EFFECTS OF FIRE ON THE REPRODUCTIVE ECOLOGY OF TEPHROSIA VIRGINIANA (L.) PERS. IN THE CAROLINA SANDHILLS

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by

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INTRODUCTION AND LITERATURE REVIEW

Fire is an important natural component of many ecosystems around the world
(Bond and van Wilgen 1996). Although fires pass very rapidly, their effects on
population or community dynamics can be long-lasting (Whelan 1995). Fires can cause
dramatic changes in the structure and composition of plant communities by killing some
species, stimulating reproduction in others, and providing conditions suitable for
recruitment (Gill 1981, Bond and van Wilgen 1996). Furthermore, changes in the fire
regime such as increased intervals between fires or increased fire intensity may affect the
ability of a plant species to survive or reproduce following fire (Rebertus, et al. 1993).

Herbaceous species that grow in fire dominated ecosystems often exhibit traits
such as underground bud protection and fire-stimulated reproduction which enhance
survival and reproduction following fire (Gill 1981). Subterranean buds borne on
underground rhizomes, tubers, or roots are protected from temperature extremes during
fires by the soil (Heyward 1938, Gill 1981, Bond and van Wilgen 1996). The removal of
apical meristems during fires, (Matlack, et al. 1993), post-fire nutrient release (Hulbert
1988, Dudley and Lajtha 1993), and increased light from canopy and litter removal lead
to the release and growth of these buds. Furthermore, the bud release and resulting shoot
density and size can be influenced by the seasonal timing of the burn (Brewer and Platt
1994) and the frequency of fire (Whelan 1995).

Fire-stimulated flower and seed production is common for plant species in fire-
prone ecosystems (Gill 1981). Mass flowering events following fires may serve to
increase pollination, leading to increases in fruit and seed set (Platt, et al. 1988, Robbins
and Myers 1992). These increases could play an important role in satiating seed predators
(Mark 1965), which could then lead to enhanced seedling establishment (Whelan 1995).
The timing of flowering and fruiting may be shifted towards or away from beneficial

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pollination or seed dispersal periods by alterations in the seasonal timing of fire (Robbins and Myers 1992).

The longleaf pine (Pinus palustris) ecosystem of the southeastern United States is one system for which fire has long been known to be an important natural component (Garren 1943). Fire plays an important role in structuring the longleaf pine forest (e.g. Hodgkins 1958, Christensen 1981, Mehlman 1992, Streng, et al. 1993), affecting species diversity and composition (Lewis and Harshbarger 1976), and influencing reproduction and recruitment of species native to this ecosystem (Platt, et al. 1988, Brewer and Platt 1994, Streng, et al. 1993, van Eerden 1997). Historically, the longleaf pine system burned frequently, with a return interval of 1 to 5 years (Christensen 1981), most likely during the growing season (mid-April through July) when lightning strikes are most common (Komarek 1964, Streng, et al. 1993). Early settlers modified this regime by setting fires during the dormant winter season because fires were easier to control due to lower air temperatures and they were thought to minimize negative effects on the overstory pines which were important timber species (Streng et al. 1993). In recent years, conservationists have argued for a return to the use of lightning season burns in prescribed fire programs (Streng, et al. 1993).

Although declines in plant species diversity have been well documented for unburned areas in southeastern U.S. pinelands (Garren 1943, Lewis and Harshbarger 1976, Mehlman 1992, Brockway and Lewis 1997), data for season of burn effects on species composition are lacking for longleaf pine communities (Robbins and Myers 1992). One study indicates some differences in plots subjected to different seasons of burn (Lewis and Harshbarger 1976), but lack of statistical analysis hampers interpretation (Robbins and Myers 1992). Results from a study that examined species richness and community composition after 39 years of dormant season burning suggest that long-term use of dormant season burning may be equivalent to growing season burning and beneficial to sustaining the longleaf pine system (Brockway and Lewis 1997). However,

this study is hampered by the lack of a set of growing season burn treatments for comparison. Streng, et al. (1993) found that there were no differences in herbaceous composition among burn seasons after 10 years of burning. They note that this lack of difference may be due to infrequent recruitment and the long-lived perennial nature of the species involved. Thus, season of burn effects may not become apparent in short-term studies, which comprise the majority of the fire-response investigations for plant community composition in the Southeast.

Variations in the seasonal timing of fire have been shown to have strong effects on the reproduction of many plant species native to the longleaf pine ecosystem (e.g. Biswell and Lemon 1943, Parrott 1967, Platt, et al. 1988, Brewer and Platt 1994, van Eerden 1997). Fire-stimulated flowering ranges from weakly facultative in some species such as the pencil flower, Stylosanthes biflora, and the shortleaf blazing star, Liatris tenuifolia, (Streng, et al. 1993) to near-obligate in other species such as wiregrass, Aristida stricta (Parrott 1967, van Eerden 1997). The number of inflorescences produced for many species, including fall-flowering composites, has been shown to increase following growing season fires (Platt, et al. 1988). Flowering following growing season fires tends to be of shorter duration and is delayed compared to flowering following dormant season fires (Platt, et al. 1988). Proximate cues which trigger flowering have been relatively unexplored for most plant species in the longleaf pine ecosystem (but see Brewer and Platt 1994).

Few studies have examined responses to changes in the seasonality of fires for later stages of reproduction, including fruit and seed production. Furthermore, no studies known to the author have examined impacts of other factors, such as seed predation, on fecundity and recruitment. Only three studies in the southeastern Coastal Plain known to the author have examined how seed production changes with season of burn. These have focused on a graminoid (Outcalt 1994, Van Eerden 1997) and on a composite (Brewer and Platt 1994). Although flowering is useful as an indicator for successful fruit and seed

production, outside influences such as lack of pollinators, seed predation, and attack by pathogens may limit the seed crop, thereby causing flower production to be an overestimate of reproduction. These limitations on the seed crop could lead to lower levels of recruitment because of the lack of propagules, thereby playing an important role in the reproduction of a given species (Louda 1995), a role which would be missed in studies focused solely on flowering.

The reproductive response of legumes to changes in the timing of fires has received little attention despite their abundance in many sub-xeric and mesic sites in the longleaf pine ecosystem (Peet and Allard 1993). Because of their ability to fix nitrogen in root nodules, legumes are an important part of many ecosystems. The seed crop and foliage of various legume species can also be of special concern as forage for important game animals, such as quail (Stoddard 1931, Landers and Johnson 1976). Legumes have traditionally been thought to respond more favorably to dormant season burns (Stoddard 1931, Waldrop, et al. 1992), although some evidence suggests that some legumes may respond better to growing season burns (Cushwa, et al. 1970, Robbins and Myers 1992, Dudley and Lajtha 1993). Because of their ability to fix nitrogen, factors such as post-fire nutrient release may not be as important in these plants as in non-nitrogen fixing species for stimulating flowering and/or fruit and seed production following fires.

The purpose of this research was to understand the reproductive response of a legume, Tephrosia virginiana, to fire and seasonal timing of fire in the sandhills of South Carolina. The first chapter addresses the response of fruit and seed production for unburned plants and plants which have been burned during different seasons. An analysis of how seed predators modify seed production and how role of the seed predator changes following burns during different seasons is included in this chapter. Chapter two elucidates proximate factors through which fire influences flowering and fruit production of this legume. Results from this work could provide insight into management practices

which would increase seed production for this legume and legumes in general for forage for game and propagules for restoration.

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CHAPTER 1:
FRUIT PRODUCTION, SEED SET, AND SEED PREDATION IN RESPONSE TO FIRE AND SEASONS OF BURN FOR GOAT'S RUE (<u>TEPHROSIA VIRGINIANA</u> (L.) PERS.) IN THE CAROLINA SANDHILLS.[1]

Abstract:

We studied production of fruits and seeds and seed predation of goat's rue (Tephrosia virginiana (L.) Pers.) in unburned sites and sites burned during different times of the year in the sandhills of South Carolina. Fruits were counted and seed production and seed predation were estimated in 14 sites that had either been burned during the dormant season (January-March), burned during the growing season (late April-May), or was not burned in that year (1997). Fruit production was significantly higher in burned plots but was not different between the two burn periods, although plots burned during the growing season exhibited higher averages and among-replicate variation than plots burned during the dormant season. Estimated seed production was significantly greater in the plots burned during the growing season while seed predation rates were significantly lower. These results suggest that fires in the spring and summer maximize conditions for seed production and minimize the effects of seed predators, while seed predation effectively eliminates seed production for unburned areas.

Key words: fire season, fire effects, fruit production, seed production, seed predation, Tephrosia virginiana

Introduction:

Fire has long been recognized as an important natural component of the longleaf pine (Pinus palustris) ecosystem of the southeastern United States (Garren 1943). It has been shown to play an important role in structuring longleaf pine forests (e.g. Hodgkins 1958, Christensen 1981, Mehlman 1992, Streng, et al. 1993), affecting species diversity and composition (Lewis and Harshbarger 1976), and influencing reproduction and recruitment of plant species native to this ecosystem (Platt, et al. 1988, Brewer and Platt 1994a, Streng, et al. 1993, van Eerden 1997). While studies in other biomes have shown

that fire effects vary with fire regime, i.e. intensity, frequency, and seasonality (Bond and van Wilgen 1996), the consequences of differing fire regimes have not been explored extensively for longleaf pine communities (but see Platt, et al. 1988, Brewer and Platt 1994a,b, van Eerden 1997).

Historically, the longleaf pine system burned frequently, with a return interval of 1 to 5 years (Christensen 1981). Prior to European settlement, fires most likely occurred during the growing season from April to July when lightning strikes are most common (Komarek 1964, Streng, et al. 1993). Early settlers modified this regime by setting fires during the dormant winter season because fires were easier to control due to lower air temperatures and because burning at that time of year was thought to minimize negative effects on the over-story pines, which were important timber species (Streng, et al. 1993). In recent years, conservationists have argued for a return to the use of lightning season burns in prescribed fire programs (Streng, et al 1993), a practice some public land managers in the longleaf pine ecosystem have begun to use (M. Housh, personal communication).

Herbaceous under-story community composition has been shown to be influenced by season of burning for many systems including the prairies of North America (Henderson 1992, Howe 1994, 1995), semi-arid grasslands of Argentina (Boo, et al. 1996), and South African fynbos (Bond 1984). Although declines in species diversity have been documented for unburned areas in southeastern pinelands (Garren 1943, Lewis and Harshbarger 1976, Mehlman 1992, Brockway and Lewis 1997), data for season of burn effects on herbaceous composition for longleaf pine communities are lacking (Robbins and Myers 1992, but see Brockway and Lewis 1997). One study indicates some differences in plots subjected to different seasons of burn (Lewis and Harshbarger 1976), but lack of statistical analysis hampers interpretation (Robbins and Myers 1992). A later study (Streng, et al. 1993) found that there were no differences in herbaceous composition after 10 years of burning during different seasons. Streng, et al. (1993) note that this lack

of difference may be due to infrequent recruitment and the long-lived perennial nature of the species involved. Thus, season of burn effects may not become apparent in short-term studies which comprise the majority of the fire-response investigations for community composition in the Southeast.

The effects of burn season on reproductive responses of plants in the longleaf pine ecosystem have received more study than the effects of burn season on herbaceous composition. The majority of these studies have used flowering to represent reproduction (e.g. Biswell and Lemon 1943, Parrott 1967, Myers and Boettcher 1987, Platt, et al. 1988). In one study, Platt, et al. (1988) found that for many species the number of flowering stems increased, the duration of flowering decreased, and flowering phenology was shifted to later in the growing season following fires during the growing season. Parrot (1967) found that wiregrass (Aristida stricta) flowered profusely after growing season fires, a response similar to another native grass in south Florida (Myers and Boettcher 1987).

Few studies have examined the response of later stages of reproduction, including fruit and seed production, to changes in the seasonality of fires. Furthermore, no studies known to the authors have examined impacts of other factors, such as seed predation, on fecundity and recruitment. We know of only three studies in the southeastern Coastal Plain that have examined how seed production changes with season of burn and these focused on a grass (Outcalt 1994, Van Eerden 1997) and a composite (Brewer and Platt 1994a). Although flowering is useful as an indicator of successful fruit and seed production, biotic influences such as lack of pollinators, seed predation, and attack by pathogens may limit the seed crop thereby making flower production an overestimate of reproduction. These limitations on the seed crop could lead to lower levels of recruitment because of the lack of propagules, thereby playing an important role in the reproduction of a given species (Louda 1995), a role which would be missed in studies focused solely on flowering.

Most studies on the reproductive response of plants to fire in the southeast have focused on two of the dominant plant families in the longleaf pine ecosystem, the composites and grasses, while a third major plant family, the legumes, has received little attention. Studies on composition of longleaf pine forests have noted large numbers of individuals and species of legumes in many sub-xeric and mesic sites (Peet and Allard 1993). Legumes are an important part of many ecosystems due to their ability to fix nitrogen in root nodules. The seed crop and foliage of various legume species can also be forage for important game animals, such as quail (Stoddard 1931, Landers and Johnson 1976). Legumes have been traditionally thought to respond more favorably to dormant season burns (Stoddard 1931, Waldrop, et al. 1992), although some evidence suggests that some legumes may respond better to growing season burns (Cushwa, et al. 1970, Robbins and Myers 1992, Dudley and Lajtha 1993).

In this study, we examine fruit and seed production and seed predation in a native legume, Tephrosia virginiana, common to the longleaf pine ecosystem. We address these questions: (1) What is the effect of fire on fruit and seed production? and (2) How does season of burn influence fruit and seed production and seed predation?

Methods:

Study Species

Goat's Rue, Tephrosia virginiana, is an herbaceous perennial legume native to the eastern half of North America from eastern Texas to the Atlantic coast and from southern Ontario south to mid-peninsular Florida (Wood 1949), and is the most common of the seven species of Tephrosia found in the eastern U.S. (Sievers, et al. 1938, Wood 1949). Over much of its range, this species grows in rolling to steep terrain in open, acid soils (Wood 1949), typically in areas with low densities of trees (Clark 1971). In the sandhills of South Carolina, T. virginiana grows on xeric sand ridges, side-slope communities, and mesic swales where it is one of the most abundant legumes.

The typically clumped stems grow from the indeterminate end of a rhizome, eventually reaching a height of 2-7 dm. The cream and purple flowers are produced in terminal racemes during late April, but can occur as late as September if the plant is burned or a portion of a rhizome is damaged (personal observation). Its breeding system has not yet been determined, but is most likely out-crossing and bee pollinated like other legumes (Platt et al. 1974, Hermann-Parker 1978, Hendrix 1994).

The two-valved, linear legume fruit matures and dehisces explosively in August, sending seeds up to 4 m from the parent plant (Clark 1971). Approximately 10% of the seed crop, mostly the largest seeds produced, will germinate immediately under suitable conditions (personal observation). The rest of the seeds exhibit dormancy (Clark 1971), most likely due to an impermeable seed coat as in other legumes (Quinlivan 1971). Seeds have cryptic coloration, mainly in various shades of brown, gray, or black (Wood 1949), and can remain viable for several years after dispersal (Clark 1971). The larvae of a host-specific curculionid weevil (Apion segnipes) develop in the seed pod by feeding on the seeds, consuming substantial portions of the seed crop (Sievers et al. 1938, Kissinger 1968). Adult weevils either tunnel out of the legume or get flung from the legume when it dehisces (Clark 1971). Other characteristics such as seedling growth, root anatomy, and leaf morphology are detailed in Clark (1971).

Study Area

Second-growth stands of longleaf pine (Pinus palustris Miller) in the Carolina Sandhills National Wildlife Refuge (CSNWR), Chesterfield County, SC, were used for this study. The 18,000 hectares which comprise the refuge are located in the fall-line sandhills, a physiographic region found along the western edge of the Atlantic Coastal Plain characterized by rolling terrain of primarily Cretaceous-age sediments. Uplands in this region were dominated historically by xeric to sub-mesic longleaf pine/wiregrass (Aristida stricta Michx.) woodlands (Peet and Allard 1993), although roughly half of

these areas on the Refuge have been converted to silvicultural pine plantations in the past 30 years. An active fire management program on the Refuge has conducted prescribed fires on an approximately three year cycle over the past twenty years, a frequency well within the natural fire regime for these communities (Christensen 1981, Brewer and Platt 1994a). Lightning season burns (April-June) and winter burns (December-March) are both used within this fire program.

Although the majority of the pines on the lands of the Refuge were logged in the early 1900's like many other areas in the longleaf pine ecosystem (Noss 1989), herbaceous species typical for undisturbed (not cleared or plowed) old-growth stands remain (Wells and Shunk 1931), indicating minimal human soil disturbance. Sites used in this study had an open canopy (<30% cover) of mature longleaf pine with a short mid-story of turkey oak (Quercus laevis Walter). Wiregrass is the dominant species in the herbaceous layer, but many forbs, grasses, and short shrubs including Andropogon spp., Carphephorus bellidifolius (Michx) T.& G., Euphorbia ipecacuane L., Gaylussacia dumosa (Andrz.) T. & G., and Solidago odora Aiton. (follows Radford, et al. 1968) grow in the interstitial spaces between the wiregrass clumps.

