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Is leaf-level photosynthesis related to plant success in a highly productive grassland?

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Abstract We addressed the question: "Are short-term, leaf-level measurements of photosynthesis correlated with long-term patterns of plant success?" in a productive grassland where interspecific competitive interactions are important. To answer this question, seasonal patterns of leaf-level photosynthesis were measured in 27 tallgrass prairie species growing in sites that differed in species composition and productivity due to differences in fire history. Our specific goals were to assess the relationship between gas exchange under field conditions and success (defined as aerial plant cover) for a wide range of species, as well as for these species grouped as dominant and sub-dominant grasses, forbs, and woody plants. Because fire increases productivity and dominance by grasses in this system, we hypothesized that any relationship between photosynthesis and success would be strongest in annually burned sites. We also predicted that regardless of fire history, the dominant species (primarily C_4 grasses) would have higher photosynthetic rates than the less successful species (primarily C_3 grasses, forbs and woody plants). Because forbs and woody species are less abundant in annually burned sites, we expected that these species would have lower photosynthetic rates in annually burned than in infrequently burned sites. As expected, the dominant C_4 grasses had the highest cover on all sites, relative to other growth forms, and they had the highest maximum and seasonally averaged photosynthetic rates (17.6 ± 0.42 μmol m^{-2} s^{-1}). Woody species had the lowest average cover as well as the lowest average photosynthetic rates, with subdominant grasses and forbs intermediate in both cover and photosynthesis. Also as predicted, the highest overall photosynthetic rates were found on the most productive annually burned site. Perhaps most importantly, a positive relationship was found between leaf-level photosynthesis and cover for a core group of species when data were combined across all sites. These data support the hypothesis that higher instantaneous rates of leaf-level photosynthesis are indicative of long-term plant success in this grassland. However, in contrast to our predictions, the subdominant grasses, forbs and woody species on the annually burned site had higher photosynthetic rates than in the less frequently burned sites, even though their average cover was lower on annually burned sites, and hence they were less successful. The direct negative effect of fire on plant cover and species-specific differences in the availability of resources may explain why photosynthesis was high but cover was low in some growth forms in annually burned sites.

Key words Competition · Grassland · Photosynthesis · Plant cover · Tallgrass prairie

Introduction

Comparisons of rates of net photosynthesis within and among species have been a cornerstone of comparative plant ecophysiological research ever since Mooney and Billings (1961) measured leaf-level gas exchange in the field. Implicit in these studies is the assumption that short-term, leaf-level photosynthetic rates are related to various attributes of plant success – productivity, competitiveness, resistance to herbivores or pathogens, seed production – i.e., fitness (McGraw 1987; Jackson et al. 1994; Pell et al. 1994; Burton and Bazzaz 1995; Patterson 1995; Van Der Kooij and De Kok 1996). Thus, the measurement of instantaneous, leaf-level photosynthetic rates is assumed to be of predictive value for assessing the longer-term consequences of abiotic/biotic factors affecting plant performance. Despite the ubiquitous measurement of carbon dioxide uptake by leaves, empirical evidence from comparative studies designed to demonstrate a direct link between leaf-level photosynthesis and

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other measures of plant success has been equivocal (Curtis et al. 1969; Evans 1975, 1993; Fischer et al. 1981; Arjunen et al. 1990; Dey et al. 1990; Reich et al. 1991).

The lack of observed relationships between measurements of individual leaf photosynthesis at optimal resource availability (= photosynthetic capacity) with whole-plant or community growth and productivity has been termed the "photosynthetic paradox" (Elmore 1980). Good and Bell (1980) argued that while there is often a lack of correlation between leaf-level photosynthetic rates and productivity, the "photosynthetic paradox" is primarily a problem of scale. They noted that the production of biomass is a function of net photosynthesis when the rate is expressed per plant (as opposed to per unit leaf area). Similarly, Zelitch (1982) and Peterson and Zelitch (1982) reported that while most attempts to correlate instantaneous leaf-level measurements of photosynthesis with productivity have failed, attempts to relate seasonal canopy photosynthesis with productivity by building carbon budgets and relating them to dry matter accumulation have been more successful. Nonetheless, because of the ease with which changes in instantaneous leaf-level photosynthesis can be measured within or among species, gas exchange data continue to be collected with the implicit assumption that such data are related to long-term plant success.

