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Effects of spring and fall burns on C3 and C4 productivity

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Abstract

A lack of information about the differing effects of fall and spring burns on aboveground net primary production of C3 forbs and C4 grasses prevents discovery of optimal restoration management techniques for the tallgrass prairie. In order to make progress toward this goal, our study examines how the above-ground biomass and abundance of the late-flowering C3 species Lespedeza capitata *and* Solidago canadensis *variety* scabra*, as well as the late-flowering C4 grasses* Andropogon gerardii *and* Sorghastrum nutans *are affected by spring burn, fall burn, and no burn treatments. We measured total nitrogen and moisture content of the soil, as well as light availability in order to examine possible correlations of these factors with different levels of productivity of the species examined. Although most previous studies have assumed similar productivity patterns resulting from spring and fall burn treatments, we found trends of greater production in C3* L. capitata *and C4* S. nutans *in spring burn regimes as compared to fall burn regimes. We also found significantly higher productivity and abundance of* A. gerardii *in both burned treatments than in unburned treatments. There were no correlations between increased production in these species with soil moisture, total nitrogen or light intensity levels. However, rhizomatous stimulation in early season growth resulting from increased solar radiation on soil could be a possible cause for this response to fire.*

Introduction

C4 grass species dominate most prairies due to the fact that, in the presence of fire, they out-compete most forbs and C3 competitors (Howe 1995). This can be attributed to their evolutionary adaptations to the conditions of the prairie, such as more efficient usage of nitrogen and carbon dioxide, more extensive root systems for moisture acquisition, and decreased stomatal transpiration in a dry environment (Reichman 1987). These adaptations result in increased rates of photosynthetic activity under low moisture conditions (Turner and Knapp 1996). C4 grasses have adapted to narrower niches in the prairie ecosystem, which reduces competition from wider-niche C3 species (Parrish, et. al 1982).

Seasonal burning studies have compared dormant season burns with summer burns and focused on the succession, diversity, abundance, and productivity of C3 and C4 species following spring and summer burns. Howe's (1995) study, for example, found that spring burns favor C4 grasses, as opposed to "more natural" summer burns, which act to suppress late flowering C4 species. However, there have been relatively few studies comparing the effects of spring and fall burns on C3 and C4 productivity and abundance, resulting in limited information on the "best practice" for management of restored prairies. James (1985) showed that the longer the time between the burn and onset of shoot growth, the lower the soil temperature, and that growth in areas after fall burning may be lower than growth following spring burns. There is also little plant activity during the low temperature period between fall and spring burn times, a factor that lessens the effects of competition on species composition and productivity.

We hypothesized that spring and fall burns will cause little if any statistically significant variation in the productivity of C3 and C4 species, but that, as in Howe's (1995) study, we expected both burned areas to have higher C4 productivity relative to C3 species than unburned areas.

By examining three variable factors influenced by burn effects—nitrogen availability, water availability, and soil-level light availability—we attempted to identify mechanisms by which fire effects influences species productivity. We expected no significant difference in percent of available light to reach the surface between the spring and fall burned plots, or between burned and unburned areas, as the effects of canopy cover from increased grass productivity offset the effects of litter removal on light intensity (Turner and Knapp 1996). We expected, based on previous studies (Hulbert 1969; Redmann et. al 1993), to find higher soil moisture content in the unburned plots. We also expected nitrogen levels to be relatively higher in unburned plots as some nitrogen escapes when the aboveground biomass is lost in burns (Turner and Knapp 1996). However, relatively similar nitrogen levels between fall and spring burns were anticipated because of Howe's (1995) findings of similarities of burning effects between the two seasons in some studies. All of these hypotheses led us to expect increased productivity of C4 species in burned plots relative to C3 productivity due to C4 comparative advantages in the hypothesized reactions of the three variables to fire. Yet we expected little productive difference between spring and fall burned plots due to our hypothesized similarities of variable response to burn regimes.

