Establishment of apparent quantum yield and maximum ecosystem assimilation on Tibetan Plateau alpine meadow ecosystem

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Received July 14, 2004; revised January 19, 2005

Abstract The alpine meadow is widely distributed on the Tibetan Plateau with an area of about 1.2×10^6 km^2. Damxung County, located in the hinterland of the Tibetan Plateau, is the place covered with this typical vegetation. An open-path eddy covariance system was set up in Damxung rangeland station to measure the carbon flux of alpine meadow from July to October, 2003. The continuous carbon flux data were used to analyze the relationship between net ecosystem carbon dioxide exchange (NEE) and photosynthetically active radiation (PAR), as well as the seasonal patterns of apparent quantum yield (α) and maximum ecosystem assimilation (P_{max}). Results showed that the daytime NEE fitted fairly well with the PAR in a rectangular hyperbola function, with α declining in the order of peak growth period (0.0244 μmolCO_2 • μmol^{-1}PAR) > early growth period > seed maturing period > withering period (0.0098 μmolCO_2 • μmol^{-1}PAR). The P_{max} did not change greatly during the first three periods, with an average of 0.433 mgCO_2 • m^{-2} • s^{-1}, i.e. 9.829 μmolCO_2 • m^{-2} • s^{-1}. However, during the withering period, P_{max} was only 0.35 mgCO_2 • m^{-2} • s^{-1}, i.e. 7.945 μmolCO_2 • m^{-2} • s^{-1}. Compared with other grassland ecosystems, the α of the Tibetan Plateau alpine meadow ecosystem was much lower.

Keywords: Tibetan Plateau, alpine meadow ecosystem, eddy covariance, apparent quantum yield, maximum ecosystem assimilation.

DOI: 10.1360/05zd0014

The alpine meadow is widely distributed on the Tibetan Plateau with an area of about 1.2×10^6 km^2, which amounts to 30.92% of the total rangeland of Tibet Autonomous Region in China. It is not only one of the typical ecosystems in alpine areas of middle Asia, but also a representative ecosystem in alpine areas in the world. The Tibetan Plateau, named "the third pole in the world", is one of the areas with the strongest solar radiation on the earth[1] and unique environmental conditions, which make the vegetation have different photosynthetical characteristics from those on the plain. The important environmental factors include low air pressure, cool climate and low CO_2 concentration, which is less than two thirds of that on the plain. Because cool climate and low CO_2 concentration are main limiting factors to plant growth, the vegetation here will be more sensitive to the rising of air temperature and enrichment of CO_2 than plants growing on the plain. As the climate gets warmer and CO_2 concentration increases in the future, if the precipitation does not change, the biomass cumulative rate of the vegetation layer on the Tibetan Plateau would be much higher than that of the plain. This would be particularly true for the alpine meadow above 4000 m, whose productivity would be remarkably improved. These changes would emerge more rapidly and noticeably than on the plain. It is therefore of great significance to study the photosynthesis of this typical kind of alpine meadow vegetation. Such study will not only provide the photosynthetical parameters of elevated-plain plants, and forecast the response degree of the vegetation to global changes under low air pressure, but also provide the most immediate and powerful evidence for further research in this field on the plain.