Sampling Procedure

Fourteen longleaf pine/wiregrass sites in which T. virginiana grew were selected for this study (Table I). We first identified all sites on the Refuge that had been subjected to one of three fire management prescriptions during 1997: unburned, dormant season burned (burned during January-March), or growing season burned (burned during April-June). From this group, we then chose sites that met the following criteria for burn history prior to 1997 and soil characteristics. To minimize variation in fire history, we chose only sites which had been burned more than three times in the 10 years prior to 1997. Unburned sites had last burned in 1995 or 1996. All sites were located on sub-xeric to mesic sands of the Alpin, Candor or Ailey soil series (SCS soil surveys for

Chesterfield County). Many of the populations of T. virginiana found on the Refuge grow in areas where the xeric Alpin or Candor sands border the mesic Ailey sands, although several populations do grow both higher and lower along the moisture gradient (Mejeur, personal observation). Five sites each were chosen for growing season burned and unburned fire types, while four sites were chosen for the dormant season burned type due to difficulty in finding sites with T. virginiana that met the burn history criteria.

Within each site, one 10 x 20 m plot was haphazardly placed in an area with <5% slope, <20% canopy cover, and open midstory, and a standard number of T. virginiana individuals (approximately 0.5 plants/m^2). Individual T. virginiana plants were defined to be discrete groups of stems which did not appear to be connected to other groups of stems, a definition which possibly overestimates the number of individuals. Each plot was divided into eight modules, each 5 x 5 m, for ease of sampling. In August 1997, total stems, total reproductive stems (stems which had at least one fruit), and total fruits were counted for each individual in each 200 m^2 plot and the module in which each plant was located was noted. For several plots, some of the fruits had begun to dehisce prior to sampling, but the pedicels and one or both of the valves remain attached to the peduncle after dehiscence, thus minimizing the chance of underestimating fruit production. All fruits in each module were collected and marked with the module and plot number. Derivative statistics were calculated from the count data, including stems per individual, fruits per individual, reproductive stems per individual, percentage of stems producing fruit, the number of fruits per fruiting stem and fruits per stem. The percentage of individual plants that produced fruit was also recorded.

From October to December 1997, fruits were sampled for seed production and seed predation. Seed production for non-dehisced fruits was defined as the presence of seeds when the fruit was opened manually, while seed production for dehisced fruits was defined as either the presence of seeds, or the presence of a fully enlarged segment that exhibited no detritus from the weevil. Seed predation was defined as the presence of the

weevil in non-dehisced fruits or the presence of a fully enlarged segment exhibiting

detritus from the weevil. Although sampling for seed predation in this manner can lead to

an underestimation of the total effect of the seed predator on seed production (Andersen

1988), it can provide information on patterns of predation.

A total of 4788 fruits were sampled for seed production and seed predation (Table

I). Fruits from each module of a plot were sampled for seed predation and seed

production in one of two ways. Because many of the collected fruit dehisced before

sampling, each sampled fruit was noted as having either one or two valves present. If the

number of fruits in a module was under 100, all fruits were sampled. If the number of

fruits in a module was over 100, either 25% of the fruits were selected randomly and

sampled or 100 fruit were selected randomly and sampled, whichever resulted in a higher

sample. Since one-valved fruits potentially could have been counted twice, module

averages for fruits counts, seed production per fruit, and seed predation per fruit were

calculated by taking one-half of the one-valve value, adding the two-valve value, and

dividing by two. Two unburned plots were not sampled for seed production because both

produced too few fruits (0 and 4 fruits) to estimate seed production and predation.

These values were then used to determine the number of predation events per

predated fruit, the percentage of fertile fruits, and the percentage of fruits predated. All

module values for the count data and derivative statistics were averaged to obtain a plot

value for each plot sampled. These plot averages were multiplied by the total number of

fruits counted within the plot to estimate the seed production per plot, fruits with at least

one seed per plot (fertile fruits/plot), predation events per plot, and fruits with at least one

predation event per plot.

Statistical Analyses

A one-way analysis of covariance test (Ott 1993) was used to analyze stems per

site and fruits per stem, using number of individuals per plot as a covariate. All other

counted and derived site averages for fruit production, seed production, and seed predation were analyzed using a one-way analysis of variance test (Ott 1993) for the effect of burning and season of burning. All data were log transformed prior to analysis to reduce heteroscedasticity (Ott 1993). Treatment means were compared using the Student-Newman-Keuls multiple range test (alpha=0.05).

Linear correlations were used to examine the relationship between reproductive output of T. virginiana and two components which are associated with seasonality: maximum air temperature on the day of the burn and Julian day. Correlations were performed on all data regardless of the season to which a site was classified.

Results:

Stem production

The number of individual plants per plot exhibited a marginally significant difference among the different burn periods ($F=3.98$, $p=0.0528$), with dormant season burned areas tending to have fewer numbers of plants (Fig. 1A). We detected significant differences among burn periods for stem production per plot ($F=11.72$, $p=0.0013$). Growing season burned plots had significantly more stems per plot than unburned plots, but dormant season burned plots did not differ significantly from either of the other two burn types (Fig. 1B). The percentage of total individual plants that produced fruit differed significantly among burn types, with the highest percentage of individuals producing fruit in the growing season burned plots and the lowest in the unburned plots ($F=35.2$, $p<0.0001$) (Fig. 1C).

Fruiting stem production

Burned plots had significantly higher numbers of stems with fruits (reproductive stems) than unburned plots ($F=14.72$, $p=0.0008$), but did not differ between the two burn periods (Fig. 2A). Significant differences between burned and unburned plots in the

percentage of the total stems that were reproductive stems were observed (*F=6.35,*
p=0.0147). Growing season burned plots had a higher percentage of reproductive stems
than unburned plots while dormant season burned plots did not differ from the growing
season burned or unburned plots (Fig. 2B). Unburned plots also differed significantly
from burned plots in the *number* of reproductive stems per individual plant (*F=17.03,*
p=0.0004) (Fig. 2C), but no differences were detected between the two burn periods.
Growing season burned plots had the highest average density of reproductive stems per
plant, but had the largest variation as well.

Fruit production

Fruit production was significantly higher in burned plots than in unburned plots
(*F=13.30, p=0.0012*). Growing season burned areas exhibited a higher average number
of fruits per stand than dormant season burned areas, but also a higher variation in fruit
production (Fig. 3A). Fruits per stem exhibited the same trend with burned areas having
significantly higher numbers of fruit per stem than unburned areas (*F=5.75, p=0.0150*),
but exhibiting no significant differences between the two burn periods (Fig. 3B). None of
the burn treatments differed in fruits per reproductive stem, although dormant season
burned areas had slightly higher average fruits per reproductive stem (*F=3.70, p=0.0799*)
(Fig. 3C). Fruits per individual were significantly higher in burned plots than in
unburned plots but also did not differ between the two burn periods (*F=16.86, p=0.0004*)
(Fig. 3D). Growing season burned plots exhibited the highest average fruit yield per plant
as well as the most variation, ranging from 3.1 to 28.5 fruits per plant.

Seed production

We detected significant differences in seed production both between unburned
and burned plots and between burn periods (*F=10.93, p=0.0039*). Growing season
burned plots had much higher estimated seed yields than either dormant season burned or

unburned plots, while unburned plots had the least (Fig. 4A). Estimates for seed production for growing season burned plots ranged from 79 to 3109 seeds per plot, while unburned sites had a maximum estimate of 13 seeds per plot. Dormant season burned plots averaged an order of magnitude lower seed yield than growing season burned plots (85 vs. 1076). Growing season burned plots had significantly more seeds per fruit than dormant season burned plots, but unburned plots did not differ significantly from either burn period ($F=5.13$, $p=0.0325$) (Fig. 4B). Burned plots did differ from unburned plots in seeds per individual plant ($F=8.10$, $p=0.0069$), but did not differ between burn seasons (Fig. 4C). The percentage of fertile fruits was marginally significantly higher in growing season burned plots than the other two treatments ($F=4.01$, $p=0.0569$) (Fig. 5A). Estimated number of fertile fruits produced per plot differed between the three treatments with growing season burned plots producing far more fertile fruits than the other two treatments ($F=11.0$, $p=0.0038$) (Fig. 5B).

Seed predation

We found significantly greater seed predation per fruit in unburned plots than in either of the two burn seasons ($F=11.47$, $p=0.0033$) (Fig. 6A). The amount of seed predation within fruits that had at least one predation event was not significantly different between any of the three burn types ($F=2.32$, $p=0.1540$) (Fig. 6B). The highest amount of seed predation in predated fruits was in an unburned plot (2.1 seeds eaten). The level of seed predation was significantly lower in growing season burned plots than the other two burn treatments ($F=6.04$, $p=0.217$) (Fig. 6C). Seed predation levels ranged from a low of 44% in a growing season burned plot to 94.3% in an unburned plot.

Burned plots exhibited significantly more fruits with some seed predation per plot than unburned plots ($F=7.76$, $p=0.011$) (Fig. 7A), although this is more likely due to the significant differences in fruit produced (Fig. 3A) than to seed predator populations

present at a site. The percentage of fruits exhibiting some predation was significantly higher in unburned plots than burned plots ($F=9.34$, $p=0.0064$) (Fig. 7B).

Air Temperature and Julian Date

Of all the variables examined, only the percentage of individuals fruiting was significantly correlated with both maximum air temperature ($p=0.0464$, $n=9$) and Julian date ($p=0.018$, $n=9$), while seeds per fertile fruit was significantly correlated with Julian date of the burn ($p=0.0081$, $n=9$). The percentage of individuals fruiting was positively correlated with both Julian date and maximum air temperature on the day of the burn, indicating that more individuals produced fruit as the air temperature on the day of the burn increased and as burns occurred later in the year (Fig. 8A&B). The number of seeds per fertile fruit was also positively correlated with Julian date, indicating that the later the burn was in the year, the more seeds matured in the fruits that had seeds (Fig. 8C).

Discussion:

Our results show that both fire and burn period can influence propagule production by Tephrosia virginiana in the Carolina sandhills. Burned plots had significantly higher fruit and seed production than unburned plots. The trend between seasons was higher variation in fruit production and significantly higher estimated seed production in growing season burned plots than dormant season burned plots. The results of this study are similar to others which have noted fire effects on the seed production (Clark 1971) and flowering (Dudley and Lajtha 1993) of T. virginiana.

Fire effects on flowering and seed production

Fruit and seed production are dependent upon processes like flowering and pollination which occur earlier in the season. Systems which undergo frequent burning have often been shown to undergo fire-stimulated flowering (Gill 1981), which can

involve synchronization of flowering (Platt et al. 1988), changes in the duration of flowering (Platt et al. 1988), delays in flower initiation (Snyder and Ward 1987, Platt et al. 1988, Robbins and Myer 1992), and/or extensive tillering which increase the number of flowering stems (Platt et al. 1988, van Eerden 1997). Synchronization in flowering after growing season burns has been observed in the longleaf pine system for numerous species and has been attributed to concurrent release of dormant buds and production of multiple ramets (Platt et al. 1988). This synchronization can lead to a decrease in the duration of flowering, which can then increase potential pollination and out-crossing rates (Platt et al. 1988, Robbins and Myers 1992). Because growing season burns occur after many plants have already initiated growth, flower production is often delayed. These changes can shift the timing of flower production towards or away from more beneficial pollinator times, thereby affecting fruit and seed production (Robbins and Myers 1992).

Fire-stimulated flowering has been noted for T. virginiana in the longleaf pine system (chapter 2, this thesis) and other parts of its range (Dudley and Lajtha 1993). Tephrosia virginiana plants rarely blossom if not burned, except in cases when the rhizome is damaged which then causes new shoots to be initiated from the rhizome (chapter 2, this thesis). Shoots can over-winter, exerting a dominance over basal buds on the rhizome. Upon renewing growth in the spring, T. virginiana sprouts from buds on the vital green shoot, not the rhizome (Clark 1971). These shoots rarely if ever blossom; only shoots derived from basal buds on the rhizome produce flowers (chapter 2, this thesis). Flowering in T. virginiana is delayed, more synchronized, and occurs over a shorter duration of time following fires in May than following dormant season fires (chap. 2, this thesis). Increased floral displays because of fire-stimulated flowering combined with suitable pollination would lead to initiation of the large amounts of fruit and seeds found in burned areas, and could explain a portion of the difference in the seed yield between the two burn periods. Fire-stimulated flowering is a common occurrence in regularly

burned ecosystems (Gill 1981), including longleaf pine (Platt et al. 1988), and has been shown to lead to higher seed set in some species (Mark 1965).

The causes of fire-stimulated flowering have not been well explored, but several factors which may promote fire-stimulated flowering may also contribute to continued success of initiated fruits and seed maturation, including post-burn nutrient flushes and the clearing of above-ground litter and competition (Bond and van Wilgen 1996). Christensen (1977) showed that soil fertility was higher in burned areas and that nitrogen availability increased after a burn. The nutrient flush following a burn could possibly trigger flowering and the nutrients available in a post-burn environment could be sequestered immediately following the fire and used by the plant to provide nutrients for the maturation of the fruits and seeds later in the season. For T. virginiana and other N-fixing legumes, other nutrients such as post-burn phosphorus release may be more important than nitrogen.

Fire can also significantly change soil surface conditions by clearing away litter and surrounding above-ground vegetation which changes the conditions experienced by growing shoots (Hulbert 1988, Bond and van Wilgen 1996). For some species of grasses in the prairie grasslands of the central U.S., it has been shown that removal of standing dead vegetation and the resulting change in light conditions significantly increased flowering stems (Hulbert 1988). It has been suggested that intense fires which remove a high proportion of above-ground vegetation also provide the best conditions for legume plants and seeds, although the study did not explicitly examine floral production (Cushwa et al. 1970). Other evidence suggests that this is the one of the most important factors for stimulating flowering in T. virginiana following dormant season fires and possibly growing season fires (chapter 2, this thesis).

Fire season effects

We did not detect significant differences in fruit production due to changes in season of burn for 1997 for this legume, but we did detect differences in seed production between the two burn periods. Although not significant, growing season burned plots tended to produce more reproductive stems and fruit on average than dormant season burned plots, but also exhibited much more variation. Growing season burned plots had significantly higher seed production than dormant season burned plots. Other studies in the longleaf pine system have noted similar responses to season of burn for seed production in a composite (Brewer and Platt 1994a) and the dominant grass, wiregrass (Parrot 1967, Outcalt 1994, van Eerden 1997). Higher seed outputs in these species have been attributed to adaptations to burns during the peak lightning season. The large degree of variation in fruit production within growing season burned areas and the difference in seed production suggests that other factors are also interacting with burn period to affect fruit and seed production.

One explanation for the increased variation has to do with the conditions on the day of the burn, independent of the burn season. The air temperature on the day of the burn was significantly correlated with the percentage of individuals which produced fruit. Fires on warmer days tend to be more intense (Wright and Bailey 1982). Fires in longleaf pine forests increase soil temperatures as deep as 0.64 cm under the surface for a short period of time (Heyward 1938), the depth at which many of the rhizomes of T. virginiana grow (Mejeur, personal observation). This pulse of increased soil temperature followed by higher daily soil temperatures due to the ash-blackened surface may serve as a cue for the production of flowering stems which could then lead to synchronization of flower production. It has been suggested that synchronized flowering can lead to higher pollination rates (Platt et al. 1988, Robbins and Myers 1992) and that fire season can shift flowering towards or away from optimal pollinator activity periods (Robbins and Myers 1992), both of which could influence fruit production.

The activity of pollinators and the degree of pollination may also play an important role in seed production of T. virginiana. Growing season burns shift the phenology from flowering in late April/early May to mid- to late-June and lead to decreases in the duration of flowering (from 3.5 weeks to 1.5 weeks) (chapter 2, this thesis). In the sandhills, numerous species which attract large quantities of bumblebees blossom during late April/early May, including many ericaceous species like Vaccinium arboreum Marshall and Gaylussacia dumosa (Andrz.) T & G, which may serve as competitors for pollinators. Following a growing season burn, T. virginiana is the one of the first plants to blossom (within 3.5 weeks), which in combination with its highly synchronized flowering, may make this species more apparent to pollinators following a growing season fire, thereby increasing pollination. The delay and synchronization in flowering for plants burned in the growing season coupled with competition for pollinators for plants burned during the dormant season may explain some of the differences in seed production seen between the two burn periods for T. virginiana.

Nutrient uptake following different burn season may further modify seed production in T. virginiana. Plants burned during the growing season may be more physiologically capable of extracting nutrients resulting from the nutrient flush following fires than plants which experience burns during their semi-dormant state because of the their active physiological state (Woods et al. 1959, Robbins and Myers 1992). This increased nutrient uptake could not only trigger flowering, as observed for plants in the prairies (Hulbert 1988) and a sandhills composite, Pityopsis graminifolia (Brewer 1995), but it could also serve as a storable resource for fruit and seed maturation. The capability of the plant to rapidly respond to and absorb nutrient flushes after growing season burns may then lead to higher seed set because of more available resources. This could further modify effects induced by differences in pollination, thereby yielding the large differences in seed abundances we observed between growing season and dormant season burned plots.

Effects of seed predators on seed production

Pre-dispersal seed predation drastically reduces the annual seed crop of T. virginiana, a finding consistent with an earlier study on the life history of T. virginiana (Clark 1971). We observed significant differences in seed predation between unburned and burned plots as well as differences in the percentage of seed predation between seasons. Unburned plots underwent the highest amount of seed predation, with a higher percentage of fruits exhibiting evidence of seed predation and more predation events per total fruits. Not only do unburned areas produce very few fruit, but seed predation further reduces the number of seeds produced, effectively eliminating reproductive output in unburned plots.

