Species-specific response of photosynthesis to burning and nitrogen fertilization

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Abstract
This study was conducted to examine photosynthetic characteristics of three dominant grass species (Agropyron cristatum, Leymus chinensis, and Cleistogenes squarrosa) and their responses to burning and N fertilization in a semiarid grassland in northern China. Photosynthetic rate ($P_n$), stomatal conductance ($g_s$), and water use efficiency (WUE) showed strong temporal variability over the growing season. *C. squarrosa* showed the significantly higher $P_n$ and WUE than *A. cristatum* and *L. chinensis*. Burning stimulated $P_n$ of *A. cristatum* and *L. chinensis* by 24-59% ($P<0.05$) in the early growing season but not during other time periods. Light-saturated photosynthetic rate ($A_{\text{max}}$) in *A. cristatum* and the maximum apparent quantum yield ($\Phi_{\text{max}}$) in *A. cristatum* and *L. chinensis* were significantly enhanced by burning (16-67%) in both the fertilized and unfertilized plots. The main effect of burning on $P_n$, $A_{\text{max}}$ and $\Phi_{\text{max}}$ was not significant in *C. squarrosa*. The burning-induced changes in soil moisture could explain 51% ($P=0.01$) of the burning-induced changes in $P_n$ of the three species. All the three species showed positive response to N fertilization in terms of $P_n$, $A_{\text{max}}$, and $\Phi_{\text{max}}$. The stimulation of $P_n$ under N fertilization was mainly observed in the early growing season when the soil extractable N content was significantly higher in the fertilized plots. The N fertilization-induced changes in soil extractable N content could explain 66% ($P=0.001$) of the changes in $P_n$ under N fertilization. The photosynthetic responses of the three species indicate that burning and N fertilization will potentially change the community structure and ecosystem productivity in the semi-arid grassland of northern China.

**Keywords:** Agropyron cristatum, Burning, Cleistogenes squarrosa, Leymus chinensis, N fertilization, photosynthesis
As a natural or anthropogenic disturbance, fire can cause changes in environmental conditions for plant growth due to the effects on soil physical properties and biogeochemical processes (Knapp et al. 1998; Neary et al. 1999; Wan et al. 2001). The increases in nutrient (especially N) availability after burning (Wan et al. 2001; Mack et al. 2001), together with higher incident radiation and the absence of competitors (Mullen et al. 2006), can stimulate plant photosynthesis and thus promote plant growth (Brys et al. 2005). However, soil microclimate such as soil moisture, temperature, and nitrogen content also change simultaneously after fire. Distinguishing the relative roles of the above factors in regulating plant ecophysiology will facilitate the interpretation of changes in plant growth, community structure, and ecosystem function after burning. In addition, fire can interact with other environmental factors to influence plant activities (Lesica and Martin 2003; Andrew et al. 2005). Considering the seasonal variability of environmental factors and the sensitivity of photosynthetic activities to changing growth condition (Ehleringer et al. 1997; Derner et al. 2003), we hypothesize that fire effect on plant photosynthesis may vary with season.

Nitrogen (N) is one of the most important resources in controlling plants photosynthesis. Close relationships have been observed among leaf N concentrations, Rubisco concentrations, and maximum rates of photosynthesis (Makino et al. 1994; Gonzalez-Real and Baille, 2000). It is well accepted that N fertilizer will enhance plant photosynthesis through increasing soil N availability, plant N uptake, and tissue N concentration. However, variations of other environmental factors (temperature, light, and water availability) may cause changes in the ecophysiological responses of plants to N fertilization in the natural communities. Therefore we hypothesize that N fertilization can interactive with burning to influence plant photosynthesis.