α and P_{max} are two key parameters in leaf photosynthesis. α is also named quantum efficiency under low light, which is usually stable and mainly reflects the biophysical characteristics in photosynthesis. P_{max}, defined as the maximum photosynthetic rate under saturating light, primarily reflects biochemical processes and physiological conditions of the plants. The P_{max} is affected by factors such as the plant species, environmental conditions, leaf thickness and leaf temperature[2]. Much research has been done about α and P_{max} at the leaf level. Ehleringer[3] investigated the apparent quantum yields of 44 kinds of C_3 and C_4 plants under the conditions of 330 μmol • mol^{-1} CO_2 and 30℃ leaf temperature, finding α of C_3 plant species very stable, on an average of 0.052—0.053 μmolCO_2 • μmol^{-1}PAR. The P_{max} for C_3 plant species on the plain is usually 14—39 μmolCO_2 • m^{-2} • s^{-1}[4], while for well developed wheat, P_{max} can reach 25 μmolCO_2 • m^{-2} • s^{-1} under appropriate temperature[5]. Due to the technological constraints on experimentation, little has been done about α, P_{max} on the canopy level, with the main methods being micrometeorological techniques and closure chambers. Luo et al.[6] measured α of sunflowers (*Helianthus annus*) on canopy level under ambient (399 μmol•mol^{-1}) and elevated (746 μmol • mol^{-1}) CO_2 concentrations by closure chambers, finding the canopy quantum yield being 0.0229—0.076 μmolCO_2 • μmol^{-1} PAR under ambient CO_2 and 0.0234—0.0959 μmolCO_2 • μmol^{-1} PAR under elevated CO_2. Canopy quantum yield was higher by 31.5% at elevated than ambient CO_2, increasing with canopy development and being strongly correlated with leaf area index. Monje et al.[7] also indicated the CO_2-indued increase in canopy quantum yield ranged from 9%—30%. However, for plants on the Tibet Plateau, studies on α and P_{max} have also stayed at the leaf level[8,9], and little has been reported on the ecosystem level. The eddy covariance method, as the only way to measure the CO_2, water and heat flux between the atmosphere and vegetation directly[10], provides a reliable approach to study the photosynthetically characteristic parameters on the ecosystem level. The work reported here analyzed the relationship between the daytime NEE and PAR, and the dynamic variation patterns of α and P_{max} during the growing season of alpine meadow in Damxung rangeland station from July to October, 2003 on the basis of the carbon flux data measured with the open-path eddy covariance system.

1 Materials and methods

1.1 Study area

The study area is located in the Damxung rangeland station. The vegetation here is alpine steppe-meadow which is typical in the northern Tibetan Plateau. Three dominating species are *Stipa capillacea*, *Carex montis-everestii* and *Kobresia pygmaea*, whose coverage is about 80%. The experimental site is categorized as plateau monsoon climate with characteristics of strong radiation, low air temperature, large diurnal variation and small annual differences. Annual mean air temperature is 1.3℃, with minimum mean of −10.4℃ in January and maximum mean of 10.7℃ in July. Mean daily variation temperature is 18.0℃, while the annual one is 21.0℃. The average surface soil temperature is 6.5℃. Soil frozen duration is 3 months from November to next February. Annual mean precipitation is 476.8 mm, with 85.1% of which concentrated in June and July. Annual evaporation is 1725.7 mm and average wetness coefficient is 0.28. The annual average sunlight is 2880.9 h. And the amount of sun radiation is 7527.6 MJ • m^{-2}, of which PAR is 3213.3 MJ • m^{-2}. The soil is classified as meadow soil with sandy loam. The soil has a depth of

0.3—1 m, with high gravel content of 30%. Organic matter content is 0.9%—2.97%, total nitrogen 0.05%—0.19%, total phosphor 0.03%—0.07% and pH 6.2—7.7.

1.2 Methods of analysis

(i) Observation items. The Damxung flux measurement site is located at the Damxung rangeland station, as one of the key experimental sites of the Lhasa Plateau Ecosystem Research Station, Institute of Geographical Sciences and Natural Resources Research, CAS. The station is 1 km away from Damxung town, located at 30.25°N, 91.05° E with an elevation of 4333 m. Fluxes of CO_2, sensible heat, latent heat and momentum between atmosphere and vegetation were measured at a height of 2.1 m in the Damxung observation site using the eddy covariance technique with the frequency of 10 Hz. The eddy covariance array sensors included a 3D sonic anemometer (CSAT3, Campbell Scientific Inc.) and an open-path CO_2 analyzer (Model LI7500, LI-Cor Inc.). Profiles of environmental factors, such as wind direction, wind speed, mean air temperature, mean air relative humidity, precipitation ,atmospheric pressure, photosynthetically active radiation, net radiation , soil temperature (5, 10, 20, 50, 80 cm) and soil moisture (5, 10, 50 cm) were also measured. Measurement began from July, 2003 and until now.

The green leaf area index (LAI) was also measured twice a month during the growing period (from June to mid-September) owing to the short-life of alpine meadow. On each measurement, five 0.25 m^2 samples were harvested and the green leaf area was measured with Area Meter AM200 (ADC BioScientific Ltd.). LAI was defined as the ratio of total green leaf area to square with the unit being $m^2 \cdot m^{-2}$.

