-burned and January-burned subplots, as was indicated by the weak correlation of clone size with the canonical axis (r=-0.09; Figure 4.1c).

A SPATIAL MODEL OF PHENOTYPIC VARIATION IN THE RATE OF VEGETATIVE SPREAD IN PITYOPSIS GRAMINIFOLIA

I used a general matrix model to describe the spatial pattern of vegetative spread in each fire season plot. To construct this model, shoot populations were classified on the basis of the incidence of flowering. A comparison of both the total number of shoots (Figure 4.2) and the number of bolting shoots (Figure 4.3) from March 1991 to December 1992 in May-burned and January-burned plots showed that increases in the density of vegetatively derived shoots were positively associated with the incidence of flowering during 1992. Data from a previous study (Chapter 3) indicated that May fires improved conditions for both flowering and vegetative spread in P. graminifolia by removing the
Figure 4.2. Mean shoot density/m²/plot ± SE from March 1991 to December 1992. Triangles below the abscissa represent the timing of January and May fires in 1992.
Figure 4.3. Mean number of bolting shoots/m²/plot ± from March 1991 to December 1992. Triangles below the abscissa represent the timing of January and May fires in 1992.
herbaceous canopy and litter and increasing soil fertility, but not by reducing module density. Nonetheless, unpublished field observations also revealed an increased incidence of flowering and shoot initiation by large shoots within small gaps in the groundcover during years without fire. Therefore, I assumed that flowering of shoots was positively associated with local conditions also favorable for vegetative spread during the year in which flowering occurred, regardless of whether or not these conditions were directly related to the occurrence of May fires. By contrasting spatial patterns of vegetative spread in May burned and January-burned plots, I attempted to partition the effects of May fires on rates of vegetative spread from the effects of other factors (e.g. module or clone density, genotype, gaps, etc.) on rates of vegetative spread in this species.

Using the incidence of shoot flowering as an indicator of locally favorable conditions for vegetative spread during the year in which flowering occurred, I assigned each excavated "mother" shoot that was initially tagged following senescence of reproductive shoots (from December 1990 to February 1991) to one of two spatial categories: (R) - clonally derived from a ramet containing at least one reproductive shoot; (N) - clonally derived from a ramet containing only non-flowering rosettes. I then counted the number of mother shoots in each spatial category that
survived until after the senescence of shoots that flowered in 1992. Likewise I counted the number of "daughter shoots" present following the senescence of shoots that flowered in 1992. A daughter shoot was defined as any shoot derived from an axillary bud on the same ramet as its mother shoot plus any shoot derived from a terminal bud on any daughter ramet. If the terminal shoot of a daughter ramet flowered in 1992, then the first axillary shoot that emerged from the base of the flowering shoot was also considered a daughter shoot. All other "granddaughter shoots" were excluded. Finally, I assigned each surviving mother shoot and each daughter shoot to one of the two spatial categories described above for mother shoots in early 1991. Shoots derived from seeds released during or after the 1990 growing season were not included in this demographic analysis.

A flow diagram of possible transitions between spatial categories of shoots from early 1991 to early 1993 in each plot is shown in Figure 4.4. Possible transitions between reproductive (R) and non-reproductive (N) categories between 1991 and 1993 included: 1) R -> R, 2) R -> N, 3) N -> N, and 4) N -> R. Numbers of shoots in each spatial category in 1991 and 1993 are presented in Table 4.2. Data for each plot were used to calculate 2 x 2 matrices of transition probabilities (Tables 4.3a-e).

The statistics obtained from each of these transition matrices were the maximum eigenvalue and its corresponding
Figure 4.4. Flow diagram of transitions of shoots between early (Jan-Mar) 1991 and early (Jan-Feb) 1993. "R" represents shoots derived from reproductive ramets. "N" represents shoots derived from non-reproductive ramets.
Table 4.2. Numbers of excavated mother and daughter shoots derived from reproductive ramets (R) and non-reproductive ramets (N) in early 1991 and early 1993.

