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Response of canopy quantum yield of alpine meadow to temperature under low atmospheric pressure on Tibetan Plateau

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Abstract An open-path eddy covariance system was set up in Damxung rangeland station to measure the carbon flux from July to October, 2003. The canopy quantum yield (α) of alpine meadow was calculated by the linear function between the net ecosystem carbon dioxide exchange (NEE) and the photosynthetic active radiation (PAR) under low light, and how it was influenced by the temperature was also discussed. Results showed that the canopy α decreased almost linearly with temperature, with the decrease in every 1℃ increase of temperature similar to those measured on leaf level of C_3 plant. At the beginning, the decrease of canopy α with temperature was 0.0005 μmol CO_2·μmol^{-1} PAR; while it increased to 0.0008 μmol CO_2·μmol^{-1} PAR in September, showing a rising trend with plant growing stages. Compared with the canopy α calculated with rectangular hyperbola function, the value in the paper was lower. However, the method advanced here has the advantages in examining the relationship between α and the key environmental factors, such as temperature.

Keywords: Tibetan Plateau, alpine meadow, canopy quantum yield, temperature.

As the third pole in the world, the Tibetan Plateau is regarded as an area sensitive to the global climate changes. The environmental conditions on the Plateau are unique, characterized by high elevation, cool climate and low CO_2 concentration which is less than two thirds of that on plain. Because cool climate and low CO_2 concentration are limiting factors for plant growth, the vegetation here will be more sensitive to the rising of air temperature and enrichment of CO_2 than the plants growing on the plain. Therefore, the photosynthetic characteristics of elevated-plain plant are likely to be different from those on the plain. How will elevated-plain plant respond to the changes of CO_2 concentration and temperature? And what is the difference between the photosynthetic parameters of plant growing in elevated areas and those on the plain? All these are the focus not only in the research of the elevated-plain plant photosynthesis, but also in the study on response of plant to the global climate changes.

As a key parameter in leaf photosynthesis, apparent quantum yield (α) is usually defined by the molecular number of CO_2 fixation/O_2 release per unit photons irradiated on leaf, representing the light utilization efficiency during the course of CO_2 assimilation in photosynthesis. Apparent quantum yield mainly reflects the biochemical characteristics in photosynthesis, and is usually stable under a certain temperature and CO_2 partial pressure. At present, the observed maximum α is 0.083−0.125 μmol CO_2·μmol^{-1} PAR measured with the globular alga under the optimal conditions in laboratory, i.e. the minimum requirement of quantum number in theory is 8−12[1,2]. However, the apparent quantum yield of plant growing under normal conditions is much lower. Ehleringer[3] reported that the α of C_3 plant species under the conditions of 330 μmol·mol^{-1} and 30℃ leaf temperature was 0.052−0.053 μmol CO_2·μmol^{-1} PAR on average. And α is prone to be influenced by many environmental factors, such as temperature, atmospheric pressure, water deficit and even habitats of plant[4]. For example, Shi *et al.*[5] reported that the α of winter wheat on Tibetan Plateau was about 0.0476 μmol CO_2·μmol^{-1} PAR, which was only 90.8% of that on the plain with the reason presumably being the low CO_2 partial pressure. In addition, there are some reports that the α of C_3 plant decreases nearly linearly with the increasing of temperature[3,5,6].

Now the reports about α are mainly on leaf level, while little has been done about α on canopy level with the main methods being micrometeorological technique and closure chambers. Luo *et al.*[7] studied the impact of CO_2 enrichment on the canopy α of sunflowers (*Helianthus annus*) by closure chambers, finding that the canopy α increased with the canopy development, and was strongly correlated with leaf area index. It was higher by 31.5% in elevated than ambient CO_2 conditions, which could reach 0.0234−0.0959 μmol CO_2·μmol^{-1} PAR. Monje *et al.*[8] also indicated the CO_2-indued increase in canopy quantum yield ranged from 9%−30%. The eddy covariance method, as the only way to directly measure the CO_2, water and heat flux between the atmosphere and vegetation[9], provides a reliable approach to study the photosynthetically characteristic parameters on the canopy level. Andrew *et al.*[10] have measured the α of tallgrass prairie with eddy covariance technique in Oklahoma, USA, finding that the α varied with plant growth, i.e. it was 0.0207 μmol CO_2·μmol^{-1} PAR in the early growth stage, 0.0348 μmol CO_2·μmol^{-1} PAR in the peak growth stage and 0.0109 μmol CO_2·μmol^{-1} PAR during the senescence stage. However, the values of canopy α reported are mostly fitted in rectangular hyperbolic function[10,11], which could only reflect the average changes in canopy photosynthesis over several days or in different phonologies. In fact, NEE fitted fairly well with PAR in a linear function under low light[12]. Moreover, the canopy temperature was usually stable in low light, which made it possible to study the relationship between α and canopy temperature. The work reported here calculated the canopy α of alpine meadow based on the linear relationship between NEE and PAR under low light, and how α responded to the temperature was further analyzed on the basis of the carbon flux data measured with the open-path eddy covariance system in Damxung rangeland station from July to October, 2003.