(ii) Data processing. Data pretreatment was needed in order to adjust the flux data caused by sensor malfunction, which included spike removal (±3σ), coordinate rotation, Webb-Pearman-Leuning revisal[11]. The daytime CO_2 fluxes were estimated as a function of PAR when half-hourly values were missing, while missing average night-time NEE were filled from a model based on soil temperature. We then examined the NEE-light response using the model of Michaelis-Menten[12] described as follows:

$$NEE = \frac{\alpha \cdot PAR \cdot P_{max}}{\alpha \cdot PAR + P_{max}} - R,$$

where NEE ($\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) is the daytime net ecosystem carbon dioxide exchange; PAR ($\mu mol m^{-2} \cdot s^{-1}$) is the photosynthetically active radiation; α ($\mu molCO_2 \cdot \mu mol^{-1} PAR$) is the apparent quantum yield, denoting the maximum efficiency of light utilization in photosynthesis; P_{max} ($\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) is the maximum ecosystem assimilation and R ($\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) is the respiration from soil and plant. The three parameters (α, P_{max}, R) could be got using the nonlinear least square method with the software of MATLAB 6.0.

2 Results

2.1 Seasonal variation pattern of LAI

The seasonal pattern of community LAI was as follows (fig. 1). The LAI kept rising from early June to late August with three clear stages: slow increase period—sharp increase period—and leveling-off period. In September, LAI began to decrease owing to the onset of senescence. The peak LAI (1.86 $m^2 \cdot m^{-2}$) was reached in late August, and the LAI increase rate then began to stagnate and even to drop. However, this did not mean the ceasation of plant growth, but was a result of the relative rise in the scorching rate under worse weather conditions. On September 10, the community LAI remained 1.82 $m^2 \cdot m^{-2}$.

2.2 Diurnal and seasonal variation patterns of NEE

From fig. 2, we can see that NEE of alpine

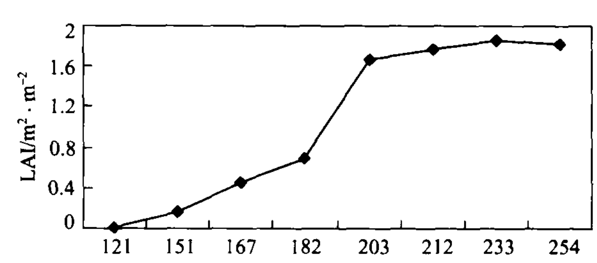

Fig. 1. Dynamic variation pattern of LAI during the growing season on the Tibetan Plateau alpine meadow (from January 1).

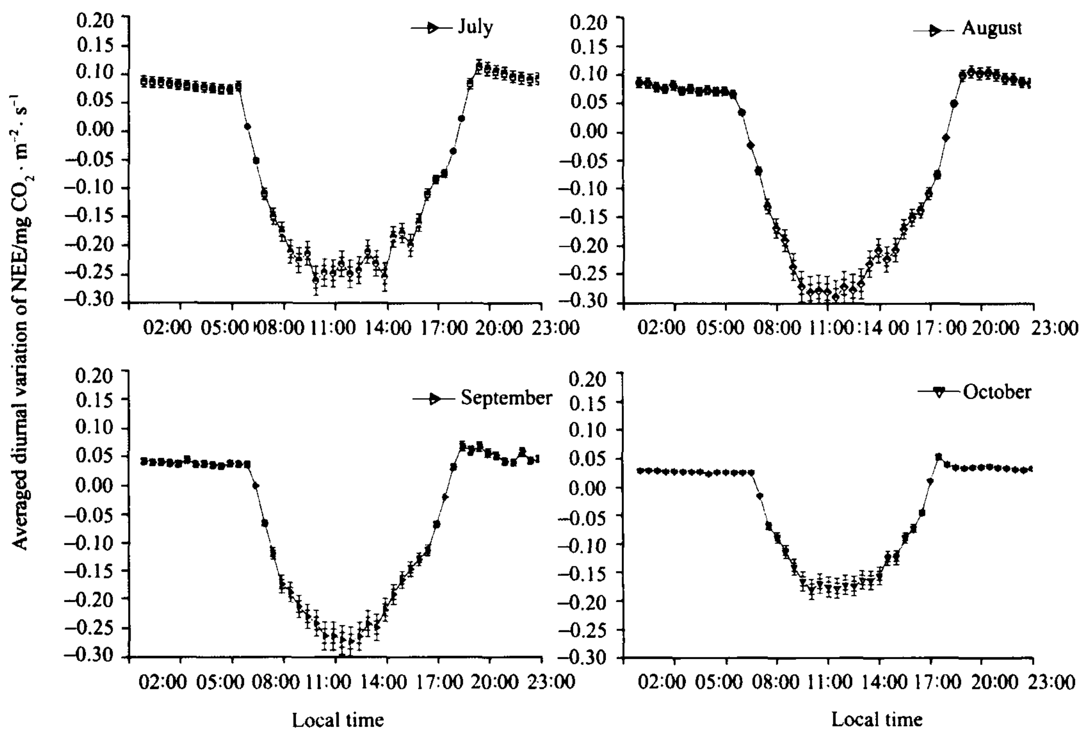

Fig. 2. Diurnal and seasonal variation patterns of NEE on the Tibetan Plateau alpine meadow ecosystem, 2003.