<table>
<thead>
<tr>
<th>Plot</th>
<th>$R_{1991}$</th>
<th>$N_{1991}$</th>
<th>$R_{1993}$</th>
<th>$N_{1993}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burned in May 1</td>
<td>19</td>
<td>17</td>
<td>44</td>
<td>73</td>
</tr>
<tr>
<td>Burned in May 2</td>
<td>10</td>
<td>29</td>
<td>20</td>
<td>81</td>
</tr>
<tr>
<td>Burned in January 1</td>
<td>6</td>
<td>28</td>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>Burned in January 2</td>
<td>2</td>
<td>24</td>
<td>5</td>
<td>48</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>37</strong></td>
<td><strong>98</strong></td>
<td><strong>71</strong></td>
<td><strong>248</strong></td>
</tr>
</tbody>
</table>
Tables 4.3a-e. Matrices of transitions between R shoots and N shoots for each fire season plot. The template of the 2 x 2 matrices is presented in table a. Actual transition probabilities for the four fire season plots are presented in tables b-e.

### a. TEMPLATE OF MATRIX

<table>
<thead>
<tr>
<th></th>
<th>N→N</th>
<th>R→N</th>
</tr>
</thead>
<tbody>
<tr>
<td>N→N</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N→R</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R→R</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### b. MAY 1

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>2.529</td>
<td>1.579</td>
<td></td>
</tr>
<tr>
<td>1.059</td>
<td>1.368</td>
<td></td>
</tr>
</tbody>
</table>

### c. MAY 2

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>2.030</td>
<td>2.200</td>
<td></td>
</tr>
<tr>
<td>0.448</td>
<td>0.700</td>
<td></td>
</tr>
</tbody>
</table>

### d. JANUARY 1

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1.250</td>
<td>1.830</td>
<td></td>
</tr>
<tr>
<td>0.000</td>
<td>0.330</td>
<td></td>
</tr>
</tbody>
</table>

### e. JANUARY 2

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1.792</td>
<td>2.200</td>
<td></td>
</tr>
<tr>
<td>0.167</td>
<td>0.500</td>
<td></td>
</tr>
</tbody>
</table>
left eigenvector. The maximum eigenvalue of each transition matrix (Leslie 1945, Caswell 1985) was considered equivalent to the per shoot population growth rate per biennial fire cycle. The left eigenvector of each transition matrix (Leslie 1948, Caswell 1985) was equivalent to the vector of vegetative reproductive values of shoots in each spatial category. Given a particular transition matrix, the shoot population generally achieves a stable distribution of vegetative reproductive values, regardless of its initial state. Once this stable distribution of vegetative reproductive values has been achieved, the shoot population continues to grow exponentially at a constant per shoot rate. Reproductive value in age-structured populations of unitary organisms was originally defined by Fisher as the expected number of offspring that remain to be born to an individual of age (x) relative to the number that remain to be born to a newborn individual. However, in this study, rather than assigning individuals to different age classes, I assigned shoots to two different spatial categories. Thus, in this case, vegetative reproductive value is defined as the sum of current shoot reproduction (including the possibility of surviving in the same spatial category to reproduce again) and a residual vegetative reproductive value that sums the probability of transition to the other spatial category times its vegetative reproductive value (Caswell 1985). The purpose of calculating vegetative
reproductive values here was not to derive hypotheses regarding the life histories of shoots, but rather to quantify the relative rates of vegetative spread in different local microsites in a shoot population that is spreading vegetatively at a constant rate.

The vector of vegetative reproductive values and the biennial population growth rates for each plot were computed by iterative multiplication of the transposed transition matrix and state vectors on a personal computer using the QUATTRO spreadsheet. State vectors resulting from each iteration were rescaled so that the elements summed to unity. The solution was checked by solving the characteristic equation (Leslie 1948, Caswell 1985):

\[ \mathbf{vA} = \mathbf{ve} \]  \hspace{1cm} (4.1)

where, \( \mathbf{v} \) = the vector of vegetative reproductive values (or the left eigenvector of \( \mathbf{A} \)), \( \mathbf{A} \) = the matrix of transition probabilities, and \( e \) = the per shoot population growth rate per biennial fire cycle (or the maximum eigenvalue of \( \mathbf{A} \)).

The major assumptions of this model include: 1) shoot population growth is density-independent; 2) the effects of fire on shoot population growth during a given two-year interval between fires are the same as those during any other two-year interval between fires; 3) the rate of
vegetative spread is equivalent to the per shoot population growth rate; 4) no migration between fire plots.