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 the 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 mean air temperature, photosynthetically active 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. ① Data pretreatment. The post-processing for the raw data was needed, including spike removal (±3σ), coordinate rotation (triple rotation) and Webb-Pearman-Leuning revisal[13], which could adjust the variation in air density due to the transfer of water vapor. The missing data was discarded.

② Calculation of α. The canopy α can be calculated based on the linear function between NEE and PAR under low light[12] (when PAR was in [0, 300] $\mu mol \cdot m^{-2} \cdot s^{-1}$). And the corresponding canopy temperature was also calculated (denoted as *T*).

$$NEE = \alpha \cdot PAR - Rd, \tag{1}$$

where *NEE* ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) is the net ecosystem CO_2 exchange (negative denoting carbon uptake; positive denoting carbon release); *PAR* ($\mu molm^{-2} \cdot s^{-1}$) is the photosynthetically active radiation; α ($\mu mol\ CO_2 \cdot \mu mol^{-1}$ PAR) is the apparent quantum yield at the stand level, denoting the maximum efficiency of light utilization in photosynthesis; *Rd* ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) is the apparent dark respiration at the stand level.

③ Relationship between canopy α and temperature. The canopy α and temperature were linearly fitted by a 10-d step to analyze how α responded to the temperature on different plant growth stages (eq. (2)).

$$\alpha = \theta \cdot T + \alpha_m, \tag{2}$$

where *T* (℃) is the canopy temperature; θ is the slope, denoting the response degree of α to temperature; α_m ($\mu mol\ CO_2 \cdot \mu mol^{-1}$ PAR) is the intercept, defined as the maximum that the canopy α tends to get on different growth stages. The data was processed with software of Origin 7.0 (OriginLab Corporation).

2 Results

2.1 *Calculation of α*

The calculation of α at stand level was illustrated with the example of July 9 (Fig. 1). Fig. 1 shows that NEE fitted fairly well with PAR in a linear function under low light with R^2 all above 0.9. Moreover, the corresponding canopy temperature was stable with the variance less than ±1℃, which reduced the influence of fluctuant temperature on the α fitting. Hence, two values of α with corresponding canopy temperature could be get by taking the slope of light response curve between NEE and PAR under low light during one day. As Fig. 1 shows, on July 9, the averaged canopy temperature in the morning was about 7.34℃ with the corresponding α as 0.0104 $\mu mol\ CO_2 \cdot \mu mol^{-1}$ PAR; the temperature rose to about 12.85℃ in the afternoon, and α decreased by 0.0031 $\mu mol\ CO_2 \cdot \mu mol^{-1}$ PAR, reaching only 0.0073 $\mu mol\ CO_2 \cdot \mu mol^{-1}$ PAR.

2.2 *Response of α to temperature*

Fig. 2 shows that the canopy α decreased almost linearly with the increasing of canopy temperature from July to September, presenting nearly as a group