The degree of seed predation differs between burn periods, with a significantly lower percentage of seeds consumed in growing season burned plots than dormant season burned plots. This, coupled with the relatively large number of seeds produced in growing season burned areas, suggests that predator satiation may occur in these later burned plots. It has been hypothesized that irregular flowering and fruiting intervals driven by variations in the frequency of fire serve as selective advantages for plants because these variations limit predator populations during inter-fire years, thereby making predator satiation more likely when seeds are produced (Gill 1981, Bond and van Wilgen 1996). If predator satiation occurs in T. virginiana, it is most likely due to an interaction between the behavior of the seed predator and the amount of seed fill in each fruit. Rarely is more than one weevil found in predated fruits (Figure 7B), regardless of the number of seeds produced within the fruit, and rarely is more than one seed consumed (Clark 1971). Because the weevils appear singly in a fruit, conditions which favor more seeds per fruit would be a method of predator satiation.

Although the seed predation rate in T. virginiana is high, and predator satiation appears to occur, the extent to which seed predators affect recruitment and population stability is unknown. The effects of seed predation on recruitment in stable populations

of long-lived perennial plants like T. virginiana is difficult to determine (Andersen 1989), and it may play little role in population dynamics despite heavy seed predation losses (Louda 1995, Andersen 1989). Seed predation becomes a limiting factor only if it reduces the total number of seeds below a threshold which then affects the total seedling establishment over the course of an adult plant life (Louda 1995). More research is needed to determine the influence of seed predation on T. virginiana population dynamics, although our observations suggest that lack of burning and chronic dormant season burning may serve to limit seed production to a level which could influence seedling establishment, especially if seed numbers are further reduced by post-dispersal predators.

It should be noted that the predation pressures experienced by these plants currently may exceed those in which the plant evolved because of the seasonal timing of many prescribed fires and the smaller extent of these fires. Historically, fires may have burned across thousands of hectares in a single event (Frost 1993), a process which may have limited predator movement. The smaller scales of prescribed fires may lead to higher rates of seed predation due to increased migration of seed predators from unburned areas into the burned areas. However, this has not been examined to the knowledge of the authors.

Management implications

The very low fruit and seed production in unburned areas suggest that fire plays a important role in reproduction of T. virginiana. Furthermore, the seasonal timing of the fires is important in determining seed production, with growing season burns providing the most optimal conditions for seed production. Chronic dormant season burning may affect long-term persistence of the legume through limited seed production and seed dispersal due in part to seed predation. Land managers interested in maximizing seed

yield for at least this nitrogen-fixing legume for restoration purposes or food for game animals should burn in late spring or early summer.

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Figure legends:

Figure 1. The mean (± SD) (a) number of individual plants counted per site, (b) number of stems per site, and (c) percentage of individuals which produced fruit for 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=4 for dormant season plots, and n=5 for growing season and unburned plots. Different letters represent significant mean differences.

Figure 2. The effect of fire and burn period on stems which produce fruit. The mean (± SD) are presented for (a) the number of reproductive stems per plot, (b) percentage of stems which produced fruit, and (c) the number of reproductive stems per individual plant for 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=4 for dormant season plots, and n=5 for growing season and unburned plots. Different letters represent significant mean differences.

Figure 3. The effect of fire and burn period on fruit production. The mean (± SD) number of (a) fruit produced per stand (plot), (b) fruits per stem, (c) fruits per reproductive stem, and (d) fruits per individual for 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=4 for dormant season plots, and n=5 for growing season and unburned plots. Different letters represent significant mean differences.

Figure 4. The effect of fire and burn period on the mean (± SD) number of (a) seeds per stand (plot), (b) seeds per fruit, and (c) seeds per individual of 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=3 for unburned treatments, n=4 for dormant season treatments, and n=5 for growing season treatments. Different letters represent significant mean differences.

Figure 5. The effect of fire and burn period on fruits that produced seeds. Mean (± SD) for (a) percentage fertile fruits and (b) number of fertile fruits per plot for 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=3 for unburned treatments, n=4 for dormant season treatments, and n=5 for growing season treatments. Different letters represent significant mean differences.

Figure 6. The effect of fire and burn period on seed predation in <u>Tephrosia virginiana</u>. Values are expressed as mean (± SD) for (a) predation events per fruit, (b) predation events per fruit that experiences seed predation, and (c) percentage of seeds predated plot for 10 x 20 m plots in dormant season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=3 for unburned treatments, n=4 for dormant season treatments, and n=5 for growing season treatments. Different letters represent significant mean differences

Figure 7. The effect of fire and burn period on the fruits that experience seed predation. Mean (± SD) are presented for (a) number of fruits exhibiting predation per plot and (b) percentage of fruits which experience seed predation for 10 x 20 m plots in dormant

season burned (DS), growing season burned (GS), and unburned (UB) sites. For all variables, n=3 for unburned treatments, n=4 for dormant season treatments, and n=5 for growing season treatments. Different letters represent significant mean differences.

Figure 8. Correlations involving percentage of individuals producing fruit and seeds per fertile fruits with Julian date and maximum air temperature. Correlations were determined using Pearson Product Moment Correlation. For all graphs, n=9 and the r-square is given. (A) The percentage of individuals producing fruit correlated with maximum air temperature ($p=0.0464$, $R^2 = 0.455$), (B) the percentage of individual plants producing fruit correlated with Julian date ($p=0.018$, $R^2 = 0.57$), and (C) the number of seeds per fruits that produce seeds correlated with Julian date ($p=0.0081$, $R^2 = 0.65$).
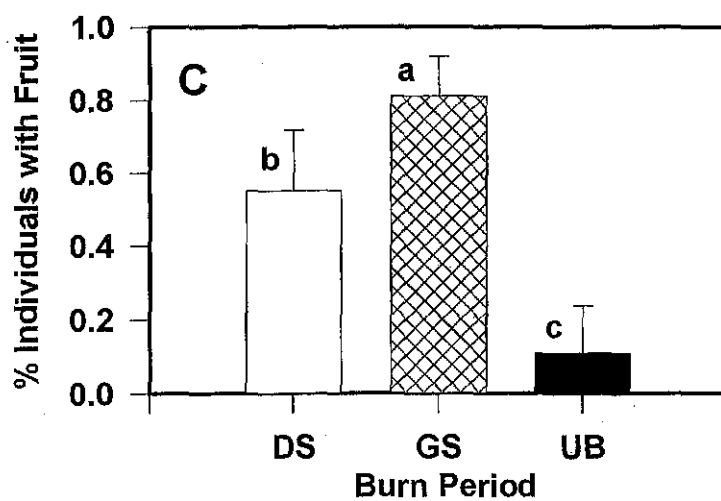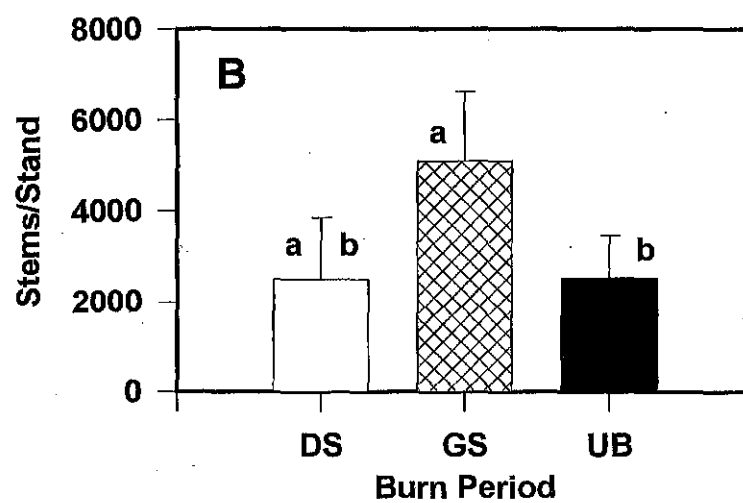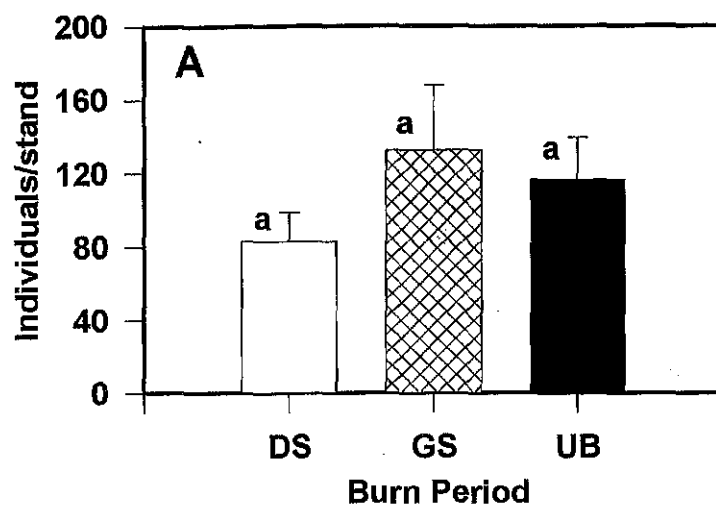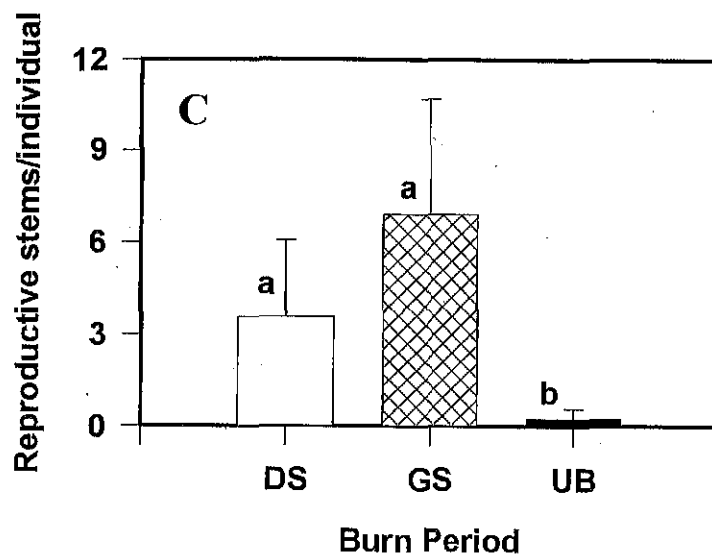
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