meadow during the growing season (from July to October) presented obvious diurnal variation patterns. During nighttime, the whole ecosystem was a carbon source because of the respiration (NEE toward atmosphere was positive, denoting carbon release); while during daytime, with photosynthesis growing, the whole ecosystem turned into a carbon sink (NEE toward vegetation was negative, denoting carbon uptake) at 06:30 am (local time), and reached its diurnal maximum carbon assimilation usually at 11:00—12:00 (local time). The diurnal maximum carbon assimilation varied with time. For example, it was highest in August, when the vegetation was in peak growth (–0.288 mg CO_2 • m^{-2} • s^{-1}, i.e. –6.538 μmolCO_2 • m^{-2} • s^{-1}) and lowest in October which was the withering period (−0.18 mgCO_2 • m^{-2} • s^{-1}, i.e. −4.086 μmol CO_2 • m^{-2} • s^{-1}). And it was similar in July and September, reaching about −0.25 mgCO_2 • m^{-2} • s^{-1}, i.e. −5.675 μmolCO_2 • m^{-2} • s^{-1} (see table 1).

2.3 Seasonal variation patterns of α and P_{max}

From fig. 3, we can see that during daytime, NEE fitted fairly well with PAR in a rectangular hyperbola function, with α declining in the order of peak growth period > early growth period > seed maturing period > withering period. It was highest during peak growth period, reaching 0.0244 μmolCO_2 • μmol^{-1}PAR, and lowest in withering time, which was only 0.0098 μmol CO_2•μmol^{-1}PAR. In early growth period and seed maturing period, it was 0.0211 μmol CO_2 • μmol^{-1} PAR and 0.0177 μmolCO_2 • μmol^{-1}PAR respectively. The P_{max} did not change greatly during the first three periods with an average of 0.433 mgCO_2•m^{-2}•s^{-1}, i.e. 9.829 μmolCO_2 • m^{-2} • s^{-1}, while the value was merely 0.35 mgCO_2 • m^{-2} • s^{-1}, i.e. 7.945 μmolCO_2 • m^{-2} • s^{-1} during the withering period.

3 Discussion

3.1 Environmental controls on the dynamic variation patterns of α and P_{max} during growing season

The patterns of photosynthetical parameter variation during the growing season in the Tibetan Plateau alpine meadow ecosystem were related to a number of

Table 1 Dynamic variation patterns of diurnal maximum carbon assimilation, α and P_{max} on the Tibetan Plateau alpine meadow ecosystem during the growing season, 2003

Month	Growing period	Diurnal maximum carbon assimilation /$mgCO_2 \cdot m^{-2} \cdot s^{-1}$	α /mg $CO_2 \cdot m^{-2} \cdot s^{-1}$	P_{max} /$\mu molCO_2 \cdot \mu mol^{-1}$ PAR	Upper α for grassland[13]
July	Early growth	0.254	0.0211	0.443	
August	Peak growth	0.288	0.0244	0.444	0.0441
September	Seed maturing period	0.258	0.0177	0.412	
October	Withering period	0.18	0.0098	0.35	