Knowing about the differences in the three variables and the productive response of species to different burn treatments, we would be prepared to suggest a 'best practice' management technique for achieving optimal biodiversity in restored prairies. While most manage prairies by burning in the spring, there is a lack of empirical evidence establishing the advantages of spring burns to fall burns.

Methods

We performed our study at 24 10x10m experimental plots in reconstructed prairies at Conard Environmental Research Area near Grinnell, Iowa between 9 October and 18 November 2002. It is unknown whether the plots in the prairies received identical plantings when they were reseeded in 1987. Burning last took place in the six randomly chosen unburned plots in the spring of 1997, in the fall plots every year since the fall of 1999, and in the spring plots in 2000, 2001 and 2002. To represent C3 plants of the plots, we chose the forbs *Lespedeza capitata* (Round-headed Bush Clover) and *Solidago canadensis* variety *scabra* (Tall Goldenrod) because of their abundance in the majority of the plots. For similar reasons, we chose grasses *Andropogon gerardii* (Big Bluestem) and *Sorghastrum nutans* (Indian grass) to represent C4 plants. All four plants are late-season species, which means that the flowers remained on the stems when we studied them. In collecting biomass and counting abundance we only included the flowering stems of C4 plants in our data in order to ensure accurate identification.

Soil Moisture

We randomly selected a point in each of six replicates of the three burn treatments and used a soil corer to extract a 31.416 cm^3 soil column. The mass of the samples were measured and placed in a drying oven at 60 degrees Celsius for 48 hours. The mass was measured again, and the percentage of soil moisture present calculated.

Light intensity

We measured light intensity on every replicate of the three burn treatments at two random points per plot. We used a quantum photometer to take a reading above the tallest grass in the area and another at soil level below litter in order to be able to calculate the percentage of available light that reached the soil.

Biomass

Slightly different methods were used for C3 and C4 plants in collecting biomass samples because of visible abundance and distributional differences. For all burn treatments we measured three samples of biomass on 28 October, 30 October, and 4 November 2002. To find biomass of selected C3 species, we randomly selected sampling points within each plot and collected the plant closest to that point by cutting the stem at ground level. For the two C4 grass species, we collected the entire aboveground portion of all flowering stems of each species within randomly chosen 0.5 x 0.5 m quadrants on each replicate plot. We then weighed flowering biomass after drying for at least 48 hours at 60°C. In calculating the mean biomass of forbs per square meter, we multiplied the abundance (plants/m^2) by the mean biomass per plant (g) for each plot. For grass species we also calculated flowering biomass in terms of grams per square meter.

Abundance

Different methods were used to measure abundance of C3 and C4 species for similar reasons. We counted all stems of *S. canadensis* within two randomly chosen 1x10m transects, on the replicates of treatments on 11 November and 18 November 2002. All *L. capitata* within each 10 x 10m plot were counted. To measure abundance of C4 species, we counted all flowering stems within the randomly chosen 0.5

x 0.5m quadrants.

Soil Nitrogen

On 13 November 2002 we took 25.133 cm^3 soil sample from three separate points within all experimental plots. The three columns from each plot were compiled into a single 75.398 cm^3 sample and sent to the Iowa State University lab for measurement of total nitrogen content.

Statistical Analysis

We analyzed the differences in biomass and abundance, soil moisture, nitrogen availability, and ground-level light availability between spring and fall burned and unburned regimes by using analysis of variance (ANOVA) tests; paired comparisons were tested for difference using Tukey's method. In simply comparing burned versus unburned treatments, we used t-tests.

Results

ANOVA yielded only one statistically significant difference in the productivity of burn regimes: 15,000% more flowering biomass of *A. gerardii* in both burn treatments as compared to the unburned treatments (Fig. 1). All other differences in biomass of species were non-significant. Trends showed that the spring burned areas yielded a mean biomass of *L. capitata* two times greater than fall burned areas and four times greater than unburned areas (Fig.2), and an increase of over 230% more flowering biomass of *S. nutans* (Fig. 1) than unburned and of 385% more than fall burned. Biomass of *S. Canadensis*, on the other hand, was insignificantly two times greater on unburned areas than burned areas (t=0.181, P=2.447) (Fig. 2).