A. $R^2 = 0.455$

% Individuals Fruiting

Maximum air temperature

B. $R^2 = 0.57$

% Individuals Fruiting

Julian Day

C. $R^2 = 0.65$

Seeds/fruits with seeds

Julian Day
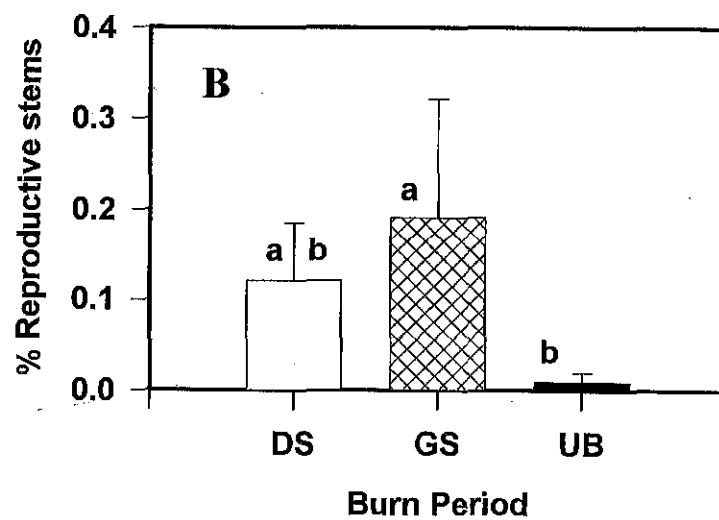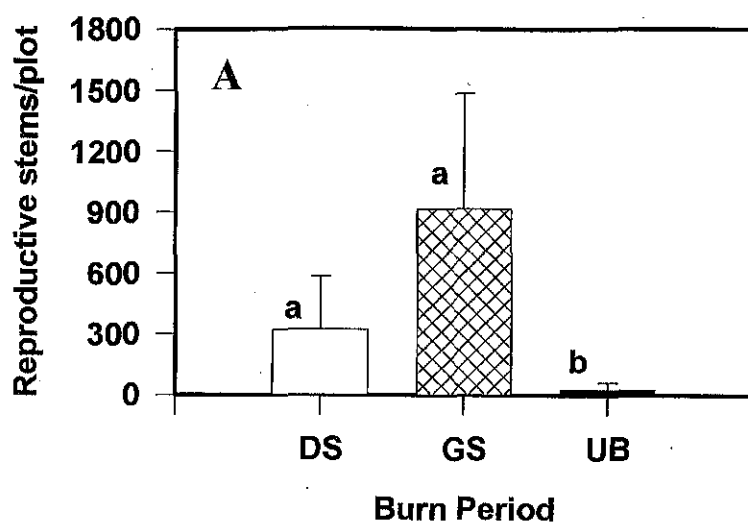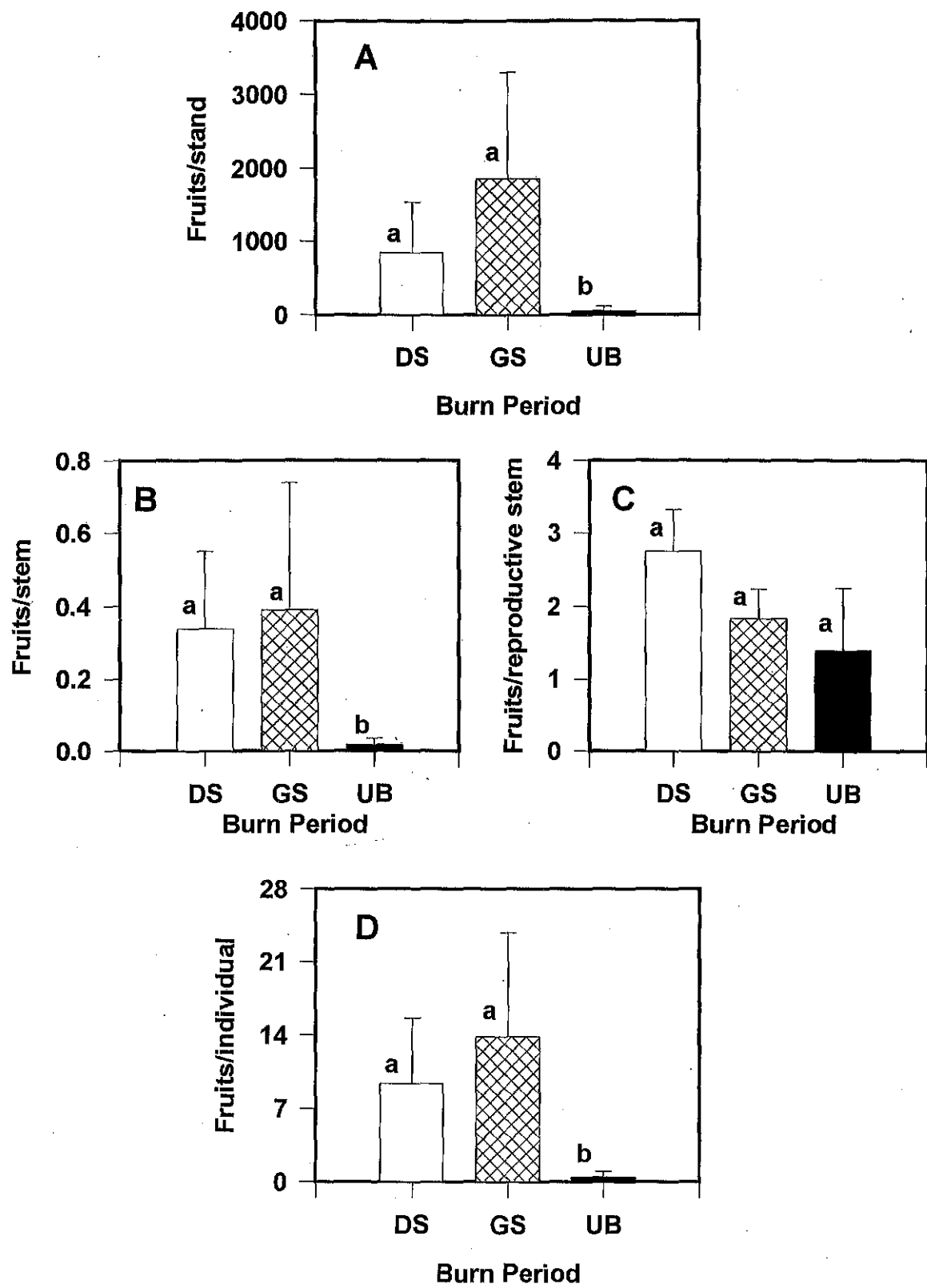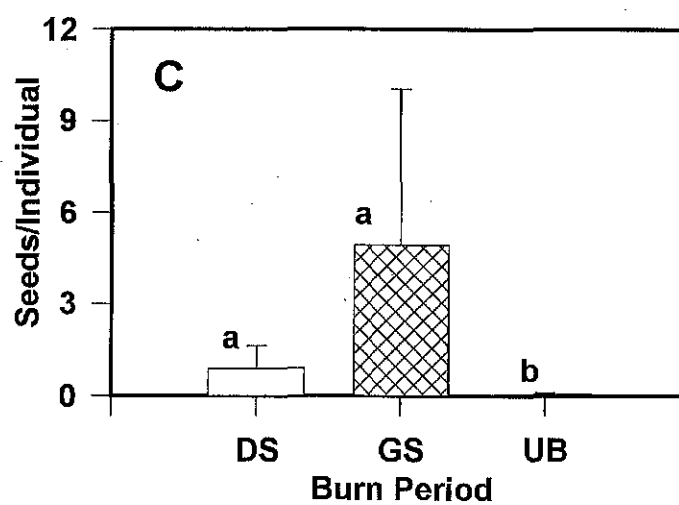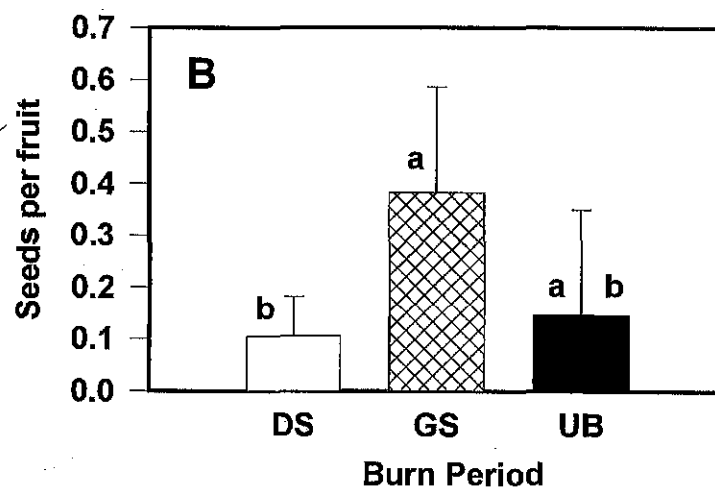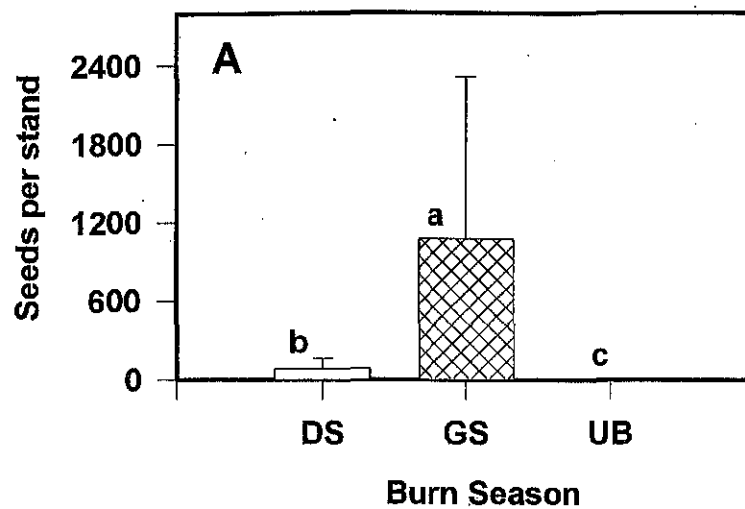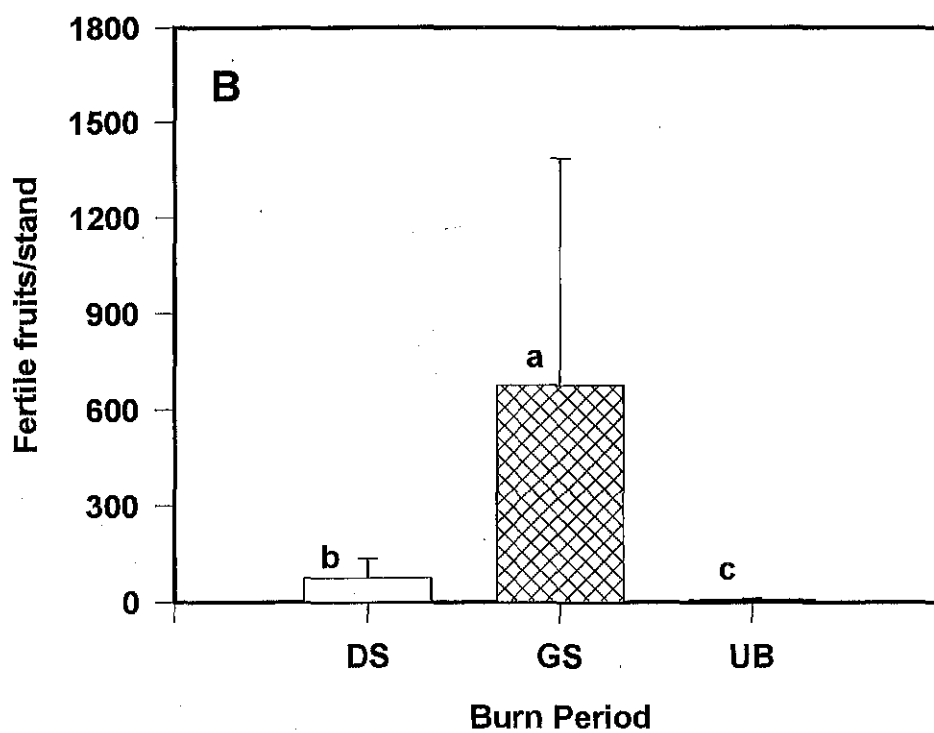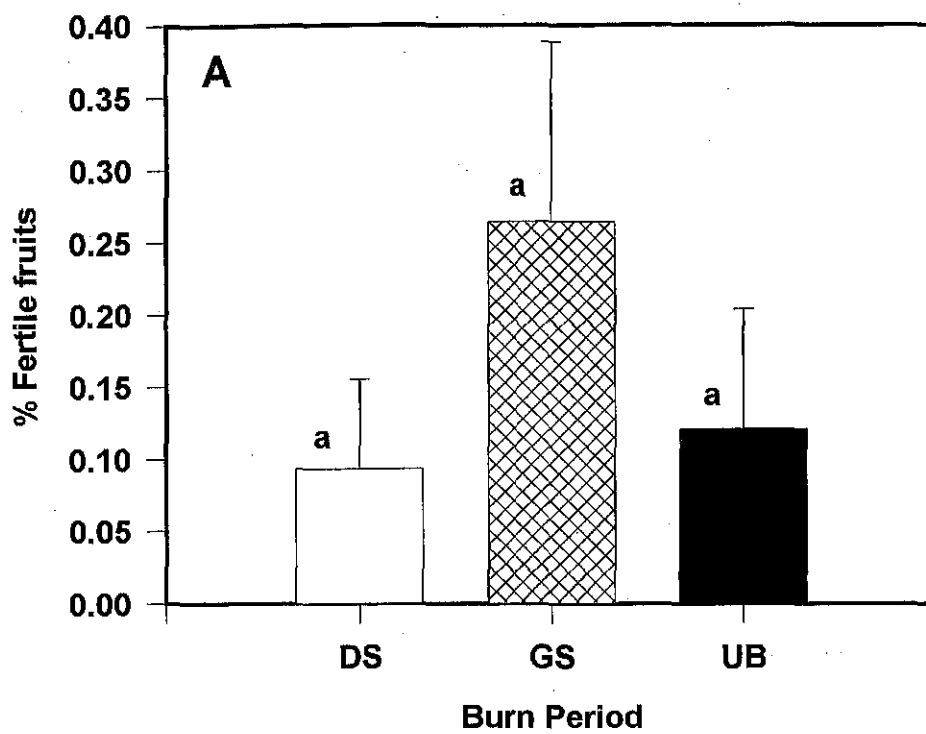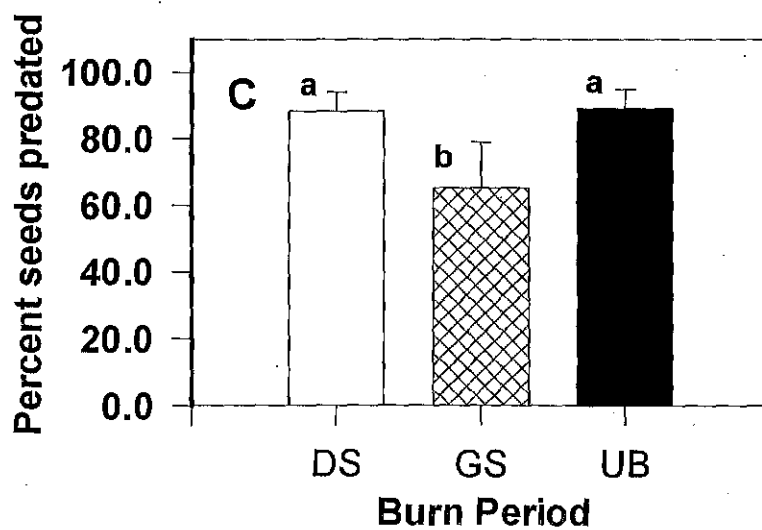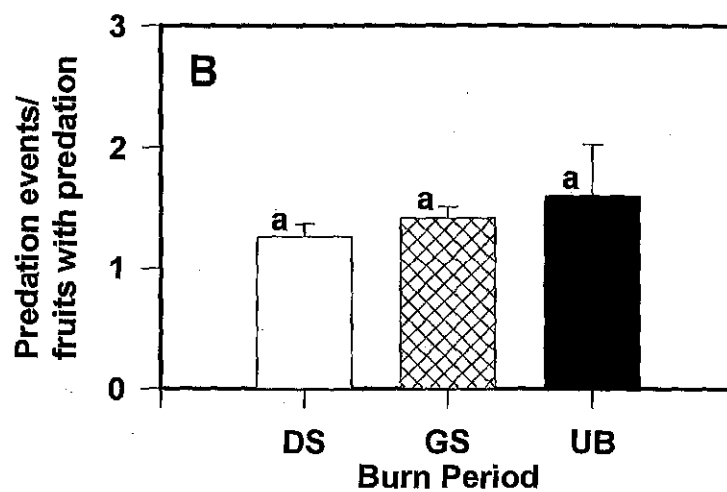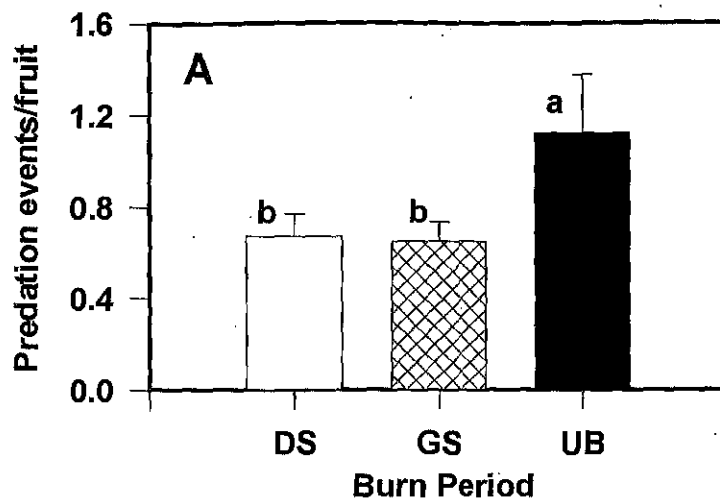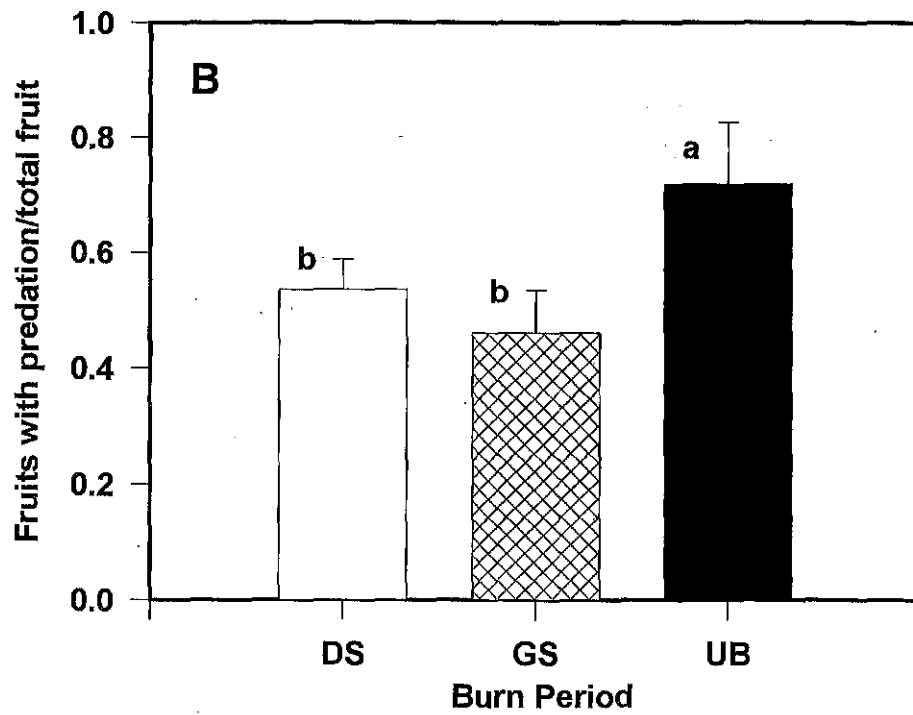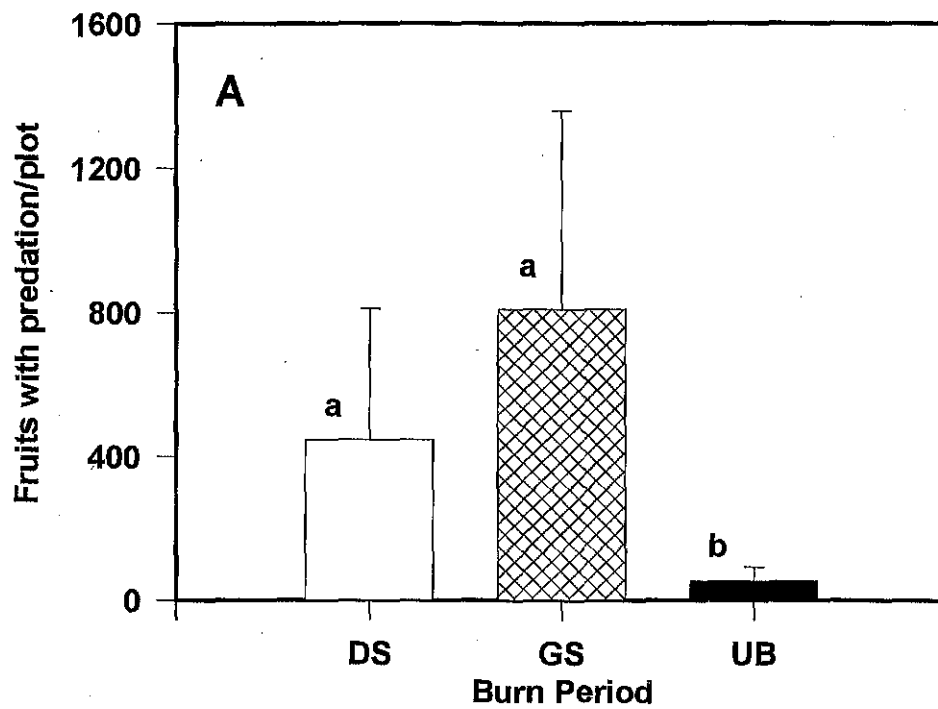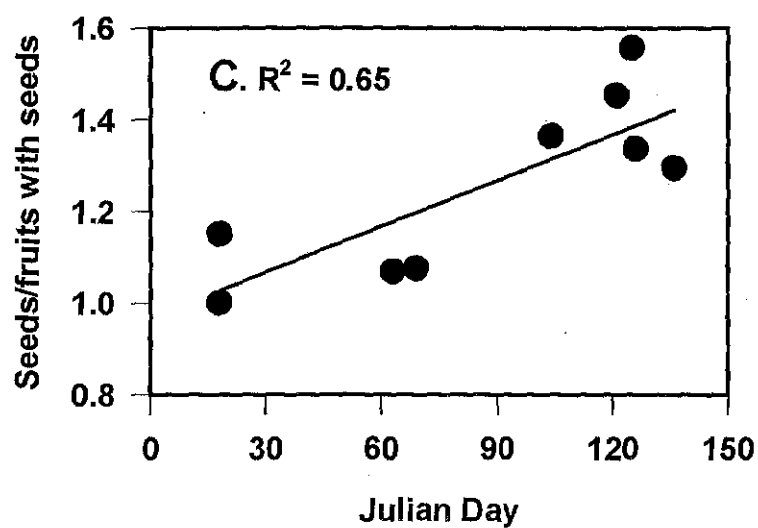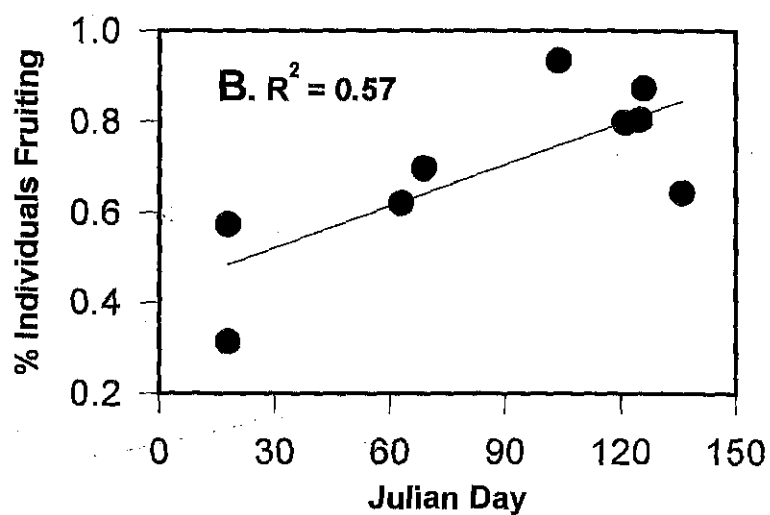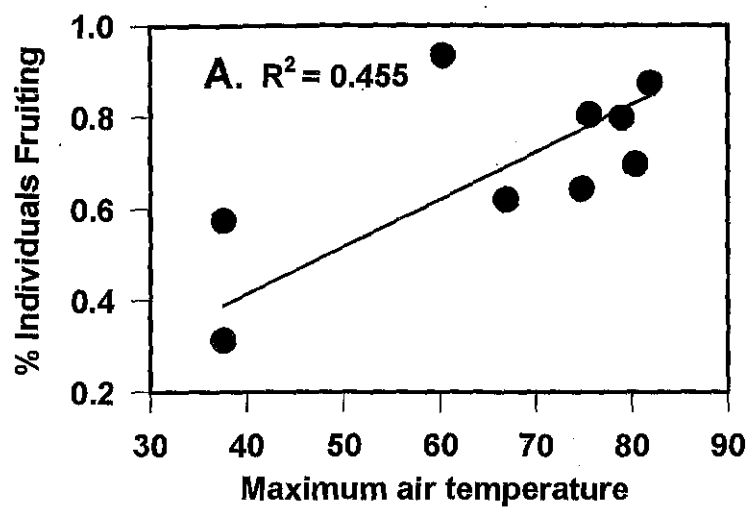
Figure 8

Table I. Summary of burn history and current burn information for all sites used in the study. Burn history indicates how many times the site was burned in the past 10 years. The table also includes the number of fruits of T. virginiana sampled for seed production and seed predation for each site. For the burn period column, DS indicates dormant season burned stands, GS indicates growing season burned stands, and UB indicates unburned stands.