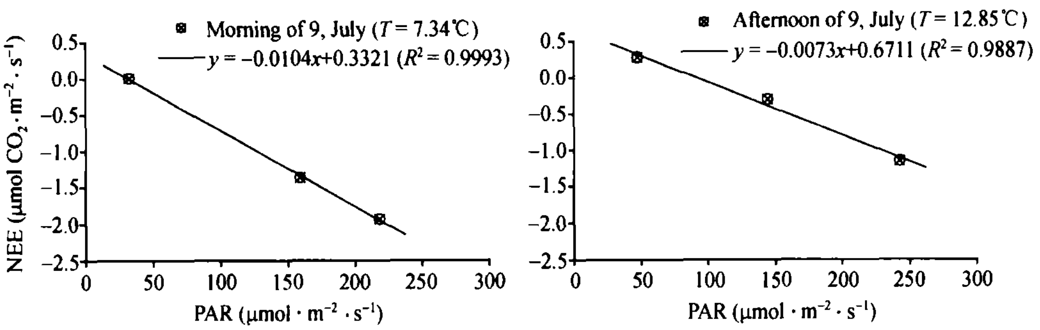

Fig. 1. Calculation of α at stand level illustrated on 9, July.

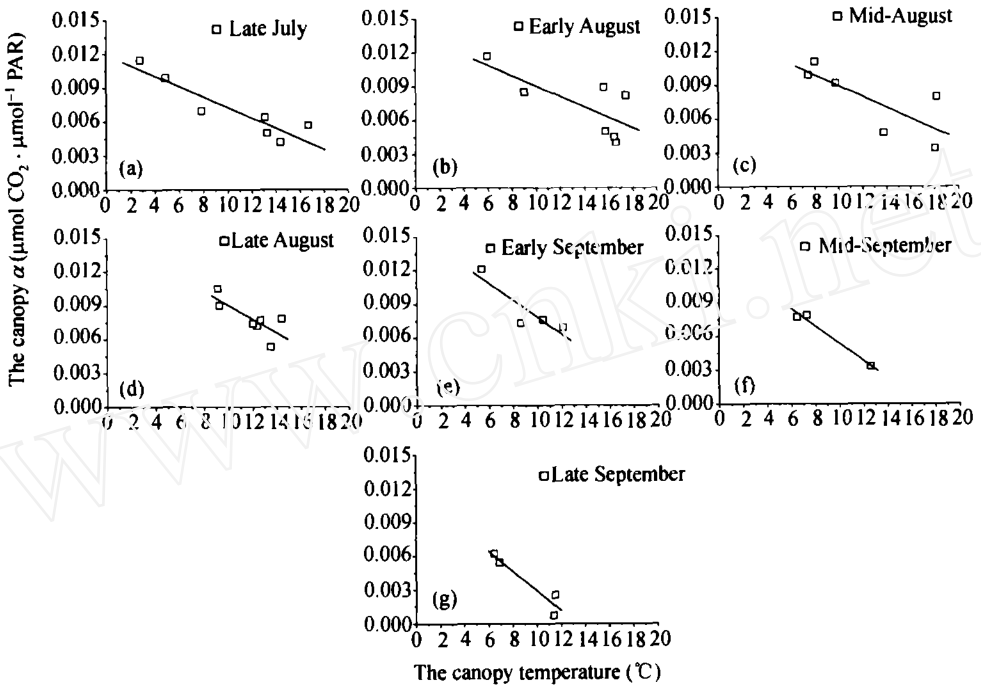

Fig. 2. Response of canopy α to temperature from July to September.

of parallel lines. The response degree of α to temperature varied on different growth stages (Table 1). From the late July to the mid-August, the decrease tendency of canopy α in every 1℃ increase of temperature was quite similar, being about 0.0005 μmol CO_2·μmol^{-1} PAR (Fig. 2(a)—(c)). Moreover, the values of α during this period varied dramatically as a result of great fluctuation of canopy temperature, which could reach 16℃ at most. For example, the α in the morning could reach 0.012 μmol CO_2·μmol^{-1}PAR with lower canopy temperature, while the value decreased to 0.004 μmol CO_2·μmol^{-1}PAR as a result of temperature increasing in the afternoon. From the late August, the response curve of α to temperature became steeper and steeper with the decrease of α in every 1℃ increase of temperature rising to about 0.0007 μmol CO_2·μmol^{-1} PAR. However, the variation range of α still kept, fluctuating between 0.012 to 0.006 μmol CO_2·μmol^{-1} PAR (Fig. 2(d) and (e)). It is not until the second half of September that the value of α began to drop markedly with the maximum merely 0.008 μmol CO_2·μmol^{-1} PAR and minimum 0.002 μmol CO_2·μmol^{-1} PAR, when the photosynthesis of the vegetation was weak.