Other assumptions of this model that relate to the spatial structuring of shoot populations are 1) the incidence of flowering is indicative of local environmental conditions that favor an increase in the number of shoots per clone, and 2) the frequency of local microsites favoring vegetative spread does not vary among fire cycles.

Results from the spatial model revealed two major findings. First, May-burned shoot populations grew faster than January-burned shoot populations. In other words, May-burned clones spread vegetatively at an overall faster rate than January-burned clones. This was indicated by the greater per shoot population growth rates in May-burned plots than in January-burned plots (Table 4.4). This confirmed previous results from the multivariate analysis of fire season effects on shoot demography. Second, the frequency of patches that were locally favorable for vegetative spread was much lower in January-burned plots than in May-burned plots (Table 4.2); however, the effect of these patches on vegetative spread was more likely to persist beyond the growing season in which fire occurred in January-burned plots than in May-burned plots. In January-burned plots, local areas that were favorable for vegetative spread in 1990 remained favorable after the 1990 growing season. This was indicated by a substantially
Table 4.4. Reproductive values and overall per shoot rates of change in shoot population size for May- and January-burned shoots.

<table>
<thead>
<tr>
<th></th>
<th>May1</th>
<th>May2</th>
<th>Jan1</th>
<th>Jan2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproductive value for R shoots</td>
<td>1.49</td>
<td>1.41</td>
<td>0.83</td>
<td>1.27</td>
</tr>
<tr>
<td>Reproductive value for N shoots</td>
<td>1.88</td>
<td>1.28</td>
<td>0.42</td>
<td>0.79</td>
</tr>
<tr>
<td>Per shoot rate of change</td>
<td>3.37</td>
<td>2.69</td>
<td>1.25</td>
<td>2.06</td>
</tr>
</tbody>
</table>
greater vegetative reproductive value of R shoots compared to
N shoots in both January-burned plots (Table 4.4). In
contrast, in May-burned plots local areas that were
favorable for vegetative spread in 1990 were not any more
favorable than any other area after the 1990 growing season.
This was indicated by the similar vegetative reproductive
values of R shoots and N shoots in both May-burned plots
(Table 4.4).

DISCUSSION

Effects of Fire Season on Clone Structure in Pitvopsis
graminifolia

The multivariate model of clone structure indicated
that fire season had a major effect on shoot demography and
shoot size, but not clone size in P. graminifolia. Shoots
had a longer period to grow before excavation (January and
February 1993) following January (1992) fires than following
May (1992) fires. This may partly explain why January-burned
shoots were larger than shoots in May-burned plots at the
time of excavation. However, May-burned clones excavated in
mid-February 1993 were similar in size to January-burned
clones excavated in early January 1993. This suggested that
a trade-off in the proportional allocation of resources to
mother and daughter shoots was more important than the
length of time between fire and excavation in determining
differences in shoot size between May-burned and January
burned plots. Sizes of excavated clones were similar in May burned and January-burned plots, but clone structure differed. May fires caused clones to shift the allocation of biomass from older, larger mother shoots to more numerous, smaller daughter shoots emerging from axillary and terminal buds on rhizomes immediately after fire and after flowering. In contrast, following January fires, shoot initiation rates were lower. Therefore, much of the residual biomass was allocated to the replacement of aboveground parts of mother shoots that survived the fires. Thus, phenotypic plasticity in allocation patterns among integrated shoots within clones probably contributed to most of the differences in shoot size and shoot demography between January-burned and May-burned plots. The results of this multivariate approach to characterizing clone structure call into question the use of modular demography models to quantify growth rates if clonal structure involves integrated ramets or shoots.

Models that quantify growth rates of clones on the basis of shoot demography within clones would have predicted that clones of *P. graminifolia* would have been larger in May-burned plots than in January-burned plots. This is because May fires stimulated greater rates of net shoot production than did January fires. A major shortcoming of modular demographic models is that they do not allow for a trade-off between the effects of shoot size and shoot number on clone size. I suggest that trade-offs between shoot size
and shoot number are likely within physiologically integrated clones subjected to chronic aboveground disturbance (e.g. fire).