Indeed, some studies have demonstrated a positive relationship between leaf-level photosynthesis and plant success in both agricultural and natural systems. These have occurred in highly productive, competitive environments where irradiance and other resources were non-limiting and when single growth forms with similar phenologies have been compared (Snaydon 1991; Evans 1993). For example, variations in relative growth rate have been linked to variations in photosynthetic rates in early successional northern hardwood forest species, but only in areas without light, water, or nutrient stresses (Walters et al. 1993). In contrast, Turner et al. (1995), working in tallgrass prairie, found few consistent differences in maximum rates of gas exchange between the dominant C_4 grass *Andropogon gerardii* and five less common C_3 forbs. They concluded that, at least for this small group of species, leaf-level gas exchange responses were not indicative of success. The purpose of the present study was to examine the relationship between leaf-level photosynthetic rates and "success" in a highly productive, species-rich grassland (tallgrass prairie). We used a wide range of species and growth forms to test the hypothesis that a relationship does exist between instantaneous measurements of photosynthesis and long-term patterns of plant success (defined as aerial plant cover).

We measured gas exchange characteristics for 27 grassland species on three sites with documented long-term differences in productivity and species composition. We hypothesized that the relationship between success and photosynthetic rates would be strongest in the most productive (competitive) sites. In tallgrass prairie, such sites are usually those that are burned frequently (Briggs and Knapp 1995). Fire removes the standing litter layer, resulting in increased light availability and soil temperatures, eventually culminating in increased leaf area and productivity (Knapp 1984). We also predicted that regardless of fire history, the dominant tallgrass prairie species (primarily C_4 grasses) would have higher photosynthetic rates than the less common species (primarily C_3 grasses, forbs, and woody species). Finally, we expected that, because forbs and woody species are less abundant in annually burned sites, these species would have significantly lower photosynthetic rates in annually burned than in less frequently burned sites.

Methods

Study sites

Research was conducted from June to August 1996 on the Konza Prairie Research Natural Area, a 3487-ha native tallgrass prairie preserve in northeast Kansas. Vegetation on Konza Prairie is dominated by the warm season (C_4) perennial grasses *Andropogon gerardii* Vitman, *Schyzachyrium scoparius* (Michx) Nash, and *Sorghastrum nutans* (L.) Nash (Freeman and Hulbert 1985). Average precipitation at Konza Prairie (35-year mean) is 835 mm, with 75% occurring during the April to September growing season (Bark 1987). Precipitation for June, July, and August 1996 was 70.4 mm, 89.7 mm, and 97.4 mm, respectively.

Konza Prairie, as a member of the Long Term Ecological Research (LTER) program, is a particularly appropriate site for this research because of the watershed-level experimental fire regime imposed since 1981 (Hulbert 1985; Knapp et al. 1998). As a result, Konza Prairie has adjacent sites that differ substantially in productivity and species composition due to long-term differences in fire regime. For this study, we selected sites in three watersheds: one that has been burned annually in April since 1981, one that was burned approximately every 4 years (most recently burned in a wildfire on 25 February 1996), and one burned approximately every 20 years (most recently in 1991).

Elevation on Konza Prairie ranges from 320 to 444 m and species diversity is typically higher in uplands than in lowlands (Gibson and Hulbert 1987). Thus, we selected study sites on uplands of each watershed in order to maximize potential species diversity within the study sites. Initially, 27 species were chosen (Table 1), including the three dominant C_4 grasses, a subset of less common grasses (a mixture of C_3 and C_4 species), a variety of forbs (all C_3) and woody plants (all C_3).