Site	Burn Period	Burn Date	Last Previous Burn	Burn History	Fruits sampled for seeds
C14BS21	DS	18-Jan-97	1994	3	328
C14BS31	DS	18-Jan-97	1994	3	147
C17S5	DS	10-Mar-97	1993	2	567.5
C20S63	DS	07-Mar-97	1994	2	307.5
Subtotal	4				1350
C15S9	GS	14-Apr-97	1995	2	340
C3S39	GS	16-May-97	1995	3	301
C6S13	GS	01-May-97	1995	2	209
C8S1	GS	06-May-97	1995	3	537
C9S24	GS	05-May-97	1995	3	306
Subtotal	5				1693
C14AS61	UB	-	1996	3	21
C15C60	UB	-	1995	2	149
C2S67	UB	-	1996	3	-
C3S7	UB	-	1996	3	-
C9S3	UB	-	1996	3	58
Subtotal	5				228
Grand Total	14				4788

CHAPTER 2:
EFFECTS OF FIRE SEASON, CLIPPING, AND LITTER REMOVAL ON THE
REPRODUCTION AND GROWTH OF A PYROPHILIC HERB, <u>TEPHROSIA</u>
<u>VIRGINIANA</u> (L.) PERS.[1]

Abstract:

We studied flowering, fruit production, and biomass changes of the legume Tephrosia virginiana (L.) Pers. following experimental manipulations applied to individual plants during two different seasons in the sandhills of South Carolina. Two seasons, dormant season and growing season, were crossed with six treatments: two burn treatments, a litter removal treatment, a clipping treatment, a clipping and litter removal treatment, and a control. Flower production, flowering duration and timing, fruit production, and biomass were the responses examined. Tephrosia virginiana exhibited a significant delay in flowering and shorter duration of flowering for plants burned during the growing season than plants burned during the dormant season. Flower production did not differ among the burn and litter removal treatments for plants manipulated during the dormant season, while only burn treatments exhibited flower production in the plants manipulated during the growing season. Fruit production was significantly lower in the growing season treatments, but did not differ among treatments within either season. Both burn and clipping treatments in the growing season exhibited an increase in the number of stems following treatments, although these stems were smaller in biomass than stems in dormant season treatments. These results suggest that fire differentially stimulates flowering in this legume in different seasons. Fire most likely affects fruit production indirectly by stimulating mass-flowering events and by interacting with the pollination ecology of this species.

Keywords: fire-stimulated flowering, season of burn, legume, Tephrosia virginiana, clipping

Introduction:

Herbaceous species which grow in fire-prone ecosystems often exhibit traits such as underground bud protection and fire-stimulated reproduction which enhance survival

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and reproduction following fire (Gill 1981). Subterranean buds borne on underground rhizomes, tubers, or roots are protected from temperature extremes during fires by the insulating qualities of soil (Heyward 1938, Gill 1981, Bond and van Wilgen 1996). Following fires, factors such as the removal of apical meristems (Matlack, et al. 1993), post-fire nutrient release (Hulbert 1988, Dudley and Lajtha 1993), and increased light from canopy and litter removal lead to the release and growth of these buds. Furthermore, the bud release and resulting shoot density and size can be influenced by the seasonal timing of the burn (Brewer and Platt 1994) and the frequency of fire (Whelan 1995).

Fire-stimulated flower and seed production has been noted for plants in many different fire-prone ecosystems (Gill 1981, Bond and van Wilgen 1996), including the longleaf pine (Pinus palustris Miller)/wiregrass (Aristida stricta Michx.) system of the southeastern United States (Platt et al 1988, Robbins and Myers 1992, Brewer and Platt 1994a, Streng, et al. 1993, van Eerden 1997). This response ranges from weakly facultative in some shrubs to nearly obligate for various herbaceous species (Robbins and Myers 1992, Bond and van Wilgen 1996) and can be heavily influenced by the seasonality of the fire (Robbins and Myers 1992). Mass flowering following fire may serve to increase reproduction by shifting the timing of flowering to a period more favorable to pollination (Robbins and Myers 1992), by increasing the availability of pollen through the synchronization of flowering (Platt et al. 1988), or by producing unreliable and irregular seed supplies that may increase the likelihood of seed predator satiation, thereby potentially influencing seed and seedling survival (Mark 1965, Gill 1981, chapter 1, this thesis).

Although many studies have documented differences in flowering between seasons of burn, few have examined the proximate cues which trigger flowering. van Eerden (1997) suggests that fire intensity plays an important role in determining the amount of flowering for wiregrass, with plants burned with more intense fires yielding

more fruiting culms. Other cues associated with fire, including canopy removal and post-fire nutrient flushes, have been shown to influence flowering of a composite, Pityopsis graminifolia, in the longleaf pine/wiregrass system (Brewer and Platt 1994a,b). Proximate cues which lead to fire-stimulated flowering in species that have mutualisms, like nitrogen-fixation in legumes, have not been explored in the longleaf pine ecosystem.

Studies on fire-influenced reproduction in the longleaf pine system have focused on graminoid and composite species while few studies have examined the legumes (but see chapter 1, this thesis), despite their abundance in many sub-xeric and mesic sites in the longleaf pine ecosystem (Peet and Allard 1993). Many legumes are nitrogen-fixing species and are an important component of many ecosystems. Legumes have been shown to increase in cover in the midwestern prairies of the U.S. following fires (Towne and Knapp 1996). Studies in the southeastern U.S. have shown that the number and cover of legumes did not differ in plots burned during different times of the year (Lewis and Harshburger 1976, Cushwa, et al. 1970, Balkcom 1994). Very few studies have focused on fire-stimulated reproduction of legumes in the longleaf pine ecosystem but there is evidence that at least some legumes respond positively in seed production to growing season fires (Cushwa, et al. 1970, chapter 1, this thesis).

In this study, we examine some proximate causes for fire-stimulated reproduction in the legume Tephrosia virginiana (L.) Pers. (Goat's Rue) and how these causes change following treatments in different seasons. To do this, we measured flower production, fruit production, and biomass following clipping, burning, and litter removal treatments for a population of goat's rue in a longleaf pine forest in South Carolina. We addressed the following questions: (1) What cues associated with fire influence reproduction of T. virginiana? and (2) How do these cues change following fire during different times of the year?

Materials and Methods:

Study Species

Goat's Rue, <u>Tephrosia</u> <u>virginiana</u>, is an herbaceous perennial legume native to the eastern half of North America (Wood 1949). Over much of its range, this species grows in rolling to steep terrain in open, acid soils (Wood 1949), typically in areas with a low densities of trees (Clark 1971). In the sandhills of South Carolina, <u>T.</u> <u>virginiana</u> can be found growing on xeric sand ridges, side-slope communities, and mesic swales where it is one of the most abundant legumes. The reproductive ecology of <u>T.</u> <u>virginiana</u> is highly influenced by fire (Clark 1971, chapter 1, this thesis). Fruit production is significantly higher in burned areas than in unburned areas, while seed production is significantly higher in late spring/early summer burned areas as compared to winter burned areas (chapter 1, this thesis). Other details about seed ecology, anatomy, and interactions with a seed predator have been reported elsewhere (Kissinger 1968, Clark 1971, chapter 1, this thesis).

Study site

A second-growth stand of mature longleaf pine with herbaceous species typical for undisturbed (not cleared or plowed) longleaf pine stands (c.f. Wells and Shunk 1931) located on the Carolina Sandhills National Wildlife Refuge (CSNWR), Chesterfield County, SC was used for this study. Xeric to sub-mesic longleaf pine/wiregrass communities comprise the majority of CSNWR, communities which were historically dominant in the fall-line sandhills physiographic region in which the Refuge resides (Peet and Allard 1993). The fall-line sandhills are found along the western edge of the Atlantic Coastal Plain and are characterized by rolling terrain of primarily Cretaceous-age sediments. Over the past twenty years, the CSNWR has implemented an active fire management program involving prescribed fires on an approximately three year cycle, well within the historical fire return interval for these communities (Christensen 1981,

Brewer and Platt 1994a). Lightning season burns (April-June), which historically occurred from April to October (Komarek 1964), and winter burns (December-March) are both used within this fire program.

The site was an open stand of widely scattered longleaf pine (<25% cover) with a short midstory of turkey oak (Quercus laevis Walter). The herbaceous composition and structure is similar to other sites in which T. virginiana occurs with a mature stand of wiregrass (average density of 5-8 clumps per m^2 - Clewell 1989, van Eerden 1997) and other species typical for the sandhills, including Andropogon spp., Carphephorus bellidifolius (Michx) T.& G., Euphorbia ipecacuane L., Gaylussacia dumosa (Andrz.) T. & G., and Solidago odora Aiton. (nomenclature follows Radford, et al. 1968). In areas where it occurs, T. virginiana is one of the dominant legumes with densities up to 1 plant/m^2 (personal observation). The burn history of the stand includes three fires in the past 10 years with the last burn on the site occurring in 1995.

On 28 January 1997, fourteen blocks of twelve plants each were established in a 2 ha area for a total of 168 plants, all of which were permanently marked. We randomly assigned blocks to one of two treatment application periods, dormant season (treatments applied during the winter) or growing season (treatments applied during the late spring or early summer), for a total of seven blocks in each period. Within each block, six treatments were randomly assigned to the twelve plants, creating two replicates of each treatment. The six treatments included (1) high-fuel burns (HIFU), (2) low-fuel burns (LOFU), (3) clipping of stems at ground level (CLIP), (4) removal of litter and surrounding above-ground vegetation (RAKE), (5) clipping the plant and removing surrounding litter and above-ground vegetation (CLRA), and (6) plants that were not manipulated (CONT) (Table I). The dormant season treatments were applied on 6 February 1997 and the growing season treatments were applied on 25 May 1997.

The HIFU treatments were applied by adding approximately 175 g of fine fuels (comprised of pine needle litter and dead wiregrass stems) to existing fuels in a 1-m^2 area

around the target individual and then burning the fuel, while LOFU treatments were applied by burning only the litter already present around the plant without any further additions of fuel. The fuel additions simulated deep litter conditions sometimes found over T. virginiana that had not been burned for 2-3 years in areas with high wiregrass and pine densities (personal observation). Although it was logistically impossible to measure fire intensity (fire duration and fire temperature) on the day the treatments were applied, fires for the HIFU treatments qualitatively appeared to have longer residence times and higher flame heights (personal observation) than LOFU treatments, which strongly suggest higher fire intensities in the HIFU treatments.

The three non-burn treatments (CLIP, RAKE, and CLRA) were used to independently examine potential influences of fire other than heat which may influence later growth and reproduction, including the removal of above-ground biomass of the target plant and the removal of surrounding vegetation and litter. For the CLIP treatment, all stems for the target plant were clipped at the soil surface but surrounding vegetation and litter was left intact. The RAKE treatment involved clipping all vegetation surrounding the target plant and removing litter around the target, but it did not damage the target plant itself. For the CLRA treatment, we combined the two previous treatments by clipping the target plant at the soil surface, clipping surrounding vegetation at the soil surface, and removing litter to expose mineral soil. The last treatment, the unmanipulated plant treatment (CONT), involved no manipulations to either the target plant or the vegetation and litter surrounding the target plant. These group served as a reference for the other treatments, but can not be considered a true control because of confounding effects of time since fire (or other treatment) (Platt et al. 1988). Plants in the CONT treatment group for the growing season application period did not begin growth after the treatments were applied, as true controls would have, but instead were physiologically and phenologically more similar to plants in the February treatments. They still are useful as a reference for comparison between all treatments.

The CLIP, RAKE, and CLRA non-burn treatments differed slightly for the two application times due to the phenological condition of the plants. Stem growth in T. virginiana did not begin until late March/early May, so clipping treatments applied in the dormant season (CLIP and CLRA) removed stems which had died back over the winter, while treatments applied during the growing season involved the removal of living stems. The RAKE treatment differed between application times by exposing mineral soil and open above-ground conditions for all shoots initiated after the dormant season treatment application, but only exposing mineral soil and open above-ground conditions after actively growing stems had elongated and potentially begun flowering for plants that had treatments applied during the growing season.

Fire intensity

To estimate differences in fire intensity between the two fuel regimes, we burned two plants under the same conditions as the HIFU and two plants under the LOFU conditions on 8 July 1997. Fire temperatures on the soil surface at the base of the plant were sampled every second by three sheathed thermocouple probes (3.2-mm diameter, 30.5-cm length ANSI type K quick disconnect thermocouples with standard type OST probe termination) attached to a Campbell Scientific CR10X data logger (Campbell Scientific, Inc., Logan, Utah). Sampling began at ignition and continued until temperatures were back to within 10 degrees of ambient air temperature (approximately 15 minutes). Values from the three probes were averaged to obtain the fire temperature per second per plant. Results indicate that high fuel fires can burn more intensively, both with higher temperature and longer duration and exhibit more variation in intensity than low fuel fires (Figure 1).

Sampling procedure

We measured several different responses, including flowering, fruiting, and biomass, to determine fire effects on the reproduction and growth of T. virginiana. Sampling for flower production, stem production, and number of flowering stems within both application periods began when flowering initiated and continued until flowering ceased. For plants treated during the dormant season, weekly sampling began on 29 April 1997 and continued for four weeks until 21 May 1997. For plants treated during the growing season, sampling occurred on 12 June, 28 June, and 3 July 1997. For all plants at each sampling date, the percentage of stems flowering, the average number of flowers per stem, and the average number of flowers per flowering stem were calculated. On 25 July 1997, we sampled all plants for fruit production, number of stems which produced fruits (fruiting stems), and total number of stems per plant. To allow for easier comparison among treatments, the percentage of stems producing fruit, the number of fruits per stem, and the number of fruits per fruiting stem were calculated.

Changes in stem production and biomass were also used to investigate differences among the treatments. For plants treated during the growing season, a count of the total number of stems per plant was taken on 21 May 1997 before treatments were applied and again on 28 June 1997, which was one month after treatments were applied. The percent increase in stem production from 21 May to 28 June was calculated. To minimize differences in phenological state, biomass was harvested on two separate dates for the two application periods with both occurring approximately three months after flowering ceased within that treatment period. All plants treated during the dormant season were harvested on 15 August 1997 while plants treated during the growing season were harvested on 12 September 1997. Plants were oven-dried for 72 hours at 65°C and then weighed.

Statistical treatments

We used repeated measures analysis of variance (using the multivariate approach described in Hand and Taylor 1987) to test for significant differences in the percentage of stems flowering, the average number of flowers per stem, and the average number of flowers per flowering stem among the treatments within application period (dormant season or growing season). The between-subject part of the analysis was a randomized complete block design. Seasons were tested separately because flowering times differed between seasons, the number of sampling periods was fewer for plants treated during the growing season, and differences among treatments were of more interest than any comparison between levels of response in the two seasons. It should be noted that this analysis does not allow for statistical comparison between the two seasons, but does allow for easier interpretation of treatment effects within each season.

We used a one-way analysis of variance (Ott 1993) to test for differences in fruit production (percent stems fruiting, fruits per stem, and fruits per fruiting stem) over both seasons of application. This analysis involved a split-plot design with application time as the whole-plot and the treatments as the split-plots. Values for the three fruit production variables were log-transformed prior to analysis to reduce heteroscedasticity (Ott 1993). This analysis does allow for comparisons between the two application times. We used a one-way analysis of covariance (Ott 1993) to test for differences in biomass over both seasons of application. The number of stems per plant was used as the covariate to try to control for differences in plant size. Because of missing values, data from only 153 of the plants were used in the analysis. For plants in the growing season application period, the percent increase in number of stems from prior to treatment application to after treatment application was also tested using a one-way analysis of variance for significant differences among treatments. To test for differences in flowering duration and timing of flower initiation between the two application times, we used a row x column G-test of independence (Sokal and Rohlf 1981).