The ability of physiologically-integrated clones of P. graminifolia to exhibit plastic allocation responses to fire is positively associated with the likelihood that longleaf pine savannas will burn as a result of lightning fires at a particular time of the year. Lightning fires have occurred within pine savannas in Florida for thousands of years at least (Frost 1993). The frequency of thunderstorms and thus lightning fires is higher during May than during January in Florida (Komarek 1964, Chen and Gerber 1990). January fires, while frequent, are typically anthropogenic in origin and as such are a more recent phenomenon in Florida (Frost 1993). Allocation to new shoots was greater following May fires than following January fires. The proximate cause of these differences in foraging capacity is probably related to differences in the phenological states of plants in May and January. Therefore, it is reasonable to hypothesize that the seasonal rhythms exhibited by P. graminifolia pre-adapted it to performing well in response to May fires.

I hypothesize that the ability of clones of P. graminifolia to shift the mode of resource allocation to transient vegetative spread following May fires enables them to expand into the surrounding environment and acquire resources available on a short-term basis. In the absence of
fire or following dormant-season fires, clones of this species proportionally increase allocation to existing shoots to increase shoot height and thus reduce shading. In contrast, species not adapted to frequent fires might not be expected to exhibit such plasticity. Most likely, they would be clonal fugitives, i.e., species that would consistently allocate a large proportion of resources to vegetative spread to colonize openings in the groundcover in years with or without growing-season fire. I suggest that the flexible plastic allocation strategy exhibited by *P. graminifolia* in response to frequent growing-season fires results in a more efficient means of resource allocation than would a clonal fugitive strategy.

**Effects of Multiple Factors on Rates of Vegetative Spread in *Pityopsis graminifolia***

The spatial model of phenotypic variation in rates of vegetative spread predicts that, in addition to large scale events such as fire, small scale factors affect rates of vegetative spread in *P. graminifolia*. The model also predicts that these small scale factors have more persistent effects on rates of vegetative spread than does fire and that these factors are more apparent in the absence of May fires. These small scale factors may include the size and/or genotype of individual clones (Grace and Wetzel 1981, Turkington and Harper 1979), microsite conditions (Pitelka and Ashmun 1985), and the effects of neighbors (Kenkel
Clones or genotypes that are large or are located within favorable microsites with few neighbors are expected to produce more daughter shoots and for longer periods of time than small shoots or genotypes in unfavorable microsites. In these cases, the rate of vegetative spread of a clone may be positively correlated with its growth rate or size, rather than indicating a proportional allocation strategy evolved to track the occurrence of sublethal fire.

One small scale factor that likely contributes to prolonged increases in rates of vegetative spread in longleaf pine savannas is the occurrence of small patches of favorable environmental conditions following intense disturbances. One potential cause of such patchily distributed microsites in longleaf pine savannas is spatial variation in fire intensity. Survival and rapid regrowth of perennial herbs following fire is extensive in longleaf pine savannas because surface fires typically kill aboveground parts, but not belowground parts (Platt et al. 1988a). However, these fires occasionally kill entire plants in a few localized "hot spots" associated with downed trees and areas of dense needle cast (Platt et al. 1991, Streng et al. 1993). These hot spots may be sufficient to create small gaps in the groundcover. The closure of these gaps by surrounding vegetation is likely much slower than is regrowth of vegetation following low-intensity fire outside these gaps. Those shoots or clones of *P. graminifolia* that
are able to colonize these disturbances rapidly may experience a prolonged reduction in the intensity of both aboveground and belowground competition. Therefore, in the absence of growing-season fires, increased rates of vegetative spread (and perhaps increased growth rates of clones) may be restricted to areas of low density, where the overall intensity of competition has been reduced (e.g. gaps in the groundcover).

Previous models of clonal growth have examined the effects of environmental variation that is either density-dependent or density-independent (e.g. Sarukhan and Gadgil 1974, Sackville Hamilton et al. 1987, Kenkel 1993). Few models, however, addressed the effects of both density-dependent and density-independent sources of environmental variation simultaneously (but see Loehle 1987). In the spatial model presented here, both sources of environmental variation were addressed. Results indicate that density dependent and density-independent sources of environmental variation can be distinguished on the basis of the temporal and spatial scales of their effects. In the pine savanna studied here, low-intensity fire results in large scale, transient changes in the environment without reducing shoot density, while the presence of gaps in the groundcover community results in persistent small scale spatial variation in shoot density. Thus, rates of vegetative spread in P. graminifolia are influenced by
density-independent changes in the environment associated with growing-season fires and perhaps by density-dependent environmental variation associated with the presence of gaps. I suggest that models of clonal growth in chronically disturbed habitats need to consider the duration and spatial scale of both density-dependent and density-independent sources of phenotypic variation in producing rates of vegetative spread.