2.3 Variation trend of α_m and its relationship with the environmental factors

α_m was defined as the maximum that the canopy α

tended to get on different growth stages. Because α can be easily influenced by the canopy temperature and kept varying during the daytime, it was reasonable to take α_m as an indicator for the comparison of canopy photosynthetic ability, which could basically reflect the photosynthetic ability of the vegetation. Fig. 3 shows that α_m increased slowly from late July to middle August, reached the maximum (0.0154 μmol $CO_2 \cdot μmol^{-1}$ PAR) in late August, and then began to decline. α_m and community LAI showed similar variation pattern in growing season with the maximum both reached during peak growth in late August. In mid-September, α_m and LAI both started to decline with the beginning of plant perishing, and the decrease tendency of LAI was much quicker (Fig. 3(a)). The relationship between α_m and soil moisture was illustrated in Fig. 3(b). The soil moisture began to decline in late July with little impact on α_m. In mid-August, however, the soil moisture declined to mere 0.17 $m^3 \cdot m^{-3}$, which was low enough to result in zero-increase of α_m in this period. In late August, α_m increased rapidly from 0.0138 to 0.0154 μmol $CO_2 \cdot μmol^{-1}$ PAR with the rising of precipitation, and reached the maximum in early September. From mid-September, though the soil moisture still maintained above 0.2 $m^3 \cdot m^{-3}$, α_m decreased as a result of the scorching of the plant and weakening of the whole community's photosynthetic ability.

Table 1 Results of linear regression between canopy α and temperature from July to September

Parameters	Late July (a)	Early August (b)	Mid-August (c)	Late August (d)	Early September (e)	Mid-September (f)	Late September (g)
θ((μmol $CO_2 \cdot μmol^{-1}$ PAR)℃$^{-1}$)	–0.0005	–0.0005	–0.0005	–0.0006	–0.0008	–0.0008	–0.0008
α_m (μmol$CO_2 \cdot μmol^{-1}$ PAR)	0.0119	0.0137	0.0138	0.0152	0.0154	0.0130	0.0117
R	–0.917	–0.729	–0.769	–0.775	–0.894	–0.987	–0.950
Value *P*	< 0.01	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
Sample number *N*	7	7	6	7	4	3	4

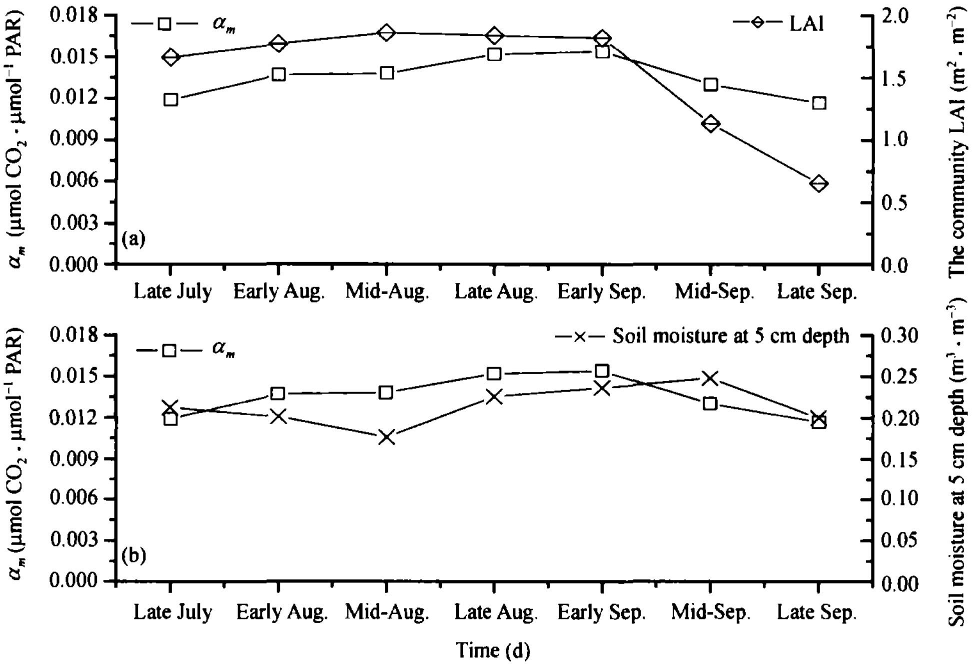

Fig. 3. Relationship between α_m and the community LAI as well as the soil moisture at 5 cm depth. (a) Relationship between α_m and the community LAI; (b) relationship between α_m and the soil moisture at 5 cm depth.