For all analyses of variances, we used planned orthogonal contrasts ($\alpha = 0.05$) to test *a priori* hypotheses about the effects of the treatments. The following five contrasts were used: (1) CONT vs. all treatments, (2) burn treatments vs. non-burn treatments, (3) HIFU vs. LOFU, (4) CLIP and RAKE vs. CLRA, and (5) CLIP vs. RAKE. Also, because one plant did not sprout following treatment application (a CLIP treatment) for the dormant season period, observations from 83 subjects were used instead of 84 for all analyses involving this application period.

Results:

Flowering

Flowering was significantly affected by the timing of the burn treatments. Plants burned during the growing season exhibited a significantly shorter flowering duration ($G=373.46$, $p<0.001$) than plants burned during the dormant season, with most plants flowering only for 1-2 sampling periods (Figure 2A). Plants in growing season burned treatments also displayed a significant delay in flowering ($G=66.62$, $p<0.001$), with flower initiation occurring 3-4 weeks after the fire and 1 month after the dormant season burned plants had finished flowering (Figure 2B). No plants burned during the growing season were observed to have any bud primordia or extant flowers on 12 June so this sampling date was excluded from the analyses. All plants that did flower following burn treatments applied during the growing season initiated flowering between 12 June and 28 June and all but 2 plants had ceased flowering by 3 July.

Flowering differed among the six treatments within dormant season and growing season application periods. For plants treated during the dormant season, the percentage of stems flowering over the four sample dates was significantly different among treatments (Table II). The CONT treatments produced significantly lower percentages of stems flowering than the other treatments, while CLIP treatments differed from only the RAKE treatment (Figure 3). Burn treatments were not significantly different from non-

burn treatments. Similar differences among the treatments were noted for the number of flowers per flowering stem with the CONT treatments exhibiting significantly fewer flowers per flowering stem than other treatments (Table IV). No differences were noted among the treatments in the number of flowers per stem (Table IV).

Treatments applied during the growing season differed significantly in their flowering response because plants which underwent the burn treatments were primarily the ones which produced flowers, although a few plants from the CLRA treatments did flower. The percentage of stems which flowered was highly significantly different among treatments over the two sample periods (Table III). However, this difference is due exclusively to the differences in the first sample period because all but 3 plants had finished flowering by the second sample period (Figure 4). Plants which underwent burns, either high fuel or low fuel burns, had significantly more stems that flowered than did plants from other treatments (Table III). Similar differences were detected in the numbers of flowers per stem and flowers per flowering stem with significantly higher average values found for the burn treatments (Table IV). It should be noted that no plants in either the CONT or RAKE treatment produced any flowers after the application of the treatments, while flowering was very rare in the other two non-burned treatments with two plants flowering in the CLRA and one plant flowering in the CLIP treatments. Also, pre- and post-treatment flowering occurred in several of the plants which underwent burn treatments applied during the growing season.

Fruiting

Despite differences in the flowering response among treatments, we did not detect any differences in fruit production within either season, although there were differences in fruiting between the two seasons. Plants exposed to treatments during the dormant season exhibited a significantly higher percentage of stems which produced fruits across all treatments than did plants exposed to treatments during the growing season (Table V).

Within the two different treatment application times, there was no significant differences among treatments (Figure 5). Similar trends in differences between season of treatment applications and lack of differences among treatments within season were noted for fruits per stem and fruits per fruiting stem (Table V).

Biomass and stem production

We observed significant differences in biomass between the two seasons of application, but detected differences among treatments only within the growing season treatments. Overall, plants in dormant season treatments had significantly higher biomass than plants in growing season treatments (Table VI). Treatments within the dormant season did not differ in biomass ($F=0.50$, $p=0.7734$). Biomass of plants treated in the growing season differed significantly among treatments ($F=14.00$, $p<0.0001$), with the burn treatments being intermediate between the RAKE and CONT group and CLIP and CLRA group (Figure 7).

Stem production following treatments applied during the growing season varied significantly among the treatments ($F=19.58$, $p<0.0001$) (Figure 6). Treatments which did not affect aboveground biomass at application time, the CONT and RAKE treatments, exhibited significantly lower changes in stem production than the other treatments ($F=87.54$, $p<0.0001$). The CLRA treatment exhibited a significantly higher percent increase in stem production over the CLIP treatment ($F=9.53$, $p<0.0029$), but neither treatment differed significantly from the burn treatments ($F=0.00$, $p=0.9815$).

Discussion:

Flower production

Our results show that fire at different times of the year interacts with the phenological condition of T. virginiana to produce the fire-stimulated flowering response. Plants burned during the growing season exhibited a significant delay in flowering as well

as a shorter duration of flowering than plants burned during the dormant season (Fig. 2).

Platt et al. (1988) documented similar delays and shorter durations in flowering following

growing season burns in Florida. These delays in flowering could shift flowering toward

or away from beneficial periods of pollinator (Robbins and Myers 1992). The decrease in

the duration of flowering may lead to increased pollination and out-crossing rates because

most individuals of the species in the population tend to flower at the same time (Platt et

al. 1988). Following a growing season fire, T. virginiana is the one of the first plants to

blossom (within 3.5 weeks). This, in combination with its highly synchronized

flowering, may make this species more apparent to the pollinators following growing

season fires and thus increase pollination.

Not only are there delays and changes in the duration of flowering following fires

at different times of the year, but proximate causes for the flowering differ slightly

between seasons as well. One effect of burning which stimulates flowering in T.

virginiana is the removal of litter and surrounding vegetation, although this differs due to

the season in which it occurs. The lack of difference between the dormant season fire

(HIFU and LOFU) and litter-clearing treatments (both RAKE and CLRA) in the amount

of flowering (Fig. 3, Table II, IV) suggests that the exposure of bare mineral soil by fire is

an important cue for floral induction, at least early in the year. The exposure of bare

mineral soil may also be important following fire later in the year, but this effect most

likely works in combination with other factors such as the top-kill of growing stems to

trigger flowering.

Fires during the growing season both directly and indirectly affect the plant to

influence flowering. Growing season fires directly affect flowering by top-killing

growing stems which then allows for the release of dormant subterranean buds. As for

plants exposed to dormant season fires, the exposure of bare mineral soil, an indirect

effect of growing season fires, may influence flower initiation on the shoots emerging

after the release of these dormant buds. Apparently, flowering is dependent upon the

complete death of the above-ground stems during the growing season, as clipping treatments applied during the growing season produced only extensive tillering with little to no floral induction. This may suggest that there are pre-determined flowering vs non-flowering tillers, although that would not explain the lack of flowering stems in unburned plants and the increase in flowering stems in dormant season litter-removal treatments. Stems produced following growing season clipping treatments all originated from the base of the stem which had been cut, not from dormant buds on the rhizome. Along with observations that plants which had undergone some herbivory exhibited increased tillering and a lack of floral induction on new stems (personal observation), these results suggest that flowering in T. virginiana is facilitated by fire but not other types of defoliation events during the growing season.

The removal of standing dead material and litter has been shown to play an important role in floral induction for other herbaceous species (Hulbert 1988, Brewer and Platt 1994a). Because much of the litter is consumed in a fire, the risk of another fire happening to the plant on a short interval is minimal. Therefore, increased light levels following litter removal may serve as a cue to confine flowering to times when loss of high nutrient and energy sinks like floral meristems are unlikely due to decreased fire probability (Brewer 1995). Changes in light quality and intensity have been shown to influence flowering in grass species following fire (Hulbert 1988), but no similar studies have been done with legumes. Some limited data suggest that flowering in T. virginiana plants burned during the growing season is not affected by changes in light quantity or quality (Mejeur, unpublished). The change in surface light intensity caused by standing dead stem and litter removal may not only change the light quantity and quality that newly initiated stems experience, but also could change the surface soil temperatures experienced by the stems. Daily temperature changes and extremes tend to be higher in burned areas than in unburned areas (Hulbert 1988). These fluctuations may serve as a potential cue for flower bud formation which would not be present under thick layers of

litter. The role of light quantity and quality and soil temperature as cues for flowering in legumes needs more investigation.

Fire-stimulated flowering may also be the result of a response to the post-fire nutrient flush. Brewer (1995) found that flowering for Pityopsis graminifolia was induced following nutrient additions and suggested that fire-stimulated flowering may be a means to capitalize on post-fire increases in nutrients. This would be especially important following a growing season burn because plants would be physiologically more capable of responding to the nutrient pulse. Pulses of nutrients, especially phosphorus, may stimulate flowering in legumes, although their nitrogen-fixing capabilities may modify or reduce the effect of these pulses. Our results suggest that, at least for plants burned during the dormant season, changes in light conditions (clearing of vegetation and litter) may play a more important role than nutrient pulses in the stimulation of flowering for T. virginiana, although further reproductive development such as fruit set and seed fill may be dependent upon these nutrient pulses. Further research in nutrient effects on fire-stimulated flowering in legumes is needed.

Fruit production

Fruit production for plants in the growing season treatments was significantly lower than fruit production in dormant season treatments, a finding which at first consideration contrasts with other studies on T. virginiana (chapter 1, this thesis). Along with the lack of differences among treatments within either season, this suggests that other factors, whether working alone or interacting with fire and season of fire, are influencing fruit production for this legume. One influential factor may be the availability of pollen. Because individual plants were burned in the growing season treatments, the flowers produced were only in small islands within the whole population as opposed to the majority of the plants in the population flowering as seen following most fires. Legumes in the mid-western prairies exhibit decreased pollination rates in

small populations or isolated plants due to the decreased ability to attract pollinators (Platt, et al. 1974, Hendrix 1994). Mass-flowering in this species may serve to increase the effective reproductive population size in a given area by producing more pollen and attracting more pollinators.

Another factor which may have affected fruit set is competition for pollinators. The reduced levels of fruits on growing season burned plants in this experiment may be due to competition from the numerous other species (e.g. Vaccinium arboreum, Gaylussacia dumosa) which were blossoming while the experimentally burned plants were blossoming. Typically, T. virginiana is one of the first species to produce flowers and finish flowering following growing season fires. This early flowering following growing season fires, compared to other species, may serve to provide easily found, abundant flowers while flowers of other species are sparse, thus reducing interspecific competition for pollinators. Unlike plants burned during the growing season, plants burned during the dormant season may experience more competition for pollinators, thereby limiting pollination and lowering fruit set, because T. virginiana flowers at the same time as many other species.

Stem production and biomass

Growing season fires lead to a significant increase in the stem production following fire, a finding consistent with other studies in the longleaf pine ecosystem (Platt et al. 1988, Brewer and Platt 1994b). Clipping treatments and fire treatments exhibited similar increases in stem production, which suggests that this tillering effect is due to the removal of above-ground biomass by fires. The removal of the apical meristems releases the subterranean buds leading to an increase in the number of stems. The increase in the number of stems increases the number of potentially reproducing units (flowering stems). Mass flowering of this legume following a fire thus may be due not only to an increase in

the number of plants blossoming, but also an increase in the number of flowering stems per plant (Robbins and Myers 1992).

Although plants produce more stems following growing season fires, these stems are smaller than shoots produced following dormant season fires or in unburned stands. Brewer and Platt (1994b) found a similar response in Pityopsis graminifolia with increased numbers of smaller shoots following growing season fires. They attributed this increase to a post-fire nutrient flush and a change in strategy from competition for light to competition for nutrients and space. Increased numbers of stems following a defoliation event (e.g. fire or herbivory) potentially allows the plant to take up more space and thus have better access to above-ground resources in following years. More study needs to be done on competitive changes caused by shifts in clonal structure for legumes following fires.

Management implications

Our findings suggest that combinations of clearing litter and mowing surrounding vegetation early in the year may lead to an increase in flowering for this species. Unlike other species such as wiregrass, mowing later in the year will not lead to flower production and cannot be used to stimulate fruit production. Large-scale fires in the growing season which lead to fires over entire populations of T. virginiana are most beneficial for fruit and seed production in this legume.

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Figure legends:

Figure 1. Temperature data for high and low fuel plots. Temperatures were recorded every second using three thermocouples at the base of each plant. The temperatures from the three thermocouples were averaged to obtain the line for each plant. Each line represents one fire with dotted lines indicating low fuel burns and solid lines indicating high fuel burns.

Figure 2. Flowering duration and delay following fire in T. virginiana. Based on 27 plants for the dormant season and 24 plants for the growing season, each bar represents the actual number of plants that (A) flowered for a given duration of time (in weeks) or (B) were noted to have begun flowering on a given date. Hatched bars represent growing season treatments while empty bars represent dormant season treatments.

Figure 3. The percentage of stems flowering for dormant season treatments over four sampling periods. Each point represents the average (±SE) percentage of stems flowering for each treatment at each sample date. Solid circles denote burn treatments, while hollow circles denote non-burn treatments.

Figure 4. The percentage of stems flowering for growing season treatments over two sampling periods. Each point represents the average (±SE) percentage of stems flowering for each treatment at each sample date. Solid circles denote burn treatments, while hollow circles denote non-burn treatments.

Figure 5. The percentage of stems which produced. Each bar represents the average (±SE) percentage of stems producing fruit for each treatment. A split-plot one-way ANOVA was used to test for differences between seasons and among treatments. Treatments were not significantly different within burn seasons, but burn seasons did differ significantly ($F=15.87$, $p=0.0018$). Hatched bars indicate dormant season treatments, while unfilled bars represent growing season treatments.

Figure 6. The percent increase in numbers of stems following application of growing season treatments. Each point represents the average (±SE) percentage increase in the number of stems following application of each treatment. A one-way ANOVA and planned contrasts was used to test for differences between treatments. Different letters indicate significantly different percentages ($\propto=0.05$).