Procedures

Measurements of leaf-level gas exchange characteristics were made for these species on all three sites, twice per month, from early June to late August (at which time the upper canopy leaves of many of the species measured began to senesce). All measurements were made during midday (11:00 a.m. to 2:00 p.m. CDT) under full sun conditions (photosynthetic photon flux $> 1500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$), using three LI-6200 portable photosynthesis systems (LI-COR, Lincoln, Neb., USA) operated simultaneously. The three systems were calibrated together in the laboratory prior to each measurement date, and against one another in the field on grass and forb species on a monthly basis. System operators and instruments were alternated among watersheds throughout the season to reduce operator and/or system bias. For each date, at least three representative plants were selected for measurements of gas exchange from each site. Sample sizes were minimal to maximize the number of species that could be measured during the period of the day when environmental variation also was minimal. For each plant, an upper-canopy, fully expanded leaf (or leaves in some species) that was naturally oriented perpendicular to the sun was measured.

Table 1 Common native tallgrass prairie species found on Konza Prairie in northeast Kansas. Each of these species was included in this study. Species are categorized according to growth form, dominance and photosynthetic pathway. Also indicated is general phenological information for each species. Flowering time indicates typical periods of the growing season when flowering begins. Some species flower for extended periods of time. Senescence times denote periods when all leaves have senesced. In several species, upper canopy leaves senesce earlier, but basal leaves remain green. Gas exchange was not measured in these basal leaves (*Sp* spring: April–May, *ESu* early summer: June, *MSu* mid-summer: July–August, *Fa* fall: September–October)

Species	Flowering time	Plant senescence
Dominant grasses (C_4)		
Andropogon gerardii	MSu	Fa
Schyzachyrium scoparius	MSu	Fa
Sorgastrum nutans	MSu	Fa
Subdominant grasses (C_3 and C_4)		
Dichanthelium oligosanthes	Sp	ESu
Panicum virgatum	MSu	Fa
Poa pratensis	Sp	ESu
Sporobolus heterolepis	MSu	Fa
Wood plants (C_3)		
Amorpha canescens	ESu	Fa
Ceanothus herbacesous	Sp	Fa
Rhus glabra	Sp	Fa
Rosa arkansana	Sp	Fa
Symphoricarpos orbiculatus	MSu	Fa
Forbs (C_3)		
Ambrosia psilostachya	MSu	Fa
Artemisia ludoviciana	MSu	Fa
Asclepias virdaflora	ESu	MSu
A. viridis	Sp	MSu
Aster oblongifolius	Fa	Fa
Callirhoe involucrata	ESu	Fa
Echinacea angustifolia	ESu	Fa
Kuhnia eupatorioides	MSu	Fa
Lespedeza capitata	MSu	Fa
Physalis pumila	ESu	Fa
Psoralea tenuiflora	ESu	MSu
Ruellia humilis	Sp	Fa
Salvia pitcheri	MSu	Fa
Solidago missouriensis	MSu	Fa
Vernonia baldwinii	MSu	Fa

After measurement, the portion of the leaf enclosed in the gas exchange cuvette was removed and placed in a moist plastic bag for transport to the laboratory where leaf area was determined with a video leaf area meter. Leaf rolling in the grasses did not occur. Most forbs and woody plants have horizontal leaves, but in the grasses leaf angles vary considerably along the length of the blade. We measured only those portions of the leaves that were fully sunlit and perpendicular to the sun. Because some species senesced earlier than others and weather constraints on one sampling day truncated the measurement period, consistent (every sampling date) data were not available for all species. However, the average number of species measured on any day was more than 22 species.

After the final leaf-level measurements in late summer, 10–30 plots (0.1 m^2 each) were located at random on each site and all aboveground biomass was harvested to estimate aboveground net primary productivity. Samples from burned sites were separated into grass and forb components, including current year's senesced tissue. Samples from unburned sites were separated into the same categories plus previous year's growth (litter). All samples were oven-dried for at least 48 h and weighed. Because previous year's litter could be distinguished from the current season's production in unburned sites, and all previous year's litter was consumed by fire in the burned sites, aboveground biomass at the end of the season is a good estimate of annual aboveground production in ungrazed tallgrass prairie (Briggs and Knapp 1995).