3 Discussion

There were some reports that α of C_3 species on leaf level usually decreased linearly with the increasing of temperature. For example, Ehleringer *et al.*[3,6] reported that the average value of *Encelia californica* and *Avena sativa* decreased 0.0009 μmol CO_2·μmol^{-1} PAR in every 1℃ increase of leaf temperature from 15 to 35℃. Shi *et al.*[5] measured the α of winter wheat on Tibetan Plateau, and found that the decrease rate of α with temperature was slower than those in the low elevation areas, which was 0.0007 μmol CO_2·μmol^{-1} PAR on average. In this study, the alpine meadow was regarded as a "big leaf"[14], and the observed decrease tendency of canopy α with temperature was similar to those measured on leaf level. At the beginning, the decrease rate of canopy α with temperature was 0.0005 μmol CO_2·μmol^{-1} PAR; while it increased to 0.0008 μmol CO_2·μmol^{-1} PAR in September. The reason might be that temperature became the main limiting factor for plant growth during the end of growing season, and the vegetation became more and more sensitive to the decrease of temperature, which resulted in the decrease rate of canopy α with temperature in a rising tendency. The major reason for the decrease of α with temperature rise on leaf level was that more NADPH and ATP produced by electronic transferring were used for respiration[1,6]; while for the community, it was much more complex. After studying the photosynthesis of wheat on Qinghai Plateau, Zhang *et al.*[15] argued that when temperature increased, the air water vapor deficit rose, some stomata closed, and the stomatal resistance increased, which resulted in the decrease of photosynthesis. In addition to plant photosynthesis, the community structure, vegetation coverage and soil respiration would all have influence on the canopy α. The vegetation in Damxung was spares, and the soil temperature increased rapidly with the strong solar radiation, which could induce the quick increase of soil respiration and the decrease of canopy α indirectly. More studies were needed for further research.

The author has analyzed the canopy α of alpine meadow before by the rectangular hyperbola function, and results showed that the maximum canopy α was usually reached during peak growth (0.0244 μmol CO_2·μmol^{-1} PAR)[16]. Compared with α measured in grassland ecosystems in low elevation areas, the lowness of α might be contributed to the low CO_2 partial press and low LAI[16]. In this study, α of alpine meadow was calculated by the linear function between NEE and PAR under low light, and the value was lower with that calculated by the rectangular hyperbola function. Lu *et al.*[17] argued that because the steepness of light response curve was variable, it might cause the value of α to be much higher if the steepness was set as 1 when simulating canopy α using the rectangular hyperbola function. Obviously, the result fitted by the linear function in the paper was reasonable. The rectangular hyperbola function has been widely used in simulating the canopy α for its advantages of being simple, convenient for further comparison between different ecosystems. However, the method advanced in this paper is very useful in analyzing the relationship between canopy α and the main environmental factors, such as temperature.

4 Conclusions

On the basis of the carbon flux data measured with the open-path eddy covariance system located in Damxung rangeland station in the hinterland on Tibetan Plateau from July to October, 2003, the canopy α of alpine meadow was calculated based on the linear relationship between NEE and PAR under low light, and how α responded to the temperature was further analyzed. The conclusions were as follow.

(1) The canopy α decreased almost linearly with temperature, with the decrease in every 1℃ increase of temperature similar to those measured on leaf level of C_3 plant. At the beginning, the decrease of canopy α with temperature was 0.0005 μmol CO_2·μmol^{-1} PAR; while it increased to 0.0008 μmol CO_2·μmol^{-1} PAR in September, representing the rising trend with the plant growing stages.

(2) It is feasible to calculate the canopy α of alpine meadow based on the linear relationship between NEE and PAR under low light, and the value was lower compared with the canopy α calculated with rectangular hyperbola function. However, the method advanced here has the advantage of analyzing the rela-

tionship between canopy α and the main environmental factors, such as temperature.

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