C3 and C4 species often coexist in natural grasslands. However, there are distinct differences in the ecophysiological traits in these two plant functional types. Generally, C3 plants have higher N and water requirements than C4 species (Pearcy and Ehleringer 1984) and thus might respond differently to burning and N fertilization. It has been reported that changes in burning frequency tend to favor or diminish the
abundance of C₄ plants relative to C₃ plants (Still and Berry 2003). Frequent burning helps maintaining the C₄-dominated ecosystem (Goldammer 1993; Bond and van Wilgen 1996; Keeley and Rundel 2005), while the absence of burning lead to the invasion of C₃ woody species into C₄ grasslands (van Auken 2000). Nevertheless, there are two contradictory aspects of how fire can impact the behavior of C₃ and C₄ species. On one hand, lower soil moisture and higher soil temperature after fire may favor C₄ species due to their greater water use efficiency and higher optimum temperature for plant photosynthesis. On the other hand, improved soil nitrogen availability under burning will favor C₃ species because of their higher N requirement and lower N use efficiency. Therefore, the net effects of C₃ and C₄ species will depend on which of the above two aspects dominates the growth of the two functional types in different grassland ecosystems.

The semiarid grassland in northern China is the representative vegetation type of the Eurasian continent which is predicted to be sensitive to climate change (Christensen et al. 2004). Water and N are the predominant limiting factors for plant growth in this area (Yuan et al. 2005). Given the changes in soil microclimate caused by burning and the differential response of C₃ and C₄ species to environmental changes, we hypothesize that C₃ and C₄ species might respond differently to burning and N fertilization. This study was conducted in a semiarid grassland in northern China to examine the potential influence of burning and N fertilization on photosynthetic activities of three dominant plant species. The questions we would like to answer are: (1) which plant functional types (C₃ vs. C₄) will be favored more by burning in term of plant photosynthesis? (2) is there an additive effect of burning and N fertilization on plant photosynthesis since both will enhance soil N availability?

**Materials and methods**

**Study site**

The study site is located in Duolun county (N42° 27', E116°40'), Inner Mongolia, China. The area is part of the Hunshandake Sandland, an area featuring great diversity
in plants and high endemism (Yang et al. 2004). Mean annual precipitation is 385 mm with peaks in July and August. Mean monthly air temperatures range from -17.5 °C in January to 18.9 °C in July, with the mean annual temperature of 2.1 °C. The soil is chestnut with 87% sand, 4% silt, and 9% clay. Soil carbon and nitrogen contents are 7.8 g kg\(^{-1}\) and 0.7 g kg\(^{-1}\), respectively. Soil bulk density is 1.42 g cm\(^{-3}\) (Liu et al. 2007).

**Experimental design**

The experimental site was located on a south-facing hillslope (approximately 15% in slope) with the altitude varying from 1,376 m at the bottom to 1,388 m at the top. The east side of the experiment site was burned by an anthropogenic burning on 5 April 2005 and the aboveground plant biomass was completely removed. Changes in wind direction during the burning left the west side unaffected by burning. Forty-eight 4×6 m plots were set up 1 week after fire in four blocks (lower slope and burned side, lower slope and unburned side, upper slope and burned side, upper slope and unburned side) with 12 plots in each block. The distance between the blocks in the upper and lower slopes is approximately 15 m in both the burned and unburned side. In addition, six of the 12 plots in each block were fertilized with urea (15 g N m\(^{-2}\)) on 10 May 2005 and the other six plots were used as unfertilized controls.

**Photosynthesis measurements**

Two C\(_3\) (*Agropyron cristatum, Leymus chinensis*) and one C\(_4\) (*Cleistogenes squarrosa*) grass species in the upper slope were selected for photosynthesis measurements.
An open gas-exchange system (Li-6400; Li-Cor, Inc., Lincoln, NE, USA) with a 6-cm² clamp-on leaf cuvette was used to measure gas exchange. Two fully expanded leaves in the upper canopy for each plant species in each plot were measured. The two values were averaged as one replicate. At least three replications per species per treatments were measured. When measuring the photosynthesis of *Cleistogenes squarrosa* which has relative small leaves, we adjusted the angle of the leaf chamber to clamp the base of the leaf and almost all the leaf parts were inserted into the chamber.