Canopy cover was used as a measure of species success in this study because long-term data are available at the species level, it is a more sensitive measure of responses to fire at the growth form level than biomass (Knapp et al. 1998), and because cover is an indication of a particular species' past reproductive and establishment success and relative dominance in the community. At Konza Prairie, canopy cover has been estimated since 1981 in 10-m^2 circular plots permanently located along four transects in selected watersheds. On each plot, cover of all species within the plot was recorded individually by cover class (modified after Daubenmire 1959). Cover was defined as the area within lines defining the extremities of the plant canopy represented by a particular species. Additional details on sampling methods are in Collins and Glenn (1991) and data and meta-data are available from the Konza Prairie LTER database (http:\\climate.konza.ksu.edu).

Data analysis

Measurements of leaf-level photosynthesis and conductance were averaged for the entire season for each watershed for all species. In addition, seasonal averages were calculated for each growth form (dominant grasses, subdominant grasses, forbs, and woody species; Table 1) within and combined for all watersheds. Monthly averages of photosynthetic rates also were calculated for each species and growth form, on each watershed. Absolute canopy cover values from 1991 to 1995 were averaged for each individual species. Absolute cover values for the dominant grasses, subdominant grasses, forbs, and woody species were calculated by combining all cover values for each species that fell within those growth form categories. Means were compared with ANOVA, and regressions were performed with a non-parametric Spearman's test because species cover data violated the assumption of normality. Statistical analyses were performed with Statistix (version 1.0 for Windows, Analytical Software, Tallahassee, Fla., USA) and significance is expressed at the $P < 0.05$ level.

Results

When cover values were combined for all watersheds sampled (Fig. 1), the dominant C_4 grasses had the highest absolute cover (73.2%), followed by subdominant grasses (36.5%), the forbs (31.7%), and woody species (7.7%; Fig. 1). Thus, cover values varied by a factor of almost 10 among growth forms. In annually burned sites, the cover of dominant C_4 grasses was similar to infrequently burned sites, but the subdominant grasses, forbs, and woody species all had higher cover in the infrequently burned sites (Fig. 1).

Total aboveground production was significantly higher on the burned sites than on the sites protected from fire for the longest period. This pattern also was seen in the biomass of all grasses combined (Table 2). Forb biomass, however, was significantly higher on the less frequently burned sites than on the annually burned site (Table 2). These 1996 data were representative of longer-term patterns documented for this site (Briggs and Knapp 1995).

Seasonally averaged photosynthetic rates across all sites for the different growth forms (Fig. 2) ranged from 17.6 ± 0.42 μmol m^{-2} s^{-1} in the dominant grasses to 10.6 ± 0.34 μmol m^{-2} s^{-1} in the woody species. Thus, there was a difference of almost 70% among growth forms in instantaneous rates of CO_2 uptake. Stomatal