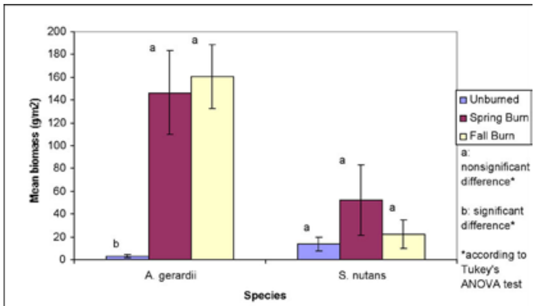

Figure 1. Mean biomass (+/- S.E.) of *A. gerardii* (n=6) and *S. nutans* (n=6) at burn treatments

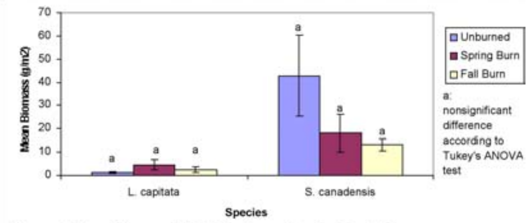

Figure 2. Mean biomass (+/- S.E.) of *L.capitata* (n=6) and *S. canadensis* (n=6) at burn treatments

However, *A. gerardii* did have a significant difference between burning treatments; similar to the results of the biomass tests, it was the only species the ANOVA tests for abundance showed having significant differences. Unburned areas had a mean of 1.11 *A. gerardii* plants per square meter (+/- S.E. 0.54), while the means for spring burned and fall burned areas were 55.78 plants/m^2 (+/- S.E. 12.20) and 57.78 plants/m^2 (+/- S.E. 6.88), respectively (Fig. 3). Our data showed some trends in the abundance of other species, although insignificant: the mean flowering abundance of *S. nutans* on spring burned areas was about twice the means of fall and unburned areas (Fig.3); and, the spring burned area had more *L. capitata* than the fall burned and unburned areas (F=1.79, P=0.202) (Fig. 4). In contrast, unburned areas had 154% more *S. canadensis* than fall burned areas and 131% more than spring burned areas (Fig. 4).

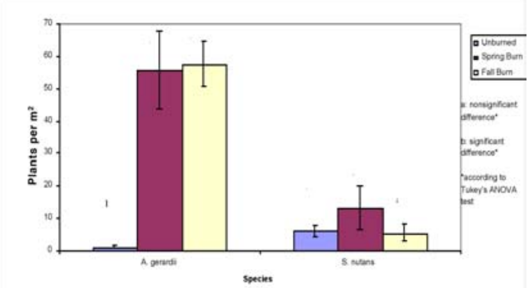

Figure 3. Mean abundance (+/- S.E.) of *A. gerardii* (n=6) and *S. nutans* (n=6) at burn treatments

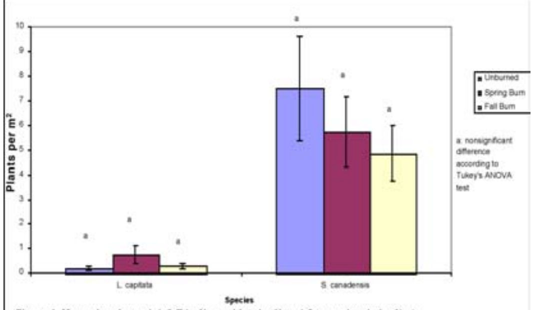

Figure 4. Mean abundance (=/- S.E.) of *L. capitiata* (n=6) and *S. canadensis* (n=6) at

The tests also found the three other variables we measured at the plots not statistically different. However, trends in the data showed the percentage of available light reaching the ground only slightly greater on unburned and spring burned areas than fall burned areas with respective means of 5.975% (+/- S.E. 1.897), 4.960% (+/-S.E. 0.900), and 3.347% (+/-S.E. 0.465) (Fig. 5). Burned areas had more mean soil moisture than the unburned areas (Fig. 6), and nitrogen content remained almost the same between burned and unburned areas (F=1.22, P=0.324) (Fig. 7).