Figure 7. Biomass for the six treatments in two seasons. Each point represents the average (± SE) biomass adjusted by the co-variate of number of stems for each treatment. Seasons differed in their response ($F=56.35$, $p=0.0001$). Hatched bars indicate growing season means, while unfilled bars represent dormant season means. Different letters indicate significant differences in biomass within season ($\propto=0.05$).
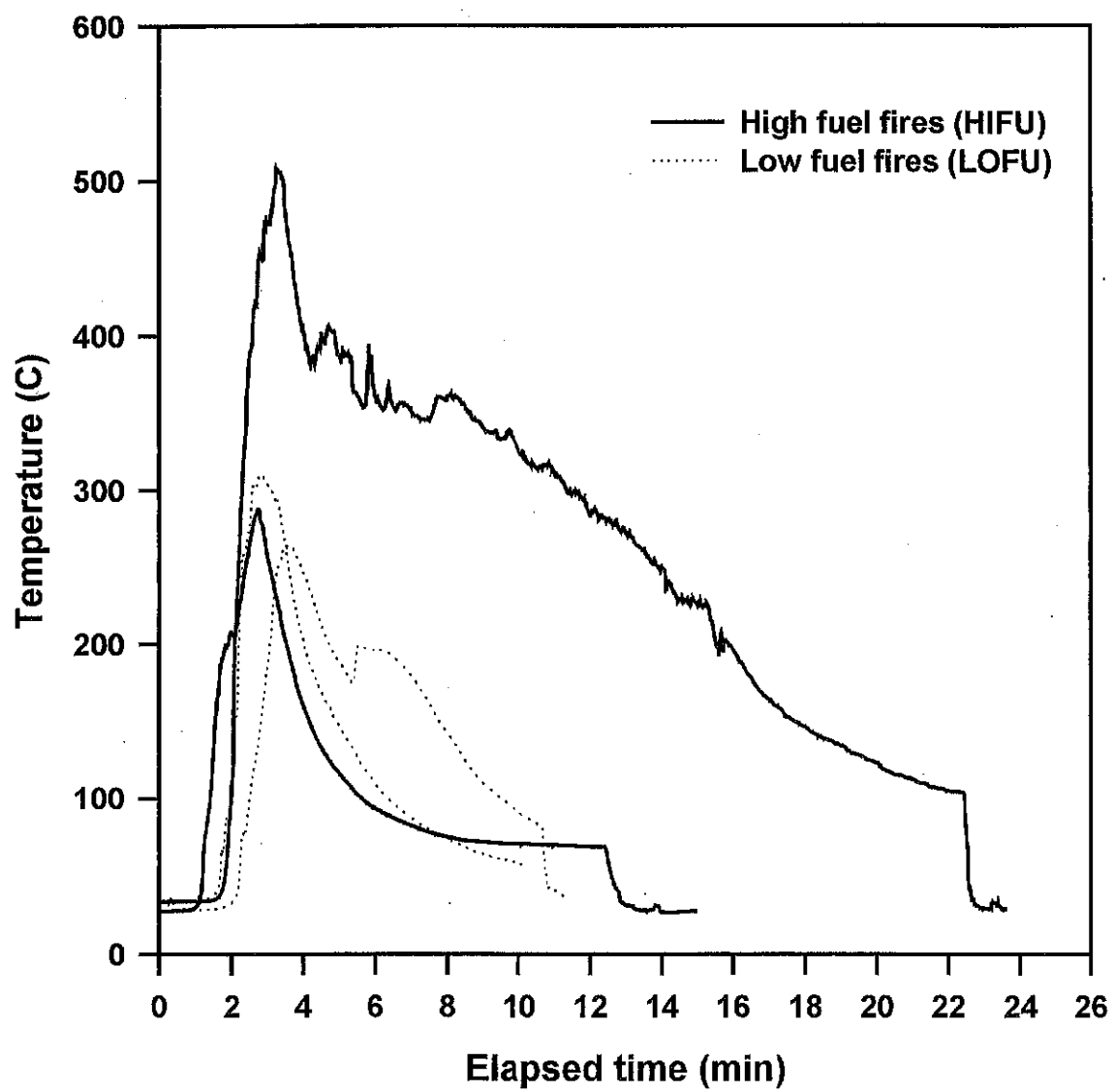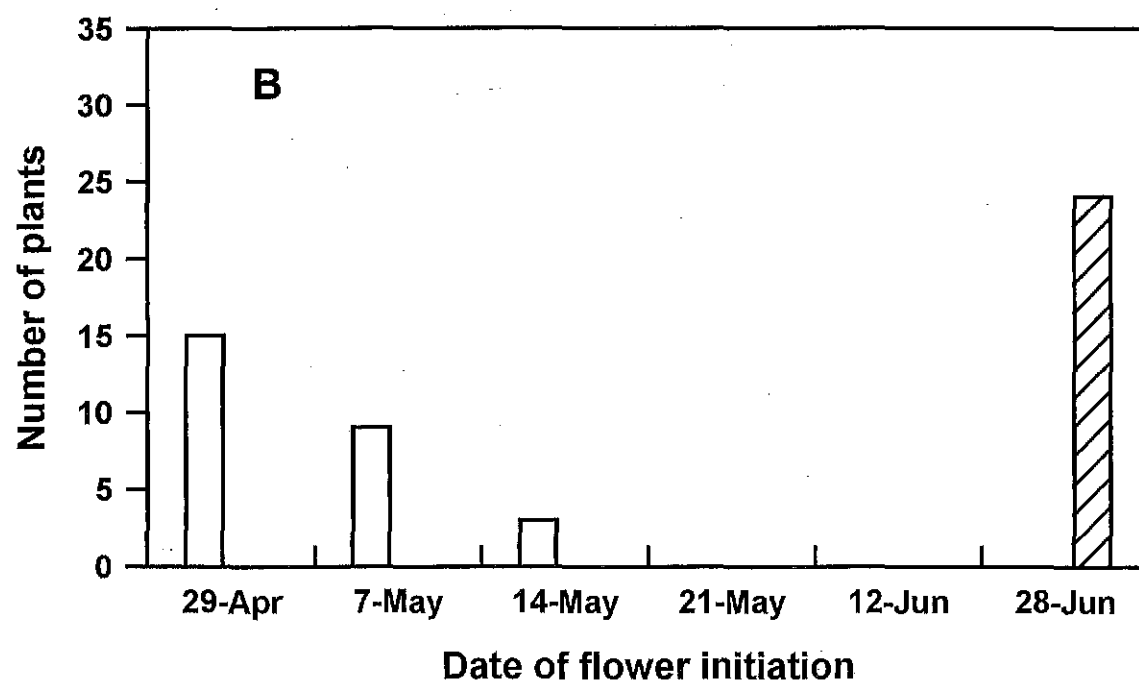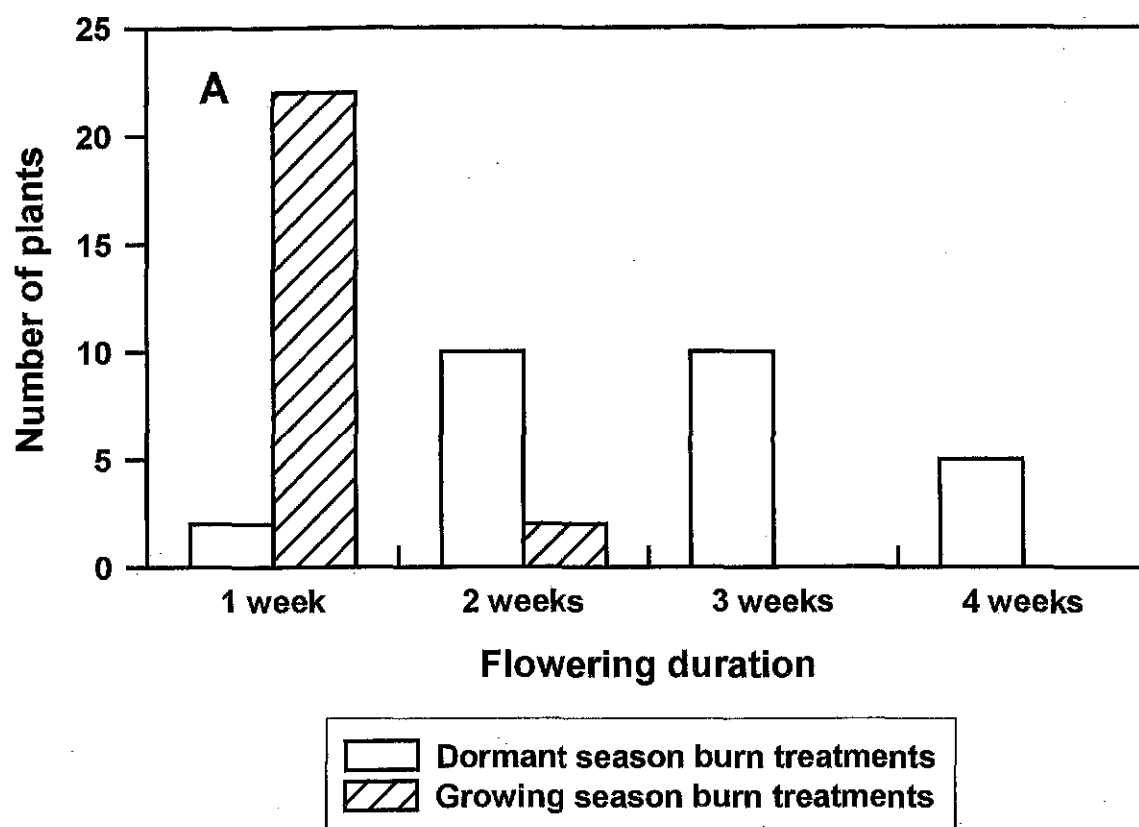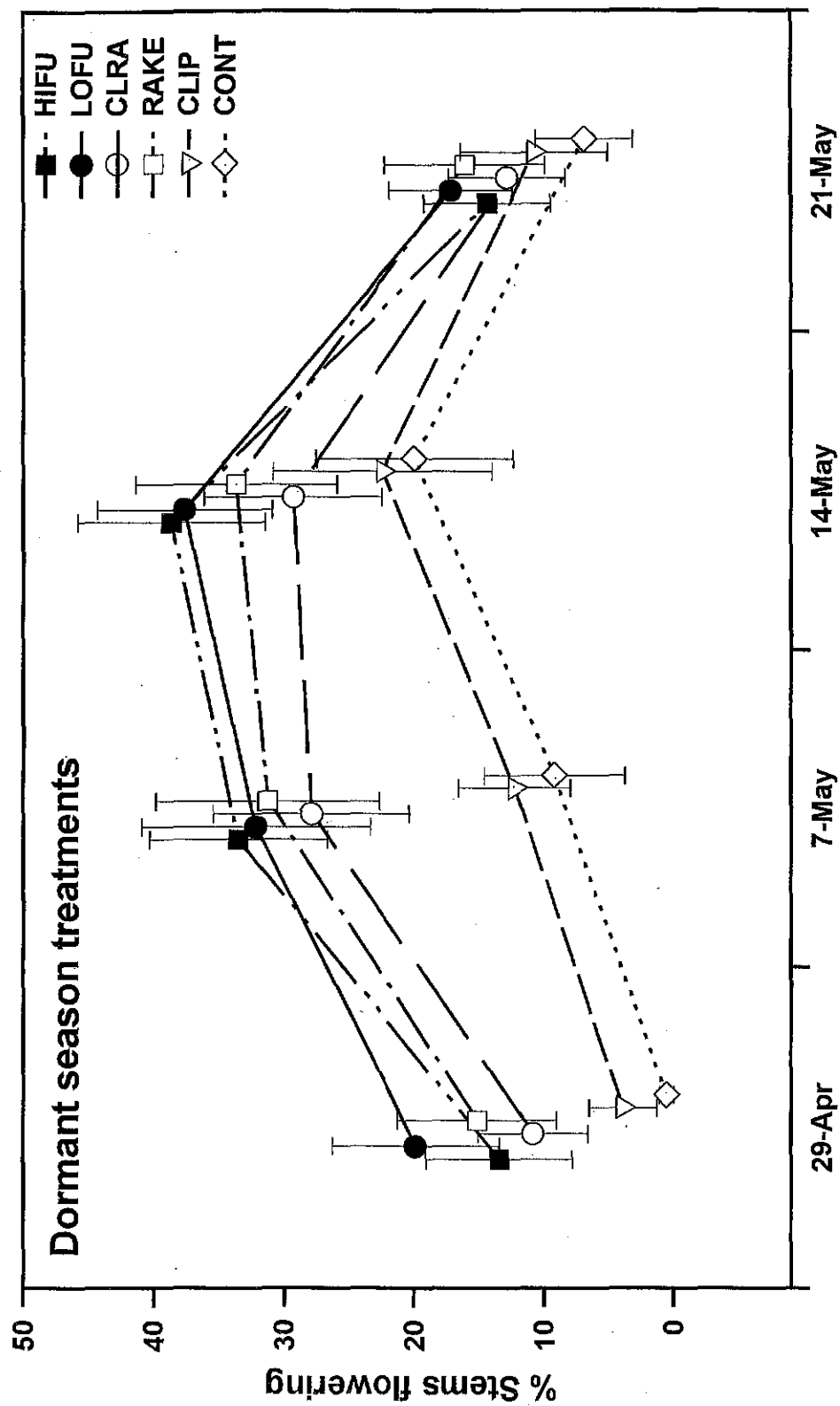
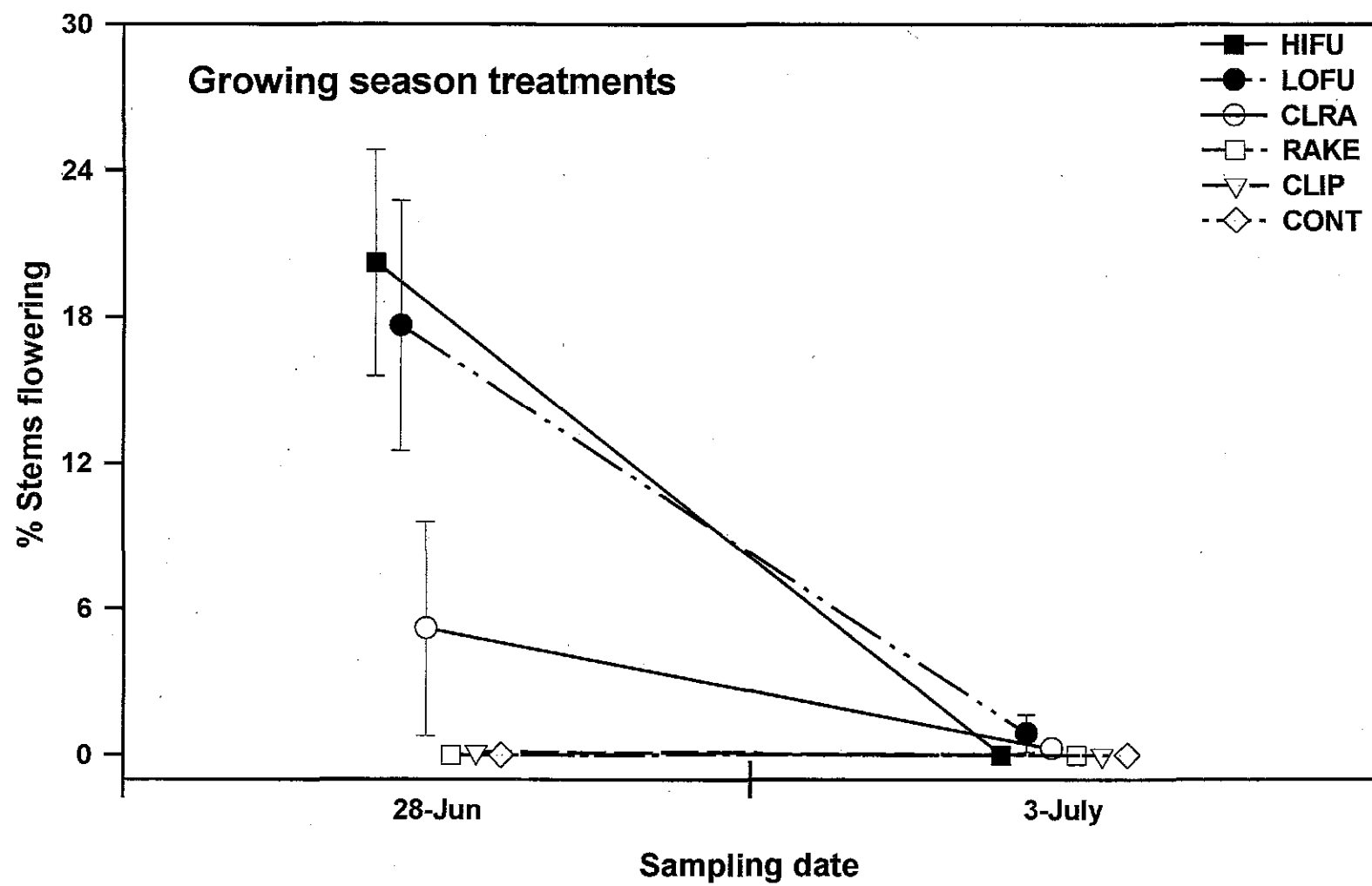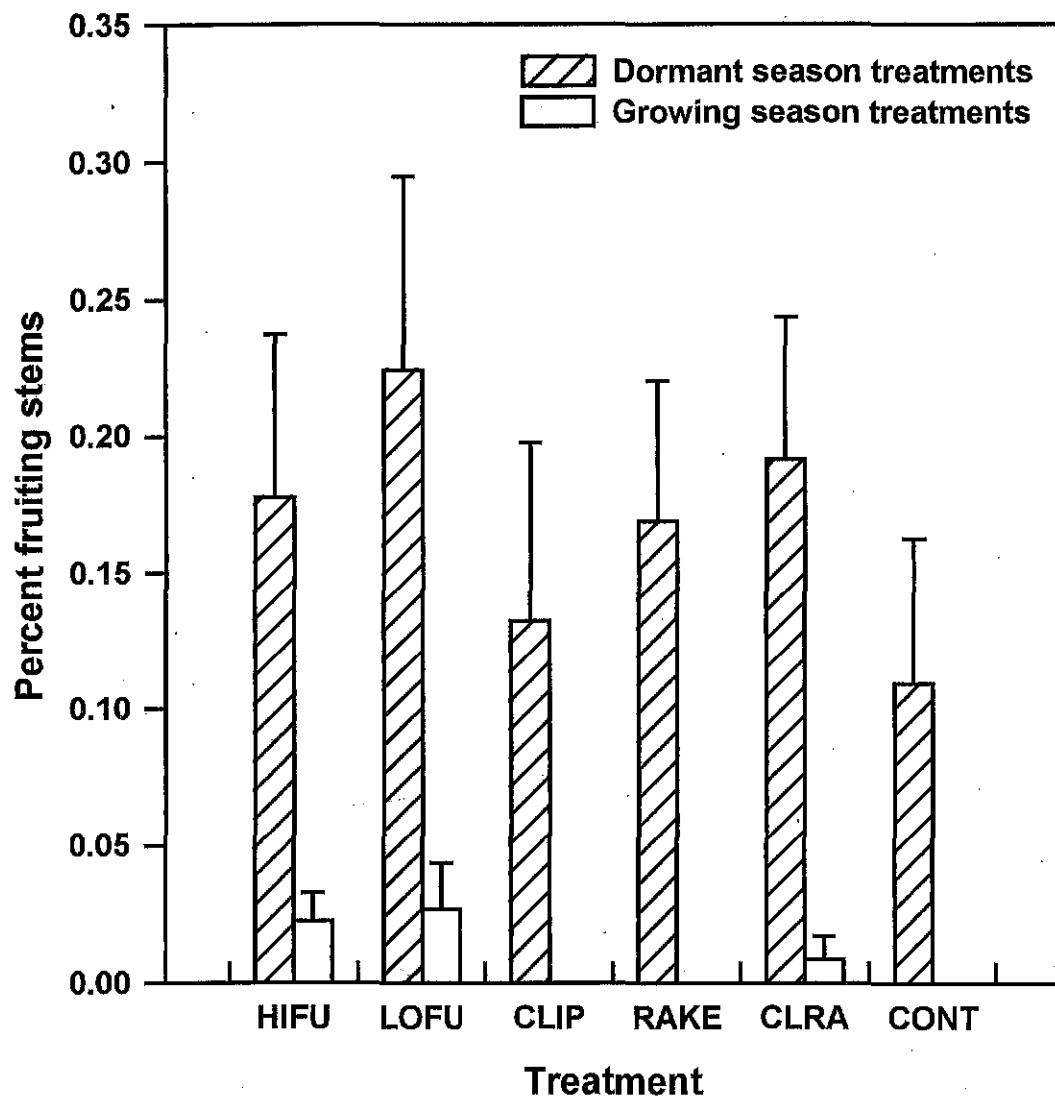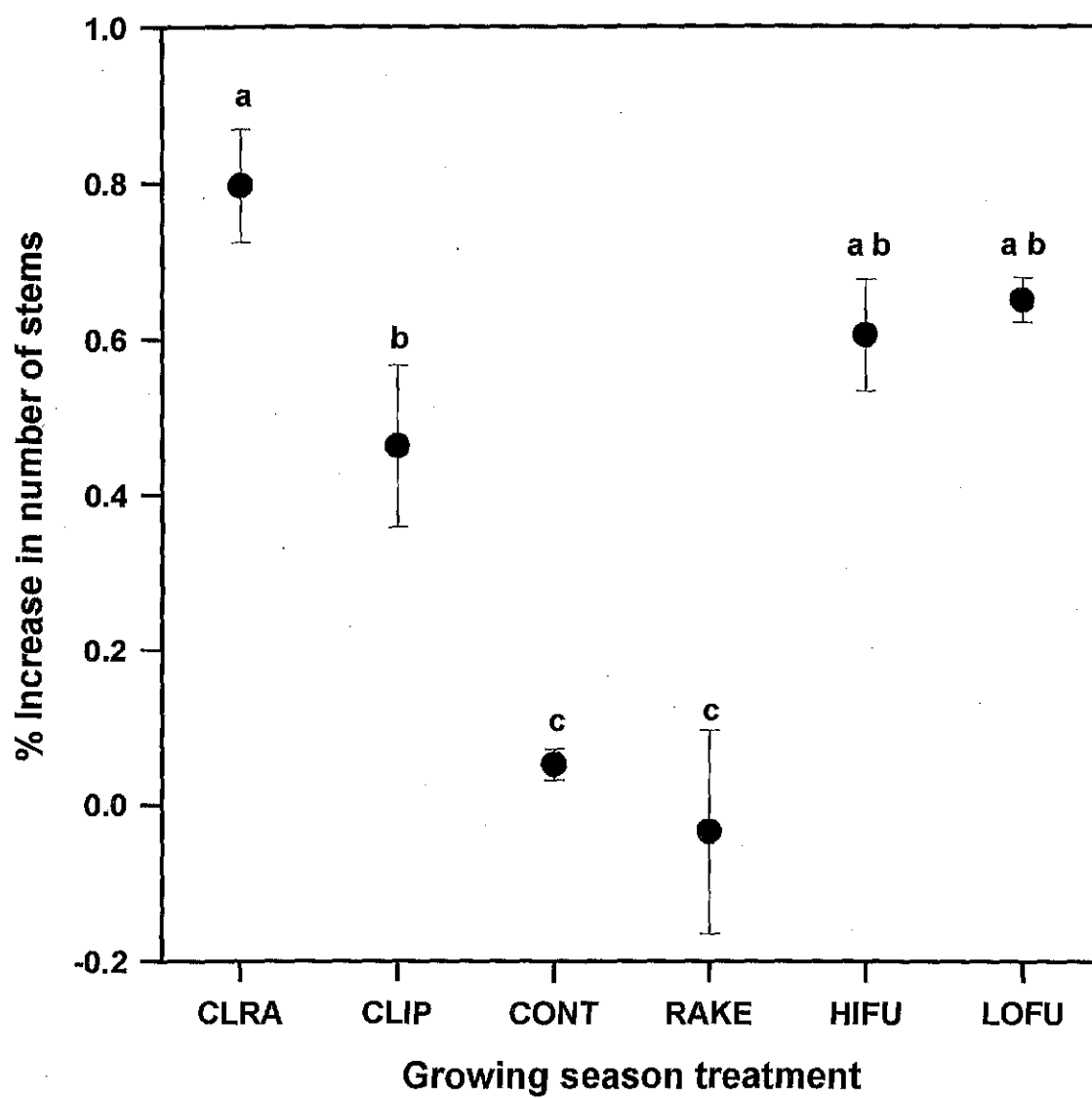Figure 1