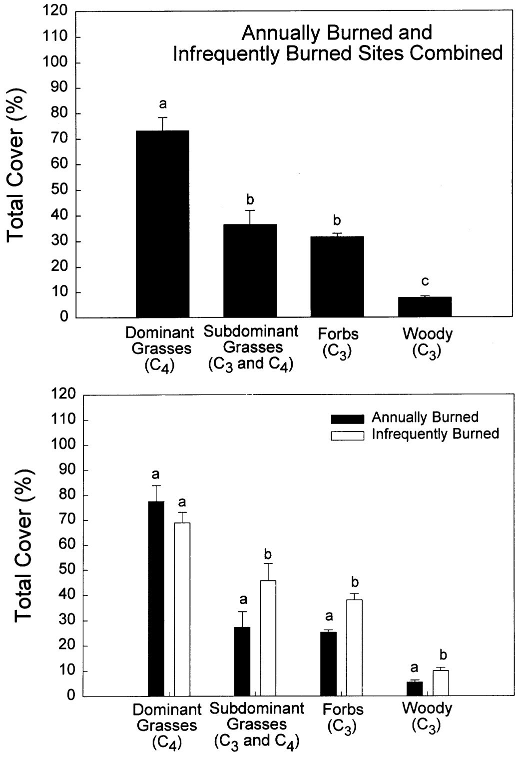


Fig. 1 (Top) Total cover (%) of the four common growth forms found on Konza Prairie, a native tallgrass prairie in northeast Kansas, USA (Table 1). Data from years 1991–1995 were averaged, and cover values for all species in each group were averaged for the annually burned and infrequently burned sites. (Bottom) Total percent cover of each of the growth form groups (1991–1995 data) in sites that differed in fire frequency. *Error bars* represent +1 SE of the mean and different *letters above bars* indicate significant differences (top) among growth forms and (bottom) between sites

conductance varied from 591 ± 15.0 mmol m^{-2} s^{-1} in the forbs to 263 ± 6.0 mmol m^{-2} s^{-1} in the dominant grasses. When seasonal photosynthetic and conductance values were examined on each site combining all growth forms (Fig. 3), photosynthetic rates were significantly higher in the annually burned relative to the infrequently burned sites. Similar patterns were seen for stomatal conductance (Fig. 3).

Monthly patterns of photosynthesis in the dominant grasses were similar in annually burned and infrequently burned sites (Fig. 4). In this comparison and the remaining analyses, we combined data for the two infrequently burned watersheds because they behaved similarly relative to the annually burned site. Photosynthesis in the dominant grasses was significantly higher in the annually burned site than in the infrequently burned sites in June, but not during the remainder of the season. This is typical of results from previous studies in tallgrass prairie (Knapp 1985). A similar pattern was seen in the subdominant grasses (Fig. 4). The forbs had the highest photosynthetic rates in the annually burned site in two out of the three months (June and August), and in the woody plants (Fig. 4), photosynthesis was greater in the annually burned site every month.

Table 2 Mean end-of-season total aboveground biomass and the graminoid and forb components (g m^{-2}) from upland tallgrass prairie sites on the Konza Prairie. Data are from an annually burned and two infrequently burned watersheds. Standard errors of the means are indicated in parentheses and means followed by different letters are significantly different ($P < 0.05$) within a row

	Annually burned	Infrequently burned (1 in 4 years)	Infrequently burned (1 in 6 years)
Total	384.8^a (17.6)	396.3^a (37.3)	297.6^b (24.1)
Graminoid	366.0^a (29.5)	337.5^a (43.5)	248.5^b (31.9)
Forb	18.8^a (5.3)	58.8^b (18.7)	49.1^b (11.5)

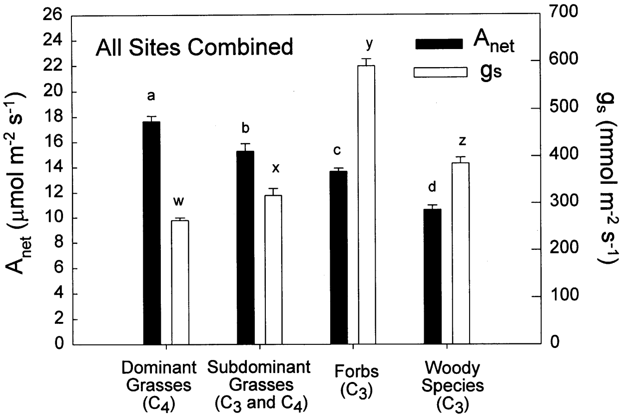


Fig. 2 Seasonal average net photosynthesis (A_{net}) and stomatal conductance (g_s) for growth forms common in tallgrass prairie (see Table 1). Data from all 3 sites and all 6 sampling dates in 1996 were combined. *Error bars* represent + 1 SE of the mean and different *letters above bars* indicate significant differences among growth forms

A number of correlational analyses, based on a priori predictions, were performed between measures of photosynthesis for each species (e.g., seasonal mean and maximum, monthly mean and maximum) and cover (e.g., absolute, relative, long-term average, maximum) for burned and infrequently burned sites, independently and combined. Most analyses yield weak or non-significant relationships, but a relatively strong relationship was found between individual species cover averaged across all sites in 1995 and the seasonal average photosynthetic rate also averaged across all sites (Fig. 5). This analysis included the 16 species for which data from all sites/dates were available. These species are notable in that they are all found within the "core" species group identified for Konza Prairie by Collins and Glenn (1991).