The seasonal dynamics of assimilation rate were measured in the morning between 9:00 am to 11:00 am (local time) on clear days on 14 June, 25 June, 9 July, 10 August, 23 August, and 7 September 2005. At each measuring date, leaf temperature was initially measured. The cuvette was applied to the leaf, and then temperature was held constant at the measured ambient level using the thermoelectric block within the cuvette. To avoid the influence of changing PPFD levels during the year, leaves were illuminated at 1500 mol m⁻² s⁻¹ using the LED light system at each measuring time.

Other environmental conditions within the cuvette were controlled to match the ambient conditions. Air temperature (*T*<sub>air</sub>), photosynthetic rate (*P*<sub>n</sub>), stomatal conductance (*g*<sub>s</sub>), and transpiration rate (*E*) were recorded. Instantaneous water use efficiency (WUE) was calculated as *P*<sub>n</sub>/*E*.

**Light response curves**

Light response curves were taken in the early July by fitting and attaching the light emitting diode array after removing the chamber window. Artificial illumination was applied to leaves from a red-blue LED light source attached to the sensor head. A range of light intensities between 0 and 2000 µmol m⁻² s⁻¹ were provided starting at 2000 µmol m⁻² s⁻¹ and ending at 0 µmol m⁻² s⁻¹ at a 2-minute interval. Measurements were made at 350 µmol mol⁻¹ CO₂ concentration. Light-saturated photosynthetic rate (*A*<sub>max</sub>) was calculated from the light response curve of each sample as the photosynthetic rate at the saturated light. The maximum apparent quantum yield (Φ<sub>max</sub>)
was calculated as the slope of the linear portion in the photosynthetic light response curve at PPFD below 100 µmol m\(^{-2}\) s\(^{-1}\) (Long and Bernacchi 2003). All the parameters can be determined by fitting data to a quadratic equation:

\[
A = \frac{\Phi_m Q + A_m - \sqrt{(\Phi_m Q + A_m)^2 - 4\Theta\Phi_m QA_m}}{2\Phi} - R_d
\]

where \(A\) is net assimilation rate (µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)), \(\Phi_m\) is the maximum apparent quantum yield of CO\(_2\) (mol CO\(_2\) mol\(^{-1}\) photons), \(A_m\) is the maximum photosynthetic rate (µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)), \(Q\) is the light level (µmol m\(^{-2}\) s\(^{-1}\)), \(\Theta\) is the convexity coefficient (0 < \(\Theta\) < 1), and \(R_d\) is the dark respiration rate (µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)).

**Data analysis**

Repeated measures ANOVA was used to test the effects of burning, N fertilization, and their interactions on photosynthetic rate \((P_n)\), stomatal conductance \((g_s)\), and water use efficiency (WUE). The difference in light-saturated photosynthetic rate \((A_{max})\) and apparent quantum efficiency \((\Phi_{max})\) among treatments were analyzed by one-way ANOVA. All ANOVA were followed by L.S.D.0.05 to show significant differences among treatments. Linear correlations were conducted to examine the relationships of photosynthesis and its response with other environmental factors. All the analyses were conducted using SPSS (SPSS 11.0 for windows, USA).

**Results**

**Soil temperature and moisture**

Burning caused significant changes in both soil moisture and temperature at most of the measuring dates whereas N fertilization had no impacts on these two parameters (Fig.1). Averaged across the growing season, burning decreased soil moisture by 0.3 and 0.2% and increased soil temperature by 2.0 and 1.4°C in the unfertilized and fertilized plots, respectively.

**Photosynthetic rate**
Photosynthetic rate of the three measured species fluctuated significantly across the growing season (Fig. 2, Table 1). *A. cristatum* and *L. chinensis* showed the peak $P_n$ on 10 August, while *C. squarrosa* showed its peak $P_n$ on 25 June in the control plot (Fig. 2A-C). *C. squarrosa* had, on average, 27 and 22% higher $P_n$ than *A. cristatum* and *L. chinensis*, respectively ($P<0.05$, Fig. 2A-C).