Figure 2

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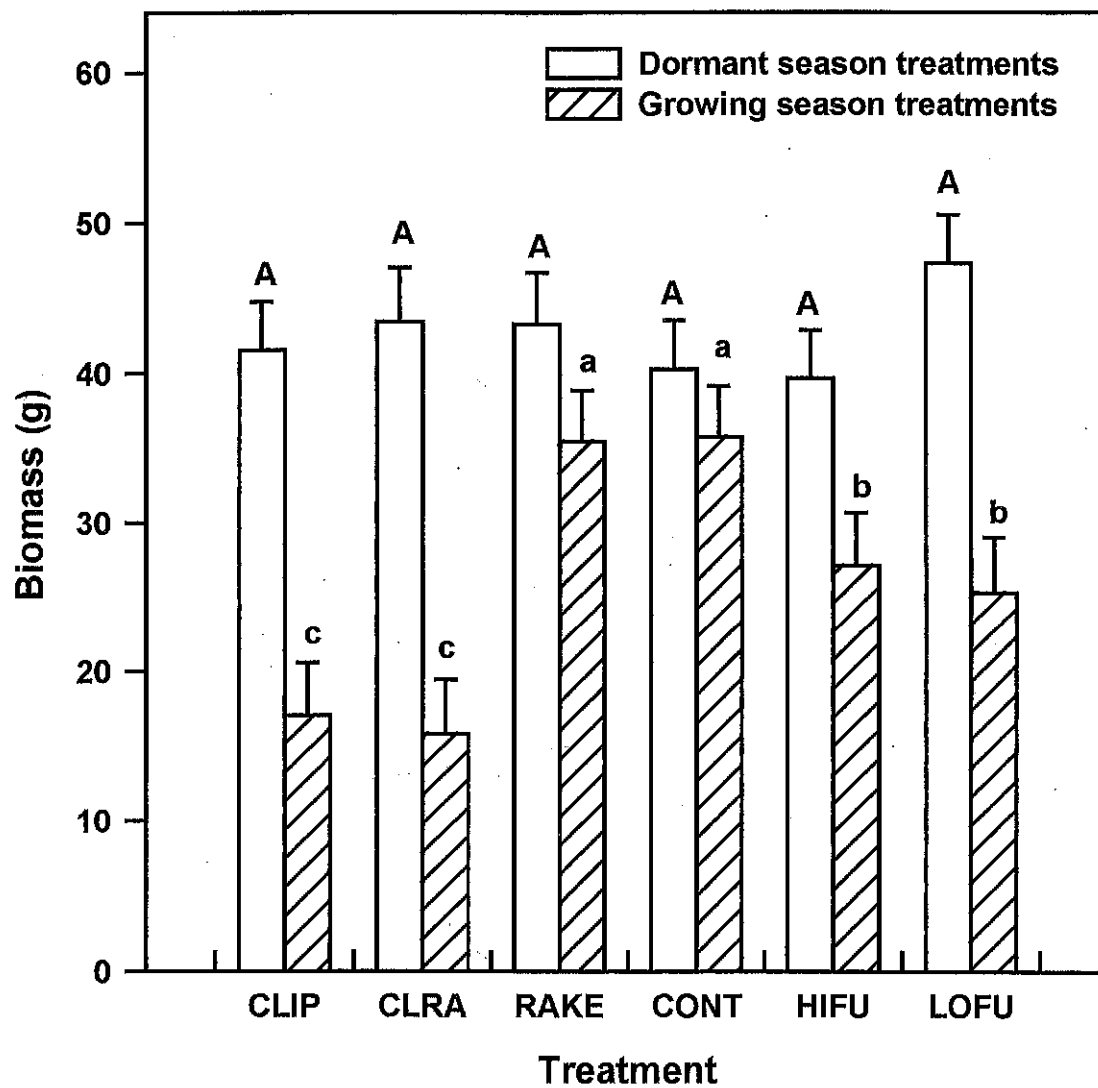Figure 4

Figure 5

Figure 6

Figure 7

Table I. List and definition of treatments applied. DS indicates a treatment applied during the dormant season while GS indicates a treatment applied during the growing season.

Treatment	Season	Definition of treatment
HIFU	DS	Target individual was burned with resident fuels plus additional 175 g of fine fuel
LOFU	DS	Target individual was burned with only resident fuels.
CLIP	DS	All dormant or dead stems grown the previous year (1996) were clipped at ground level and surrounding litter and vegetation was not manipulated.
RAKE	DS	Litter was removed around target individuals and all vegetation in 1 m^2 area around the target plant was clipped at ground level.
CLRA	DS	All stems grown the previous year (1996) were clipped and all vegetation was clipped at ground level and litter was removed in 1 m^2 area around target individual.
CONT	DS	Target plant was left unmanipulated.
HIFU	GS	Target individual was burned with resident fuels plus additional 175 g of fine fuel.
LOFU	GS	Target individual was burned with resident fuels.
CLIP	GS	All stems initiated in 1997 plus dormant or dead stems grown in 1996 were clipped at ground level and surrounding litter and vegetation was not manipulated.
RAKE	GS	Litter was removed from around stems initiated in 1997 and all vegetation in 1 m^2 area around target was clipped at ground level.
CLRA	GS	All stems initiated in 1997 plus dead stems grown in 1996 were clipped at ground level and all vegetation was clipped at ground level and litter was removed in 1 m^2 area around the target plant.
CONT	GS	Target plant was left unmanipulated.

Table II. Repeated measures ANOVA table for the percentage of stems flowering following dormant season treatment application.

Between-subjects

Source of variation	df	MS	F	P>F
Block	6	0.518	5.76	0.0001
Treatments	5	0.064	3.26	0.0105
(1) CONT vs. all	1	0.730	8.11	0.0057
(2) burn vs. non-burn	1	0.324	3.60	0.0618
(3) HIFU vs. LOFU	1	0.008	0.09	0.7642
(4) CLIP & RAKE vs. CLRA	1	0.014	0.16	0.6885
(5) CLIP vs. RAKE	1	0.384	4.27	0.0425
Error	71	0.090		

Within-subject

Source of variation	df	MS	F	P>F	Adj. P>F (G-G)
Time	3	0.718	27.76	0.0001	0.0001
Time x Block	18	0.075	2.90	0.0001	0.0003
Time x Treatment	15	0.016	0.63	0.8477	0.8032
Time x (1)	3	0.024	0.93	0.4291	0.4074
Time x (2)	3	0.016	0.64	0.5921	0.5475
Time x (3)	3	0.009	0.36	0.7807	0.7208
Time x (4)	3	0.010	0.37	0.7726	0.7130
Time x (5)	3	0.022	0.85	0.4683	0.4407
Error (Time)	213	0.026			

Greenhouse-Geisser $\epsilon = 0.7464$

Table III. Repeated measures ANOVA table for the percentage of stems flowering following growing season treatment application.

Between-subjects				
Source of variation	df	Type III SS	F	P>F
Block	6	0.019	2.42	0.0347
Treatments	5	0.064	8.18	0.0001
(1) CONT vs. all	1	0.046	5.89	0.0177
(2) burn vs. non-burn	1	0.258	33.14	0.0001
(3) HIFU vs. LOFU	1	0.014	1.74	0.1909
(4) CLIP & RAKE vs. CLRA	1	0.001	0.13	0.7209
(5) CLIP vs. RAKE	1	0.000	0.00	0.9795
Error	72	0.0078		

Within-subject					
Source of variation	df	MS	F	P>F	Adj. P>F (G-G)
Time	1	0.206	31.25	0.0001	.
Time x Block	6	0.014	2.17	0.0552	.
Time x Treatment	5	0.059	8.92	0.0001	.
Time x (1)	1	0.041	6.25	0.0147	.
Time x (2)	1	0.238	36.03	0.0001	.
Time x (3)	1	0.011	1.67	0.2010	.
Time x (4)	1	0.004	0.64	0.4257	.
Time x (5)	1	0.00	0.00	0.9778	.
Error (Time)	72	0.007			

Table IV. Summary of a repeated measures ANOVA table for the flowers per stem and flowers per flowering stem in both dormant season and growing season treatments. F-values for the treatment, time, and time x treatment interaction are given. The main effect of treatment is partitioned into five orthogonal contrasts when treatment means are significantly different: (1) CONT vs. all treatments, (2) burn treatments vs. non-burn treatments, (3) HIFU treatments vs. LOFU treatments, (4) CLIP and RAKE treatments vs. CLRA treatments, and (5) CLIP treatments vs. RAKE treatments. Statistical significance is denoted by * - $p < 0.5$, ** - $p < 0.01$, *** - $p < 0.001$, and ^{ns} - not significant. DS indicates the dormant season application period, while GS indicates the growing season application period.

Variable	Between-subjects		Within-subjects			
	Treatment	dfn, dfd	Time	dfn, dfd	Time x Treatment	dfn, dfd
DS - Flowers per stem	1.52^{ns}	5,71	12.81	3,213	0.86^{ns}	15,213
GS - Flowers per stem	5.76***	5,72	19.85	1,72	6.03***	5,72
(1)	4.01*	1,72			3.97^{ns}	1,72
(2)	20.46***	1,72			19.79***	1,72
(3)	2.61^{ns}	1,72			4.55*	1,72
(4)	1.73^{ns}	1,72			1.84^{ns}	1,72
(5)	0.00^{ns}	1,72			0.00^{ns}	1,72
DS - Flowers per flowering stem	2.96*	5,71	17.33***	3,213	1.09^{ns}	15,213
(1)	10.58**	1,71				
(2)	2.09^{ns}	1,71				
(3)	0.23^{ns}	1,71				
(4)	0.02^{ns}	1,71				
(5)	1.85^{ns}	1,71				
GS - Flowers per flowering stem	14.01***	5,72	41.82***	1,72	13.41***	5,72
(1)	9.78**	1,72			8.36**	1,72
(2)	57.65***	1,72			50.07***	1,72
(3)	0.70^{ns}	1,72			7.16**	1,72
(4)	1.91^{ns}	1,72			1.42^{ns}	1,72
(5)	0.02^{ns}	1,72			0.02^{ns}	1,72

Table V. Summary of an ANOVA table testing the effect of season, block, treatment, and treatment by season interactions on percent stems fruiting, fruits per stem, and fruits per fruiting stem.

Variable	Source	d.f.	Sum of Squares	F-value	P>F
Percent stems fruiting	Season	1	0.405	15.87	0.0018
	Block	12	0.306	3.75	0.0001
	Treatment	5	0.039	1.15	0.3392
	Season * Treatment	5	0.014	0.42	0.8352
	Error	142	0.965		
Fruits per stem	Season	1	1.971	12.97	0.0036
	Block	12	1.82	4.09	0.0001
	Treatment	5	0.158	0.85	0.5147
	Season * Treatment	5	0.098	0.53	0.7561
	Error	142	5.273		
Fruits per fruiting stem	Season	1	6.956	20.94	0.0006
	Block	12	3.957	3.81	0.0001
	Treatment	5	0.823	1.89	0.0996
	Season * Treatment	5	0.201	0.46	0.8044
	Error	142	12.364		

Table VI. Summary of an ANOVA table testing the effects of season, block, treatment, and season by treatment interaction on biomass of T. virginiana.

Source	d.f.	Sum of Squares	F-value	P>F
Season	1	8008.772	56.35	0.0001
Block	11	1563.322	0.99	0.4553
Treatment	5	2217.977	3.10	0.0112
Treatment * Season	5	2598.808	3.64	0.0041
Error	129	18441.220		

SUMMARY AND CONCLUSIONS

Fire is an important natural component of many ecosystems around the world, including the longleaf pine ecosystem of the southeastern United States. For most of these systems, fire plays an important role in determining structure and species composition. The response of species in fire-prone areas can be greatly affected by changes in the fire regime of the system, especially changes that might shift fire to seasons or intensities unlike those under which the plants evolved. Therefore, to provide better management prescriptions, it is important to know how different species respond to fire.

Goat's rue (<u>Tephrosia</u> <u>virginiana</u>) is a pyrophilic legume which is common in the longleaf pine ecosystem. Fruit and seed production is strongly influenced by fire. Seasonal differences in fire do not seem to affect fruit production for this legume, but do affect seed production. Plants which are burned during the growing season, or late-April through mid-July, produce more seeds than plants burned in the dormant season. Seed production is almost non-existent for unburned plants. Seed predation effectively eliminates any reproduction in unburned plants. Seed predator satiation appears to take place for plants burned in the growing season. I hypothesize that increased seed production was due to a delay in flowering and shorter durations of flowering as well mass flowering following fire. These delays in flowering and shorter durations of flowering following growing season burns may have led to reduced levels of competition for pollinators with other species. Mass-flowering also would have increased the availability of pollen and the visibility of the flowers.

Fire season also causes flowering in different ways. Dormant season fires most likely increase flowering for this legume by clearing vegetation and litter from over the

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plant. We hypothesize that this litter removal changes the light quantity and quality which may stimulate stems to produce flowers. Growing season fires influence flowering by top-killing the stems which then releases subterranean buds. More research is needed to determine factors which cause stems to produce flowers following growing season fires. Fruit production was very low in plants burned in the growing season in the study described in chapter two compared to fruit production levels in the study described in chapter one, a finding I attribute to lack of pollination success. Burn treatments in the study described in chapter two were localized. Flowers produced following these fires lacked a population wide mass-flowering event. I hypothesize that the very localized flowering following these burn treatments led to low availability of pollen and low visibility of flowers to pollinators.