Discussion

The tallgrass prairie in general, and Konza Prairie in particular, provides an excellent opportunity to examine the relationships between leaf-level photosynthesis and plant success. This is because the tallgrass prairie is species rich and very productive (Briggs and Knapp 1995), and the experimental fire regime creates sites with a wide range of productivity, species richness and resource availability (Knapp and Seastedt 1986; Hulbert 1986; Collins et al. 1995). Frequent fire in tallgrass prairie leads to lower species richness, but higher productivity relative to less frequently burned sites (Table 2; Abrams et al. 1986; Briggs and Knapp 1995). In contrast, higher cover and greater diversity of forbs and woody species (Fig. 1) characterize less frequently burned areas. Although annual fire may reduce soil N and water availability at certain times of the growing season (Knapp 1985; Hulbert 1988; Seastedt et al. 1991; Ojima et al. 1994), it increases light levels throughout the canopy due to the removal of dead material and increases shoot density, potentially leading to increased competitive interactions (Kucera and Koelling 1964; Knapp and Seastedt 1986; Hulbert 1986; Collins 1987). Indeed, these resource alterations in burned sites (high light, low N, periodic water stress) are key to the success of the C_4 dominants (Knapp et al. 1998). Tallgrass prairie is a stable, fire-maintained ecosystem, but if fire is eliminated, woody species can invade and eventual conversion to forest occurs (Bragg and Hulbert 1976; Knight et al. 1994).

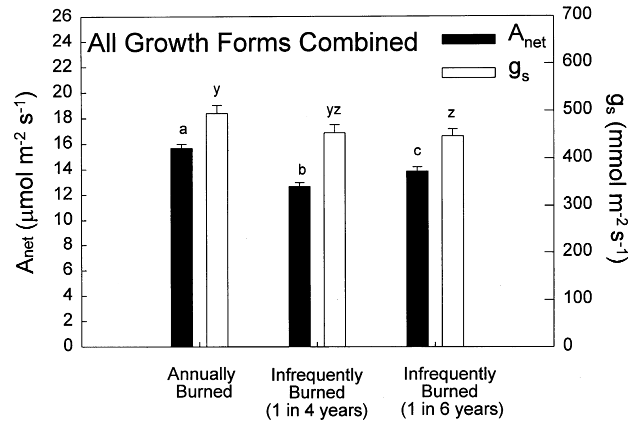
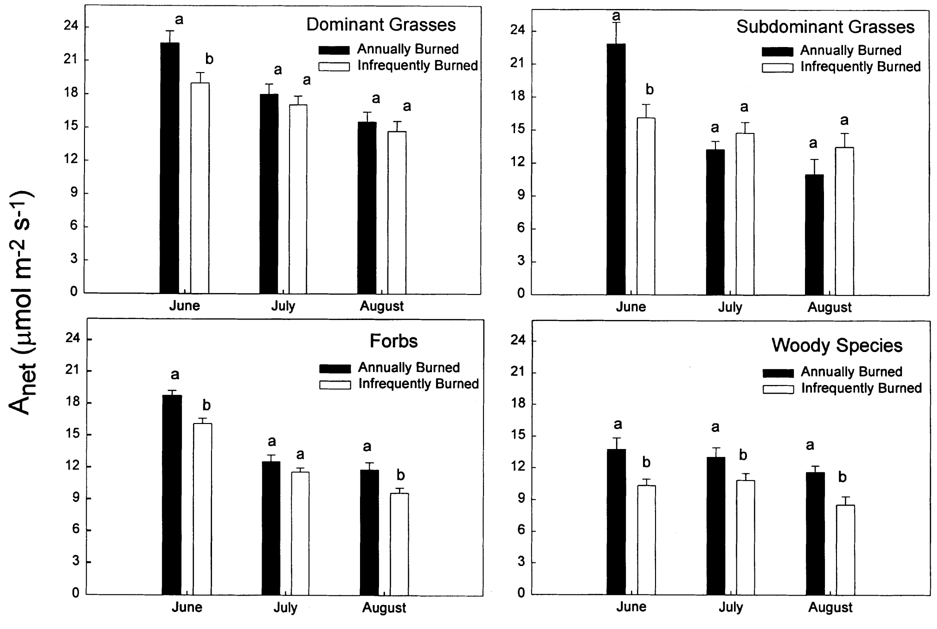