Adaptive Significance of Allocation Responses to Chronic Sublethal Aboveground Disturbance

Most discussions of the adaptive significance of allocation patterns within clones following aboveground disturbance have considered only the responses of graminoids to herbivores (e.g. McNaughton 1984, Coughenour et al. 1985b, Milchunas et al. 1988). The model of plant-grazer interactions presented by Milchunas et al. (1988) predicts that plant species that have coevolved with grazers should most likely respond to moderate levels of grazing with increased allocation to new shoots. Increased numbers of shoots or tillers/clone and regrowth of defoliated shoots or tillers have different effects on the subsequent mode of competition (Milchunas et al. 1988). It is suggested that increasing the numbers of shoots/clone following aboveground disturbance allows clonal plants to take advantage of windows of relaxed aboveground competition by more efficiently "foraging" for soil resources. Results from the
current fire study indicate that aboveground disturbances such as fire and grazing may interact with plant phenology to determine the ability of clones to respond to aboveground disturbance with increased allocation to new shoots. Results from a previous study (see Chapter 3) showed that neither dormant-season fires (e.g. January fires) nor fires occurring late in the lightning season (e.g. August fires) were effective at shifting the allocation of resource to new shoots within clones of P. graminifolia. I predict that shifting the season of grazing or fire away from "natural" peak periods of occurrence might affect the ability of clones to respond to relaxed aboveground competition following grazing or fire with increased allocation to new shoots.

If results from the current study of fire effects apply to other aboveground disturbances such as grazing by generalist herbivores, then in years marked by the absence of grazing or fire during the natural peak season, the effects of numerous factors such as clone size and genotype, soil conditions, and the density of neighbors on rates of vegetative spread should become more apparent. I hypothesize that while increased rates of vegetative spread following grazing or fire may reflect an altered pattern of allocation, it is possible that higher rates of vegetative spread resulting from other, more persistent, sources of phenotypic variation (e.g. large clone size, location in
gaps, low module density) reflect faster growth rates or larger sizes of clones. It is likely that the effects of sublethal disturbances on clonal growth interact with more persistent sources of phenotypic variation. For example, transient increases in rates of vegetative spread of grazophilic or pyrophilic clones following moderate grazing or fire might enable such clones to readily colonize sparsely distributed, but longer-lasting, favorable microsites (e.g. gaps).

To understand the adaptive significance of clonal growth responses to environmental variation in chronically disturbed habitats, it is important to consider multiple causes of clonal growth responses. The chronic occurrence of sublethal disturbances likely favors those clones capable of shifting the proportional allocation of resources to and away from new shoots in such a way as to enable them to track the occurrence of sublethal disturbances. In contrast, increased rates of vegetative spread resulting from large clone size or location within gaps enables clones to take advantage of small-scale variation in density or the availability of resources.
CHAPTER 5 - SUMMARY AND CONCLUSIONS
The goal of this dissertation was to examine how fire season influences components of fitness (e.g. reproductive success and clonal growth) in a pyrophilic forb of longleaf pine savannas. I examined the relationship between the performance of *Pityopsis graminifolia* following fires at different times of the year and the expected frequency of lightning fires occurring at different times of the year in north Florida.

To study the effects of fire season on reproductive success in *P. graminifolia*, I experimentally manipulated fire season in a longleaf pine sandhill community in north Florida and studied floral induction, bud herbivory, clone fecundity, and seedling dynamics. In addition, some proximate cues of fire-related floral induction were examined using a factorial arrangement of clipping season and fertilization treatments in 1992.

Flowering was induced by fire. Results from the clipping/fertilization experiment showed that removal of canopy and litter was an important inductive cue associated with fire. Floral induction of clipped shoots was further influenced by soil fertility and the season during which clipping occurred.