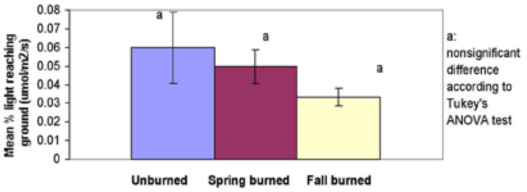

Figure 5. Mean percent of available light (+/- S.E.) reaching ground in burn treatments (n=6)

Figure 6. Percent of moisture in the soil (+/- S.E.) at burn treatments (n=6)

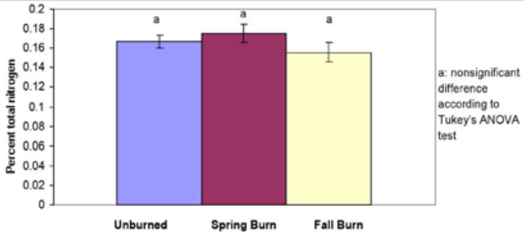

Figure 7. Mean percent total nitrogen (+/- S.E.) of soil at burn treatments (n=6)

Discussion

Although we hypothesized that the two C4 species would uniformly show advantages in productivity over the two C3 species in burned plots, we found more mixed responses. As expected (Hulbert 1969; Howe 1995; Turner and Knapp 1996), we found a statistically significant greater mean production of the C4 *A. gerardii* and a non-significant mean decrease in production of C3 *S. canadensis* in both burned plots. We also found large mean increases, though non-significant, in productive responses of *S. nutans* and *L. capitata* to spring burn relative to other regimes. This was consistent with similar findings of positive C4 *S. nutans* response to annual burning (Collins, et. al 1995), but contradictory to the findings of McGinley and Tilman (1993), which identified slightly negative responses of C3 *L. capitata* to burning. The large, though non-significant mean differences between spring and fall burns in both plants suggest one or several factors is involved in the similar productive increases of both plants.

Snaydon (1991) and Turner and Knapp (1996) both identified three primary limiting factors to prairie species productivity: nutrients (emphasizing nitrogen), moisture, and light availability. C3 plants in grasslands are generally limited by their comparative disadvantage in allocating and retaining nutrients and water for two primary reasons: 1) C4 grass species' root growth is deeper and more extensive allowing them to out-compete C3 species; 2) the C4 photosynthetic pathway allows for decreased water transpiration in allocating carbon (Reichman 1987; Snaydon 1991). The comparative advantages of colonizer C3 forbs include higher fecundity, faster initial growth, and lower light requirements for photosynthesis as compared to C4 species. Colonizer C3 species quickly form a canopy over their slow-growing C4 competitors and may effectively suppress C4 species under conditions of high water and nutrient resource availability by limiting light availability during early succession (Wilson and Tilman 1991; Turner and Knapp 1996). Spring and, similarly, fall burns may effectively eliminate the comparative advantage of C3 species by removing litter and destroying early growth.

Light Availability

Turner and Knapp (1996) showed that, while the soil-level light availability is high following spring burns when litter cover is removed, shading by canopy cover in spring burned plots surpasses litter cover shading of unburned plots by mid-summer, due to the growth stimulatory affect of fire and increased light availability on rhizomatous activity (Ewing and Engle 1988). We found similar results in that the percentage of available light reaching soil level was non-significantly greater in the unburned compared to the fall burned plots. This suggests that light limitations suppressed productivity of C4 grasses in unburned plots. However, light was not a limiting factor to C4 grass productivity in burned plots, consistent with Turner and Knapp's (1996) findings.