Burning significantly affected $P_n$ in *A. cristatum* and *L. chinensis* but not in *C. squarrosa* (Table 1). Over the growing season, burning increased mean $P_n$ of *A. cristatum* and *L. chinensis* by 8-10%. However, the response of $P_n$ to burning varied with measuring date. Significant increases in $P_n$ were observed in June and July for *A. cristatum* (17-46%), in June for *L. chinensis* (25-59%), and on 25 June for *C. squarrosa* (11%, all $P<0.05$). $P_n$ of the three species were not impacted by burning on other measuring dates (Fig. 2A-C).

The main effect of N fertilization on $P_n$ was statistically significant in *C. squarrosa*, with an average increase of 13% over the growing season (Table 1, Fig. 2C). N fertilization significantly interacted with measuring date to impact $P_n$ in all the three species (Table 1). For example, N fertilization elevated $P_n$ of *A. cristatum*, *L. chinensis*, and *C. squarrosa* by 21, 25, and 19% (all $P<0.001$), respectively on 25 June across the burned and unburned sides. However, N fertilization did not affect $P_n$ of the three species on 10 August (Fig. 2A-C).

**Stomatal conductance ($g_s$)**

Stomatal conductance of the three measured species changed greatly over the growing season (Fig. 2D-F). *A. cristatum* and *L. chinensis* showed the peak $g_s$ on 10 August (Fig. 2DE) while *C. squarrosa* showed the peak $g_s$ on 14 June (Fig. 2F) in the control plots. Across the growing season, *C. squarrosa* had 32 and 18% higher $g_s$ than *A. cristatum* and *L. chinensis*, respectively (Fig. 2D-F). Stomatal conductance showed positive linear correlation with $P_n$ (Fig. 3). None of the main effects on $g_s$ of burning, N fertilization, or their interactions were
statistically significant in any of the three species (Table 1). However, N fertilization interacted with measuring date to influence $g_s$ in *L. chinensis* (Table 1), which was elevated by 68% ($P<0.05$) on 9 July but was not changed on 25 June by N fertilization (Fig. 2E).

**Water use efficiency (WUE)**

There was strong seasonal variability of WUE for all the three measured species (Table 1). Over the growing season, *C. squarrosa* showed, on average, 35% higher WUE than *A. cristatum* ($P<0.05$, Fig. 4). Burning significantly impacted WUE only in *A. cristatum* (Table 1). Burning also interacted with the measuring date to affect WUE for *A. cristatum* and *C. squarrosa*. On 10 August, WUE of *A. cristatum* and *C. squarrosa* was increased by 56 and 76% (all $P<0.05$), respectively, by burning in the unfertilized plots (Fig. 4DF). However, there was no difference in plant WUE between the burned and unburned sides on 25 June. The main effect on WUE of N fertilization was significant only in *A. cristatum*, which was increased, on average, by 27% across the growing season (Fig. 4D). There were interactive effects of burning and N fertilization on WUE in *A. cristatum* and *C. squarrosa* (Table 1).

**The light saturated photosynthetic rate ($A_{\text{max}}$) and the maximum apparent quantum yield ($\Phi_{\text{max}}$)**

Burning significantly stimulated $A_{\text{max}}$ of *A. cristatum* by 16% in the unfertilized plots and by 20% in the N fertilized plots ($P<0.05$, Fig. 5A). $A_{\text{max}}$ of both *L. chinensis* and *C. squarrosa* was slightly but insignificantly increased by burning (Fig. 5BC). N fertilization enhanced $A_{\text{max}}$ in *A. cristatum* by 18 and 14% in the unburned and burned sides, respectively (Fig. 5A), and by 19% in *C. squarrosa* in the burned side (Fig. 5C, all $P<0.05$). Burning significantly increased $\Phi_{\text{max}}$ of *A. cristatum* in the fertilized plots (by 57%, Fig. 5D), and $\Phi_{\text{max}}$ of *L. chinensis* in the unfertilized plots (by 67%, Fig. 5E). N fertilization stimulated $\Phi_{\text{max}}$ of *A. cristatum* in the burned side and $\Phi_{\text{max}}$ of *L.*
Correlations between soil traits and photosynthesis traits