Fig. 3 Seasonal average net photosynthesis (A_{net}) and stomatal conductance (g_s) for three tallgrass prairie sites that differed in fire frequency. Data from all growth forms (Table 1) and from all 6 sampling dates were combined in this analysis. *Error bars* represent +1 SE of the mean and different *letters above bars* indicate significant differences among sites

Canopy coverage is generally more sensitive to burning than aboveground production, thus it was used in this study as a more responsive and predictable measure of plant success (Knapp et al. 1998). Because cover can be determined for individual species, but also can be expressed relative to other species in the community, it can be used as an indication of a species' dominance on a given site. As expected, the three dominant C_4 grasses (*A. gerardii*, *S. scoparius* and *So. nutans*) had the highest absolute cover overall, as well as on each watershed individually (Fig. 1). Also as predicted, the dominant grasses had the highest seasonal average, maximum, and monthly photosynthetic rates and lowest stomatal conductances, two key physiological traits that contribute to their dominance in this system (Fig. 2). In contrast, the woody species had the lowest average cover as well as the lowest average photosynthetic rates. The subdominant grasses and the forbs were intermediate in terms of both cover and photosynthesis. In the subdominant grasses and forbs, seasonal and monthly means for gas exchange may have been affected by the early senescence of some species (Table 1). Although its not known if these species have shorter leaf life spans, which are correlated with higher photosynthetic rates (Reich et al. 1991), than others in their group, gas exchange measurements for these species were not atypical of others in their respective growth forms. Thus, the lower number of measurements included in means for these species late in the year did not bias growth form averages. Overall, these patterns sug-

Fig. 4a–d Monthly patterns of net photosynthesis (A_{net}) for each growth form (Table 1) in tallgrass prairie sites that differed in fire history. Patterns were similar on both of the infrequently burned sites, so these data were combined for analysis. *Error bars* represent +1 SE of the mean and different *letters above bars* indicate significant differences between sites within months



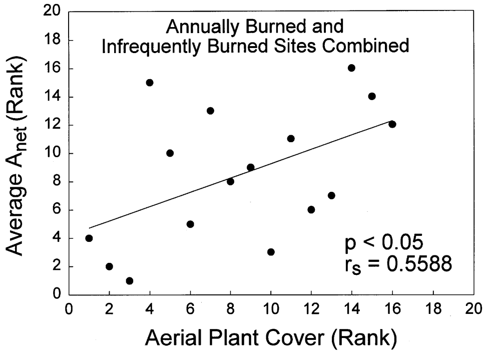


Fig. 5 Relationship (Spearman's rank correlation) between average net photosynthesis (A_{net}) and aboveground plant cover for 16 "core" species common at Konza Prairie (Collins and Glenn 1991) that were measured on both annually and infrequently burned sites. Cover data were from 1995. For each species, A_{net} and cover were combined for all sites

gest that there is a positive relationship between instantaneous measures of leaf-level photosynthesis and cover (success) in this grassland.