Soil Moisture

Contrary to our hypothesis, we found non-significantly greater mean moisture content in both fall and spring burns. Hulbert (1969) found that litter on unburned grassland reduces water evaporation from the soil. Extending this argument, and using Turner and Knapp's (1996) observation that C4 grass species increase productivity and cover due to stimulatory effects of spring and fall burns, we can conclude that the increased plant cover limited evaporation from wind and solar radiation, as noted by Reichman (1987).

Nitrogen content

Long-term annual burning reduces the level of nitrogen in the soil, thus decreasing species diversity and productivity (Collins, et. al 1995). Most non-legume colonizer C3 species, such as *S. canadensis*, cannot be maintained in nitrogen deficient soil. Nitrogen-fixing C3 legumes, and specifically *L. capitata* (Becker and Crocket 1976; Ritchie and Tilman 1995), along with dominant C4 grasses, are able to acquire and allocate nitrogen more efficiently than other C3 species through their comparative advantage. Positive though non-significant *L. capitata* and *S. nutans* response to spring burns suggests decreased nitrogen content in the spring burned soil as a result of annual nitrogen-removing burns over a three year period. This positive response also suggests that nitrogen is the primary limiting factor to productivity in burned areas (Turner and Knapp 1996).

However, our data do not indicate any conclusive trends in nitrogen content as a result of burn treatment. The similarities in nitrogen content between all three treatments suggest that short-term annual burning may not have negative affects on nitrogen content. Noticeable nitrogen losses may only occur following long periods of frequent burning. Reichman (1987) observes that microbial bacteria in the accumulated litter of unburned plots intercept nitrogen from rain, thus blocking nitrogen input. This effect may balance out short-term losses of nitrogen from burned prairies, yet long term frequent burning seemingly lowers soil nitrogen content to levels that would significantly decrease productivity, as Collins, et al (1995) discovered.

Productivity and Abundance

Annual burning in the first three years of this experiment has apparently maintained its positive effect on productivity. We question part of our initial hypothesis because of the greater mean responses of *S. nutans* and *L. capitata* to spring than fall burns and greater response in general of *L. capitata* to annual burns. Ewing and Engle (1988) argued that late-season burns, similar to mid-summer burns, could damage late-season species to a greater extent than spring burns as more nutrients may be available in the shoots following mid-season maturation. This supports our finding that *fall burns do not positively affect* S. nutans. However, our hypothesis was supported by responses of *A. gerardii*, which showed little mean difference between fall and spring productivity, suggesting little difference in damage to shoots in fall compared to spring.

Conclusion

As James (1985) concluded, lower soil temperatures in fall burn plots limit the growth of late-flowering species during their period of maximum growth. Soil temperature decreases proportionally to the increase in time following burns as a result of increase in canopy cover, and thus decreases solar heating of the soil. The period of maximum shoot growth of late-flowering species (June 15 to July 15) follows sooner after spring burns than fall burns (Ode et al. 1980). Harsh winter conditions inhibit growth several months subsequent to fall burns. Yet the early-season C3 growth of these regimes (February through May), not reduced by spring burning, may hinder C4 growth by shading out the shorter dominants, utilizing a comparative advantage of sunlight acquisition. This competitive reduction of dominants is similar to, yet less pronounced than that of unburned regimes.

Knapp (1984) concluded that early season fire might stimulate greater rhizomatous activity in late-season species as a result of the temporarily increased soil temperature due to the early removal of canopy cover. Early season burning may also increase the length of the growing season by allowing early season solar radiation to warm the soil, thereby favoring late-flowering C4 grasses.

We found statistically greater productivity in *A. gerardii* in burn regimes compared to unburned, and trends of greater productivity in *L. capitata* and *S. nutans* in spring and compared to fall and unburned regimes. Measuring in the October-November period, we found little differences in suspected mechanisms of fire's effects on productivity between burn regimes.