\( P_n \) and \( g_s \) in both \( A. \) cristatum and \( L. \) chinensis were positively correlated with soil moisture across the growing season \( (P < 0.05, \) Fig. 6\). Changes in \( P_n \) in response to fire also showed positive linear correlations with burning-induced changes in soil moisture for the three species \( (\text{Fig. 7A}). No correlations were found between burning-induced changes in \( P_n \) and burning-induced changes in soil temperature or soil extractable N content \( (P > 0.05). Comparing with the control plots, N fertilization enhanced soil extractable N by 33-131\% \( (P < 0.001). Fertilization-induced changes in \( P_n \) of the three species linearly increased with changes in soil extractable N content under N fertilization \( (\text{Fig. 7B}). \)

Discussion

Seasonal dynamics of photosynthetic characteristics

Seasonal dynamics of \( P_n \) and \( g_s \) for the two C3 species \( (A. \) cristatum and \( L. \) chinensis) were similar with each other \( (\text{Fig. 2ABDE}), but were different from that of C4 species \( C. \) squarrosa \( (\text{Fig. 2CF}). The different seasonal dynamics of photosynthetic characteristics between the measured species could facilitate the temporal partitioning in their resource requirements and thus are helpful for their co-existing. Seasonal differentiation in photosynthetic characteristics between C3 and C4 species have previously been attributed to the different temperature responses of net CO2 assimilation of C3 and C4 species \( (\text{Kemp and Williams 1980}). However, in our study, we suggest that the differential response of \( P_n \) and \( g_s \) to soil moisture between \( A. \) cristatum, \( L. \) chinensis, and \( C. \) squarrosa might cause their different seasonal dynamics. Positive relationships of \( P_n \) and \( g_s \) of \( A. \) cristatum and \( L. \) chinensis with soil moisture \( (\text{Fig. 6AB}) \) and no such relationship for \( C. \) squarrosa suggest that soil moisture drives changes in \( P_n \) and \( g_s \) in \( A. \) cristatum and \( L. \) chinensis but not in \( C. \)
squirrosoa over the growing season. It has been well studied that C₄ species have higher water use efficiency than C₃ species (Chapin et al. 2002), which was also observed in our study (Fig. 4). Therefore, C. squarrosa was more insensitive (less sensitive?) to soil moisture changes than A. cristatum and L. chinensis.

C. squarrosa had lower gs and higher Pn and WUE in comparison with A. cristatum and L. chinensis (Fig. 2, 4). The differences in A, gs, and WUE between the C₃ and the C₄ species were consistent with the difference between the two photosynthetic pathways reported previously (Niu et al. 2003).

Effects of burning on photosynthetic characteristics

Burning changed soil temperature and soil moisture greatly in this study (Fig. 1). When a fire scorches a large fraction of the aboveground canopy, evapotranspiration is reduced greatly (Beringer et al. 2003; Mullen et al. 2006). Therefore, transient higher soil moisture was observed on 25 June (Fig. 1). By contrast, higher plant transpiration and soil evaporation caused by burning-elevated temperature when the canopy grown up (Fig. 1B) led to the lower soil moisture in the burned side (Fig. 1A). The burning-induced changes in soil moisture and temperature can potentially impact plant photosynthetic characteristics.

The expected burning effect on photosynthetic characteristics was observed in our study (Table 1). Burning enhanced Pn, Amax, and Φmax of all the three species, which lead to 42% increase in aboveground biomass in 2005. The positive effects of burning on plant growth were also reported in the previous studies (Knapp 1985; Svejcar and Browning 1988; Bowen and Pate 2004). The species-specific responses of photosynthetic characteristics to burning observed in our study suggest A. cristatum and L. chinensis were more sensitive to burning than C. squarrosa. Our results were in accordance with those of a previous study (Mccarron and Knapp 2003) which also reported differential responses of C₃ and C₄ species after burning. The different effect of burning on grasses and forbs were also observed by Turner et al (1995).