Twenty-five years of annual spring fires on the annually burned site has resulted in a highly productive watershed, with high cover of the dominant C_4 grasses and a decrease in subdominant grasses, forbs, and woody species. When comparing mean seasonal photosynthetic rates for all species combined in each watershed, the annually burned site clearly had higher rates than either of the less frequently burned sites (Fig. 3). Indeed, if these calculations had been weighted for the differences in cover between burned and unburned watersheds (lower cover of species with low photosynthetic rates in annually burned sites; Gibson and Hulbert 1987, Fig. 1), differences would be ever greater. Thus, at the watershed level, there appears to be a positive relationship between instantaneous, leaf-level photosynthetic rates sampled periodically through the season and productivity. The significant difference in photosynthetic rates in the two infrequently burned sites may be due to a winter fire that occurred in one of the sites. Winter fires reduce soil moisture earlier in the spring (Anderson 1965), and this may lead to decreased photosynthetic rates. Perhaps most importantly, a positive relationship was found between leaf-level photosynthesis and cover at the level of individual species when data for the 16 "core" species (Collins and Glenn 1991) were combined for all sites (Fig. 5). These core species are thought to be superior competitors in tallgrass prairie relative to the "satellite" species, whose abundance may be more likely controlled by stochastic events (Collins and Glenn 1991).

In contrast to the above relationships, we also found evidence suggesting that leaf-level photosynthesis was not related to success when other comparisons were considered. Most notably, the subdominant grasses, forbs and woody species all had higher photosynthetic rates in the annually burned site, yet the highest absolute cover values for each of these groups occurred in the unburned watersheds. This inconsistency has several possible explanations. First, this could be due simply to the loss of the less competitive species from these growth forms in the annually burned site. That is, the species persisting in annually burned watersheds are all highly competitive with the dominant grasses and have high photosynthetic rates. However, there was >90% overlap in the species measured in the annually burned site with the other watersheds (indeed, few species are unique to any particular fire regime on Konza Prairie, but their abundance varies substantially). Within each growth form, there are other possible explanations. For example, the forbs had the highest mean stomatal conductances compared to the other growth forms (Fig. 2). This could be a function of their deeper rooting habit (Weaver 1968), resulting in access to a potentially greater water supply than the more shallow-rooted grasses. Access to deep soil moisture for C_3 species may be particularly important in burned sites where water limitations are most severe (Knapp 1985; Briggs and Knapp 1995). Therefore, during dry periods in burned sites, forbs may have greater rates of gas exchange than the grasses (Turner et al. 1995) and because light availability is greater in burned sites, photosynthesis in forbs may be higher than in unburned sites. In this study, all data were collected on clear days during midday, and thus interactive effects of light availability and access to soil moisture could have strong effects on leaf-level responses.

Finally, in woody species, high leaf-level photosynthetic rates should not be expected to be indicative of cover in burned sites. This is because all perennial aboveground woody tissue is lost annually in spring fires. Thus, the direct negative effects of fire, not differences in photosynthetic rates manifest through competitive success and increased cover, may explain the pattern observed in woody species. Indeed, direct negative effects of fire also may be important for some of the other C_3 species that initiate growth before spring fires occur. The critical role that fire plays in maintaining this grassland was noted previously. Without fire, woody species (with their low leaf-level photosynthetic rates) will dominate. However, this success is achieved not through a growth rate advantage, but because the elevated perenating organs of woody plants allow for greater leaf area/plant and increased access to sunlight.

In summary, results of this study indicate that there does appear to be a positive relationship between instantaneous leaf-level rates of photosynthesis and plant success in this grassland. The relationship was most clearly seen when growth forms were compared among a variety of sites. Such a relationship was not always apparent, however, within individual sites, species or growth forms due to specific environmental and/or resource constraints on particular species. Given that such exceptions occurred in subsets of the data we collected, it is noteworthy that the strongest relationship between leaf-level photosynthesis and plant success was found in the most broadly based analysis (i.e., data from multiple sites combined with gas exchange measurements from throughout the season). This suggests that instantaneous leaf-level photosynthesis can be related to long-term success in this highly productive, native grassland.

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