Apparent quantum yield of photosynthesis of winter wheat and its response to temperature and intercellular CO_2 concentration under low atmospheric pressure on Tibetan Plateau

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Abstract The Tibetan Plateau is characterized by lower atmospheric pressure, lower air temperature and high daily and seasonal variation due to high elevation. The photosynthesis of plants is significantly influenced by these alpine environmental factors. Apparent quantum yield (α_A) is one of the basic parameters of photosynthesis and mass production. Its accuracy determination is of significance to model photosynthesis of C_3 plants and global change on the plateau. In the Lhasa Plateau Ecological Station with 65.4 kPa of atmospheric pressure at an elevation of 3688 m, Li-Cor 6400 portable photosynthesis system was used to measure light response curves of winter wheat in different temperatures and intercellular CO_2 concentration (C_i). The slope of light response curve in weak light area of PFD from 0 to 150 μmol $m^{-2} s^{-1}$ was used to evaluate the value of α_A. The dependence of α_A on temperature and intercellular concentration was analyzed. In 30℃, the average value of α_A was 0.0476 ± 0.0038. It is not quite different from the values in low elevation areas. α_A is influenced both by temperature and by the ratio of CO_2 and O_2 partial pressure ($[CO_2]/[O_2]$). The measured values in the previous study were much lower. This might be due to systematic errors from instrument and data processing methods. The values of α_A decreased linearly with temperature. It decreased 0.0007 in every 1℃ increase of temperature. The decrease slope is similar to those of C_3 plants in the previous researches. While $[O_2]$ is constant, α_A increases with C_i with a hyperbolic relationship. In comparison with low elevation areas, the α_A on the Tibetan Plateau is more sensitive to increase of CO_2.

Keywords: Tibetan Plateau, low atmospheric pressure, C_3 plant, apparent quantum yield, temperature, intercellular CO_2 concentration.

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Quantum efficiency is the maximum use of photosynthetically active radiation (PAR) in the course of photosynthesis. It reflects biochemical characteristics of photosynthesis[1]. The maximum quantum yield (α_0) is fairly steady under a certain temperature and CO_2 partial pressure. In the condition of ca. 1 standard atmospheric pressure near the sea level, the value of α_0 of C_3 plant is 0.083—0.125 when O_2 partial pressure is 1 kPa, i.e. the minimum requirement of quantum number in theory is 8—12[1,2]. The average value of quantum yield (α) of C_3 plant is 0.0524 in O_2 pressure of 21 kPa with temperature of 30℃[3]. The value was commonly used in the lowland areas with nearly one atmospheric pressure. However, whether α in the Tibetan Plateau with high elevation is the same as lowland areas is in doubt. There is little information on the measurement of α for C_3 plants on the plateau. Some measurements for winter wheat were reported. To date, we are still not clear the value of α for C_3 plant on the Tibet Plateau and we do not know anything about the response of α on CO_2 partial pressure and temperature in the scenario of future global change. The α in leaf level is the characteristic parameter reflecting light utilization efficiency, CO_2 uptake and mass production[4]. Especially in modeling photosynthesis, α is a necessary input parameter. And therefore, determination of the values of α for C_3 plants in current and future global change scenario is one of key works. It is of great significance to assess photosynthetic efficiency in the global change scenarios.

In fact, α is strongly dependent on CO_2 partial pressure and temperature. There were some reports that α increased with the ratio of RuBP carboxylase to oxygenase with increase of CO_2 concentration. On the contrary, α decreased when carboxylase of RuBP increased with temperature[1,3]. However, in a condition of certain energy uptake, the value of α is the result long-term adaptation and is not prone to change. It reflects the biochemical characteristics of a type of photosynthetic pathway. However, apparent quantum yield (α_A), i.e. the slope of linear part of light response curve in weak photosynthetic flux density (PFD) between 0 and 150 μmol m^{-2} s^{-1}, is influenced by environmental factors such as atmospheric pressure, temperature, water deficit, and even habitats of plants[5]. α_A is usually lower than α_0 when environment is not optimal.