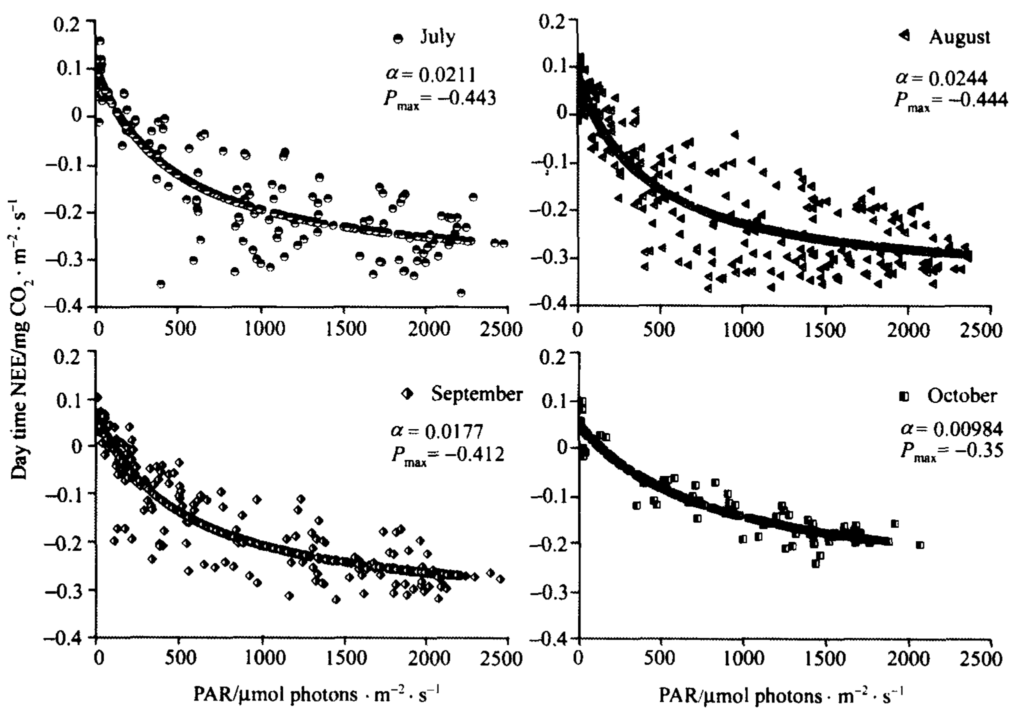

Fig. 3. Seasonal variation patterns of α and P_{max} in the Tibetan Plateau alpine meadow ecosystem, 2003

variables, such as light, precipitation, temperature and plant growth. During July and August, the average diurnal maximal air temperature (16℃) and PAR (1750 μmolPAR $\cdot m^{-2} \cdot s^{-1}$) were similar, but the maximal water vapour pressure deficit in July (1.1 kPa) was higher than that in August (0.97 kPa). Furthermore, plants in August were in peak growth, the above-ground biomass reaching maximum; appropriate temperature and plentiful precipitation made α and P_{max} highest. In September, though the diurnal maximal PAR was highest (1850 μmolPAR $\cdot m^{-2} \cdot s^{-1}$) and the diurnal maximal VPD was lowest (0.77 kPa), mean air temperature began to drop and the photosynthetic ability began to fall with the onset of senescence in late September. As a result, α declined quickly to 0.0177 μmol $CO_2 \cdot \mu mol^{-1}$PAR. On the other hand, just as Yi et al.[14] suggested, the gradual worsing of the weather only caused the vegetation scorching rate to rise relatively, the LAI increase rate to stagnate and even to drop; however, the existing above-ground green biomass still kept up. The diurnal maximum carbon assimilation and P_{max} could therefore still maintain a comparatively high level. In October, plants began to scorch entirely, the mean air temperature dropped rapidly and was only 5℃ below zero at the early morning; the temperature of surface soil was also near zero degree, and the total precipitation was only 9.6 mm, though the sunshine was still high (1580 μmolPAR • m^{-2} • s^{-1}), the whole ecosystem's photosynthetic ability was weak, the α and P_{max} hit rock bottom.

3.2 Comparison of α with that of other grassland ecosystems in the world

Compared with other grassland ecosystems in the world, the diurnal maximum carbon assimilation and α in the Tibetan Plateau alpine meadow ecosystem were extremely low. For example, the maximum carbon assimilation in Damxung during the peak growth period was only −0.288 mgCO_2 • m^{-2} • s^{-1}, i.e.−6.538 μmolCO_2 • m^{-2} • s^{-1}, while in North American prairie grasslands, the maximum CO_2 exchange could reach −1.3 mgCO_2 • m^{-2} • s^{-1}, i.e. 30 μmolCO_2 • m^{-2} • s^{-1}[15], −1.2 μmolCO_2 • m^{-2} • s^{-1}, i.e. 27.2 μmolCO_2 • m^{-2} • s^{-1}[16] during the growing season. The reasons for this may be that all these sites had much higher LAI, around 4—5 m^2 • m^{-2}, and often included drought tolerant C_4 species[17]. However, the vegetation in Damxung was composed of C_3 plant species, which could merely 3—5 cm high with low above-ground biomass and low LAI (maximum 1.86 m^2 • m^{-2}). These effects can be attributed to the cold climate and low precipitation in the northern Tibetan Plateau.