Therefore, we suggest that light and moisture availability may be more differentiated between burn regimes in the spring than the fall. Following this, we also suggest that these mechanisms are more influential on the C3/C4 productive relationship in the spring than in the fall, while nitrogen effects are influential following long periods of frequent burning.

From a management perspective, trends in our evidence suggest that spring burning is more effective than fall burning in increasing relative productivity of some late-season species, but result in no recognizable difference in productivity between C3 and C4 species. This is due to fire's effects on the different photosynthetic pathways of C3 and C4 species. This suggests that there will be little difference in biodiversity because of spring and fall burns. However, further studies, similar to that of Parrish and Bazzaz (1982), of spring and fall burn effects on early-flowering annuals and late-season perennials may more accurately reveal methods of prairie management for increasing biodiversity.

Studies such as ours that measure only aboveground biomass neglect belowground productivity, a measurement that more accurately reflects the competitive advantages of C4 species on grasslands (Snaydon 1991). We would therefore recommend a belowground study comparing the differences between burned and unburned plots; this study could better measure the competitive interactions between C3 and C4 species. A more thorough and diverse survey of nutrient availability may also be of great benefit. Ritchie and Tilman (1995), for example, studied the competitive interactions of legume species to multiple nutrient and herbivore variables. This study suggested that herbivores targeted legume species because of the supply of nitrogen in their plant tissue, and that nutrients other than nitrogen prevented legume dominance in grasslands. Further studies accounting for these factors may indicate the primary mechanisms by which fire influences species productivity and provide solutions to optimizing biodiversity.

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Literature Cited

Becker, Donald A. and Jerry J. Crockett. 1976. Nitrogen fixation in some prairie legumes. *American Midland Naturalist* **96**: 133-143.

Collins, Scott L.; Susan M. Glenn; and David J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* **76**: 482-492.

Ewing, A.L. and D.M. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* **120**: 212-223.

Howe, Henry F. 1995. Succession and fire season in experimental prairie plantings. *Ecology* **76**: 1917-1925.

Hulbert, Lloyd C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* **50**: 874-877.

James, Samuel W. 1985. An unexpected effect of autumn burning on tallgrass prairie. *The American Midland Naturalist* **114**: 400-403.

Knapp, Alan. 1984. Post-burn differences in solar radiation, leaf temperature, and water stress influencing production in a lowland tallgrass prairie. *American Journal of Botany* **71**: 220-227.

McGinley, Mark A.; David Tilman. 1993. Short-term response of old-field plant communities to fire and disturbance. *American Midland Naturalist* **129**: 409-413.

Ode, David J.; Larry L. Tieszen; and Juan Carlos Lerman. 1980. The seasonal contribution of C3 and C4 plant species to primary production in a mixed prairie. *Ecology* **61**: 1304-1311.

Parrish, J. A. D. and F. A Bazzaz. 1982. Competitive interactions in plant communities of different successional ages. *Ecology* **63**: 314-320.

Redmann, R.E.; B. Pylypec; and J.T. Romo. 1993. Impacts of burning on primary productivity of Festuca and Stipa-Agropyron grasslands in central Saskatchewan. *The American Midland Naturalist* **130**: 262-273.

Reichman, O.J. 1987. *Konza Prairie*. University Press of Kansas, Lawrence, KS: 58-114.

Ritchie, Mark E. and David Tilman. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen poor soil. *Ecology* **76**: 2648-2655.

Snaydon, R. W. 1991. The productivity of C3 and C4 plants: a reassessment. *Functional Ecology* **5**: 321-330.

Turner, C.L. and A.K. Knapp. 1996. Response of a C4 grass and three C3 forbs to variation in Nitrogen and light in tallgrass prairie. *Ecology* **77**: 1738-1749.

Wilson, Scott D. and David Tilman. 1991. Component of plant competition along an experimental gradient of nitrogen availability. *Ecology* **72**: 1050-1