The semi-arid grassland of northern China is characterized by a low-N and water-stressed environment, particularly after fire (Liu et al. 2007). These conditions
favor the species with higher water use efficiency. *A. cristatum* and *L. chinensis* in our study showed the lower WUE than *C. squarrosa* (Fig. 4), suggesting that these two species will be more impacted by water condition than *C. squarrosa*. This might lead to more sensitive responses of *A. cristatum* and *L. chinensis* to burning than *C. squarrosa*. Photosynthesis of the plants in the arid or semi-arid area was always stomata-limited (Cornic 2000; Niu et al. 2005), which was reflected by the close correlations between $P_n$ and $g_s$ (Fig. 3). $g_s$ of *A. cristatum* and *L. chinensis* was greatly dependent on soil moisture (Fig. 6B), which resulted in the sensitive response of $P_n$ to soil moisture (Fig. 6A).

In our study, the burning effects on photosynthesis varied greatly over the growing season. The positive burning effects on $P_n$ were found in the early growing season but not on other measuring dates (Fig. 2A-C). In the early growing season, specifically in June, no reductions in soil moisture or even increases in soil moisture on 25 June (Fig. 1A), in combination with elevated temperature and N availability, might have stimulated photosynthesis. Whereas in the middle and late growing season when plants need uptake more water from soil and ecosystem evapotranspiration was higher due to the high temperature, burning-induced decrease in soil moisture (Fig. 1A) might have aggravated water limitation on plant growth. The negative effect of burning caused by lower soil moisture might counteract the positive effect resulted from the increases in nutrient availability (Wan et al. 2001; Mack et al. 2001) or the higher radiation (Mullen et al. 2006). Over the whole growing season, the burning-induced changes in monthly mean soil moisture could explain 51% ($P<0.001$) of the burning-induced changes in $P_n$ of all the three species (Fig. 7A), suggesting that burning-induced soil moisture was the main driving factor for plant photosynthetic responses.

**Nitrogen fertilization effect on photosynthesis**

The effects of N fertilization on leaf-level net assimilation rate were reported inconsistently. Fertilization stimulated $P_n$ in some cases (Mitchell and Hinckley 1993;
Shangguan et al. 2000), but not in other cases (Lovelock and Feller 2003; Gough et al. 2004). In our study, the effects of N fertilization on photosynthesis were season-dependent for all the three species (Table 1), which might be ascribed to the seasonal variation of soil extractable N content. N fertilized plots had 93-116% higher soil extractable N content than the unfertilized plots in the early growing season (before July) across both burned and unburned sides (Liu et al. 2007), which stimulate photosynthesis of fertilized plants (Fig. 2A-C). However, the increases in soil extractable N by N fertilization diminished during the rest of the growing season (Liu et al. 2007), probably due to both plant N uptake and high leaching rate in the sandy soil. Thus plant photosynthesis was not different between the fertilized and unfertilized plots in the late growing season (Fig. 2A-C). Across the whole growing season, the N fertilization-induced changes in soil extractable N content could explain 66% of N fertilization-induced changes in $P_n$ (Fig. 7B), suggesting N-dependence of the responses of plant photosynthesis in the three species. The strong dependence of photosynthesis on N resource has also been observed in other grasslands (Field and Mooney 1986; Lee et al. 2001). The enhancement of photosynthesis leads to the increase in aboveground biomass (by 76%) in the N fertilized plots in this study. Our results indicate that N input might be a good method to rapidly restore primary productivity in the degraded temperate steppe caused by over-grazing.