Fire season influenced the proportion of shoots that bolted, bud herbivory, and the size of bolting shoots. Rates of herbivory of capitular buds were much lower following May and August (growing-season) fires than following January
fires in 1990 and 1992. As a result, fecundity of growing-season-burned clones was greater than that of January-burned clones in 1992. Fecundity was greater in May-burned clones than in August-burned clones in 1992 because of greater shoot size.

Seedling emergence in early 1991, following 1990 fires, was highest in May-burned plots, intermediate in August-burned plots, and lowest in January-burned plots. Seedling survivorship through December 1992 was low in all fire season plots, but still varied in response to fire season (6% in May-burned plots, 2% in August-burned plots, and 0% in January-burned plots). Successful reproduction of 1991 cohorts following 1992 fires only occurred in May-burned plots.

Results from the reproductive success study suggested that reproductive success in *P. graminifolia* was greatest in May, intermediate in August and lowest in January. These rankings are the same as the relative likelihoods that longleaf pine savannas will burn at these different times of the year.

To study fire season effects on clonal growth in this species, I determined the size and demography of shoots, rhizomes, and clones from late 1990 to early 1993. In addition, I examined shoot responses to seasonal variation in canopy/litter removal and soil fertility in 1992.
May fires caused a higher short-term per shoot rate of increase in shoot density than did either January or August fires. The combination of canopy/litter removal and mineral nutrient addition as part of the clipping experiment revealed a similar effect on shoot density in May.

Fire season influenced clone structure. May fires resulted in greater numbers of shoots/clone than did January or August fires. January-burned plots had clones and rhizomes that contained larger (but fewer) shoots than did May-burned or August-burned plots. I suggest that such variation in clone structure may indicate a greater capacity of clones to "forage" for soil resources following May fires than following either January or August fires. This capacity is in part positively associated with the likelihood of being burned by lightning fires at different times of the year.

To investigate multiple sources of phenotypic variation in clone structure in this species, I developed a multivariate model and a spatial model of phenotypic variation in clonal growth responses to May and January fires. The multivariate model showed that when clones of this species were subjected to May fires, modular demography mostly reflected proportional allocation of resources within clones rather than overall growth rates of clones. These results call into question the general use of modular demography models to quantify growth rates of clones and
genets. Results from the spatial model indicated that multiple factors affected rates of vegetative spread of clones of this species. The effects of May fires on rates of vegetative spread were evident over a large proportion of the area studied, but were mostly restricted to the year of fire. The effects of other factors (e.g. clone size and/or genotype, location within gaps) on rates of vegetative spread were important at much smaller scales, but persisted for at least two years. I believe that increased rates of vegetative spread resulting from proportional shifts in resource allocation following the removal of aboveground plant parts by May fires are positively correlated with a hypothesized shift in competition from aboveground to belowground. In contrast, I suggest that higher rates of vegetative spread associated with other factors (e.g. location in gaps) may reflect faster growth rates or larger sizes of clones. Models of clonal growth, at least in chronically disturbed habitats such as the longleaf pine sandhill studied here, should incorporate differences in proportional resource allocation and growth rates and sizes of clones.

In conclusion, fire season appeared to influence components of fitness related to reproductive success and clonal growth in *Pityopsis graminifolia*. This species is one of many clonal herbaceous species in longleaf pine savannas that exhibits increased flowering following growing-season
fires (Platt et al. 1991, Streng et al. 1993). I suggest that further study of fire season effects on reproductive success and clonal growth of species from a wide variety of taxonomic groups would reveal new insights into the nature of adaptive specialization of life history traits to fire. I believe that such insights could provide the basis of an informed evolutionary approach to the conservation of longleaf pine savannas.
LITERATURE CITED


VITA

John Stephen Brewer was born on February 15, 1964, in Mountain Home, Arkansas. He graduated from Little Rock Central High School in 1982. From 1982 to 1986, he attended Hendrix College in Conway, Arkansas and received a Bachelor of Arts degree in biology. He received a Master of Science degree in botany from Louisiana State University in 1989 and has been in the doctoral program in botany at LSU since 1989. His academic interests include the ecological and evolutionary significance of disturbance in plant populations and communities and the functional morphology of clonal herbs.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: John Stephen Brewer

Major Field: Botany

Title of Dissertation: Life History Responses to Fire Season in a Clonal Herb, Pityopsis graminifolia (Asteraceae)

Approved:

William A. Platt
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

November 30, 1993