Table 1 includes magnitudes of α at various stages of alpine meadow growth (it should be noted that this value is different from α at the leaf level). The value of α was largest (on average 0.0244 μmolCO_2 • μmol^{-1}PAR) during the peak growth period when all the environmental factors were optimal. In contrast, in a tallgrass prairie site in north-central Oklahoma, USA, the α was 0.0348 μmolCO_2 • μmol^{-1}PAR when there was no moisture stress during the peak growth; when moisture stress conditions prevailed, α was considerably smaller (on average 0.0234 μmolCO_2 • μmol^{-1}PAR); when plant was in senescence period, α was only 0.0114 μmolCO_2 • μmol^{-1}PAR[18]. Ruimy[13] suggested an upper limit of 0.0441 μmolCO_2 • μmol^{-1}PAR for C_3 and C_4 grasslands during the peak growth, which agreed with the value observed in this study. Luo et al.[6] measured the canopy quantum yield of sunflowers growing under ambient and elevated CO_2 concentration, and found CO_2 enrichment resulted in a 31.5% increase in the canopy quantum yield. In addition, canopy quantum yield increased with canopy development and was strongly correlated with LAI. For example, under ambient CO_2 concentration, the canopy α increased from 0.0229 to 0.076 μmolCO_2 • μmol^{-1}PAR while LAI changed from 0.6 to 4.5 m^2 • m^{-2}. Monje et al.[7] also indicated that the CO_2-indued increase in canopy quantum yield ranged from 9% to 30%. Hence, we can see that environmental CO_2 concentration has a great influence on the canopy quantum yield. Having studied the photosynthesis of winter wheat on the Tibetan Plateau, Zhang et al.[8] and Liu et al.[9] also pointed out that it was probably the rareness of air and low CO_2 partial pressure that resulted in the lowness of α in C_3 plant species on the plateau. Xu et al.[19] suggested that drop in CO_2 partial pressure with increasing altitude might be the primary reason for the decrease in photosynthesis and α for the same kind of species. The altitude of Damxung was 4333 m, so high altitude and low CO_2 partial pressure would be likely to explain the lowness of the α on the Tibetan Plateau alpine meadow ecosystem. Furthermore, worse weather and low precipitation in the northern Tibetan would inevitably have had some influence on the α.

4 Conclusions

In this article, the dynamic variation patterns of α and P_{max} in the Tibetan Plateau alpine meadow ecosystem were analyzed on the basis of continuous CO_2 flux data measured with the eddy covariance technique during the growing season, 2003. The conclusions are as follows:

(1) The patterns of variation in photosynthetical parameters during the growing season in the Tibetan Plateau alpine meadow ecosystem mainly depended on the following variables: light, precipitation, temperature, plant growth. The α declined in the order of peak growth period > early growth period > seed maturing period > withering period. It was highest during the peak growth period, reaching 0.0244 μmolCO_2 •

μmol^{-1}PAR, and lowest in the withering time, which was only 0.0098 μmolCO_2 • μmol^{-1}PAR. In early growth period and seed maturing period, it was 0.0211 and 0.0177 μmolCO_2 • μmol^{-1}PAR respectively. The P_{max} did not change greatly during the first three periods with an average of 0.433 mgCO_2 • m^{-2} • s^{-1}, i.e. 9.829 μmolCO_2 • m^{-2} • s^{-1}, while the value was merely 0.35 mgCO_2 • m^{-2} • s^{-1}, i.e. 7.945 μmolCO_2 • m^{-2} • s^{-1} during the withering period.

(2) Compared with other grassland ecosystems in the world, α in the Tibetan Plateau alpine meadow ecosystem was extremely low. It was probably the high altitude and low CO_2 partial pressure that caused the lowness of α' Furthermore, low above-ground biomass and low LAI induced by worse weather and low precipitation in the northern Tibet would inevitably have had some influence on α.

Acknowledgements This work was jointly supported by the Major State Basic Research Development Program of China (Grant No. 2002CB412501), the National Natural Science Foundation of China (Grant Nos. 30170153 and 30470280) and the Key Innovation Project of Institute of Geographic Sciences and Natural Resources Research, CAS (Grant No. CXIOG-E01-03-03).

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