**Conclusions**

Effects of burning on plant photosynthesis are species-specific and dependent on the measuring date. *A. cristatum* and *L. chinensis* was more sensitive to burning than *C. squarrosa*, suggesting the potential shifts of plant species composition under burning condition. The seasonal variation of the response of $P_n$ to burning could be explained by the burning-induced changes in soil moisture rather than burning-induced changes in soil temperature or soil N content, suggests dominant roles of soil moisture in regulating photosynthesis in response to fire in the semiarid grassland in northern China. The positive responses of photosynthesis to N fertilization were observed in all
the three measured species, which could be explained by the soil extractable N content. The response of photosynthesis to burning and N fertilization indicates that ecosystem productivity of this area will be greatly changed under the anthropogenic perturbations.

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References


Cornic G (2000). Drought stress inhibits photosynthesis by decreasing stomatal


Table 1. The main effects of burning (B), nitrogen fertilization (F), measuring date (D), and their interactions on photosynthetic rate ($P_n$), stomatal conductance ($g_s$), and water use efficiency (WUE).

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Figure legends

Figure 1. Changes in (A) soil moisture and (B) soil temperature induced by N fertilization (UF), burning (BU), and burning plus N fertilization (BF), respectively. Positive and negative values refer to increase and decrease in soil moisture and temperature, respectively, under treatments compared with the control plots.

Figure 2. The effects of burning and N fertilization on photosynthetic rate ($P_n$) and stomatal conductance ($g_s$) (Means±SE) in Agropyron cristatum (A, D), Leymus chinensis (B, E), and Cleistogenes squarrosa (C, F). UU: unburned and unfertilized, UF: unburned and fertilized, BU, burned and unfertilized, BF, burned and fertilized.

Figure 3. The correlations between photosynthetic rate ($P_n$) and stomatal conductance ($g_s$) in Agropyron cristatum, Leymus chinensis, and Cleistogenes squarrosa.

Figure 4. The effects of burning and N fertilization on leaf level water use efficiency (Means±SE) in Agropyron cristatum (A), Leymus chinensis (B), and Cleistogenes squarrosa (C). UU: unburned and unfertilized, UF: unburned and fertilized, BU, burned and unfertilized, BF, burned and fertilized.

Figure 5. The effects of burning and N fertilization on light-saturated photosynthetic rate ($A_{max}$) and the maximum apparent quantum yield ($\Phi_{max}$) (Means±SE) in Agropyron cristatum (A, D), Leymus chinensis (B, E), and Cleistogenes squarrosa (C, F). UU: unburned and unfertilized, UF: unburned and fertilized, BU, burned and unfertilized, BF, burned and fertilized.

Figure 6. The correlations between soil moisture and photosynthetic rate ($P_n$) (A) and stomatal conductance ($g_s$) (B) in Agropyron cristatum and Leymus chinensis across the growing season.

Figure 7. The correlations of burning-induced relative changes in monthly mean photosynthetic rate ($P_n$) with burning-induced relative changes in monthly mean soil moisture (A) and the correlations of N-fertilization-induced relative changes in monthly mean photosynthetic rate ($P_n$) with the N fertilization-induced relative changes in monthly mean soil extractable N content (B).
Fig. 6

**Panel A**
- Plant A: $r^2 = 0.83$, $P < 0.001$
- Plant L: $r^2 = 0.64$, $P < 0.001$

**Panel B**
- Plant A: $r^2 = 0.32$, $P < 0.02$
- Plant L: $r^2 = 0.48$, $P < 0.001$

- Soil moisture: (%)
- $P_n$ (µmol m$^{-2}$s$^{-1}$)
- $g_s$ (mol m$^{-2}$s$^{-1}$)

The graphs illustrate the relationship between soil moisture and photosynthetic rate ($P_n$) and stomatal conductance ($g_s$) for two different plant species (A and L). The data points and trend lines show a significant correlation with the indicated coefficients of determination ($r^2$) and levels of significance ($P$).
Fig. 7

A. Burning-induced relative changes in SM (%)

B. Burning-induced relative changes in Pn (%)

C. N-induced relative changes in soil extractable N content (%)

Regression equations:

- $r^2=0.51$, $P=0.01$
- $r^2=0.66$, $P=0.001$