The Tibetan Plateau is characterized by high elevation, lower atmospheric pressure and cooler climate. The CO_2 density in air is 1/3 less than those in lower elevation areas[1)]. The cooler climate and lower CO_2 partial pressure is limitation for plant photosynthesis and growth. And therefore, plants on the plateau with lower atmospheric pressure perhaps have lower values of α_A[6]. However there is little information on the research in this field[7,8]. In recent years, portable photosynthesis systems such as ADC infrared instrument and CID portable photosynthesis system were used to measure the values of α_A of wheat in Xining and Lhasa on the plateau. The measured values, 0.023[7] and 0.034[8] respectively in Xining and Lhasa, both were significantly lower than the common recognized value 0.054[3] in lower elevation areas. The authors argued that lower atmospheric pressure and lower CO_2 partial pressure on the plateau were the main causes of lower α_A[7,8].

And therefore, can we infer that the C_3 plants on the plateau, with CO_2 partial pressure 1/3 less than standard atmospheric pressure, possess significantly lower values of α_A in the same temperature in comparison with C_3 plants in lower elevation areas? The objectives in present study are to: (1) determine the values of α_A in different temperatures; (2) clarify the relationship between α_A and temperature, $[CO_2]/[O_2]$; and (3) analyze the sensitivity of α_A to increase of $[CO_2]/[O_2]$ in future scenario in contrast to lower elevation areas.

1 Materials and methods

The study was conducted in Lhasa Plateau Ecological Station (29°40′40″N, 91°20′37″E), with an elevation of 3688 m. Due to high elevation and low air density, the site has an average atmospheric pressure of 65.4 kPa, which is 2/3 of standard atmospheric pressure. The partial pressures of $[O_2]$ and $[CO_2]$ are ca. 14 kPa and 24 Pa respectively. Average air temperature is 7.7℃. Precipitation is 425 mm, 80% of which concentrates in summer from June to August[9].

The material for measurement is winter wheat,

1) The lower elevation areas refer to the area with near 1 standard atmospheric pressure if not specifically described.

Triticum aestivum L. var. Bussyd, a kind of C_3 plant. Seed in 500 m^{-2} was planted spacing 25 cm in early October in 2000. Basic fertilizer of N, P_2O_5, and K_2O was applied 40, 18 and 11 kg hm^{-2} respectively while planting. Sheep manure was spread with 10 t hm^{-2} on surface and covered with shallow soil after seeding. Before heading, 35, 6 and 4 kg hm^{-2} of N, P_2O_5, and K_2O were re-fertilized in the cropland. The crop was harvested in September. The whole production period is about 320 d.

In the period of flowering during 20 June and 5 July in 2001, robust, fully extended flag leaves were labeled with tags. Photosynthetic rates in different PFD and CO_2 concentration were measured by Li-Cor 6400 portable photosynthesis system (Li-Cor Inc, Lincoln, Neb., USA). One day before measurement, the measure site was irrigated to ensure no water deficit during the measurement, in particular at the dry and sunny day. The measurement time was conducted in the period of 07:00—10:00 and 14:00—18:00 at local time[1)]. During measurement, temperature in leaf chamber was set varying with air temperature. In order to let instrument reach the static state, leaf temperature in the chamber was kept no less or higher than 5℃ of air temperature.

LED of Li-Cor 6400 was used to produce and control light resource during measuring light response curve of photosynthesis. We measured light response curves with PFD gradient of 0, 20, 40, 60, 80, 100, 120, 150 μmol m^{-2} s^{-1} in different leaf temperatures from 15 to 35℃ with interval of 2.5℃. There were 4—5 replicates in different leaf temperatures. In total, 43 curves of light response under 9 temperature gradients were measured. The slope of linear part of light response curve was used to estimate α_A and analyze the influence of temperature on α_A.

The influence of intercellular CO_2 on α_A was measured by light response curve under certain temperature and certain CO_2 concentration. The leaf temperature was set as 25℃ and CO_2 concentration in leaf chamber was controlled by scrubbing soda lime. The light response curves were at 25℃ and under different intercellular CO_2 concentrations. In total, 26 curves of light response in the PFD 0—150 μmol m^{-2} s^{-1} with C_i from 80 to 680 ppm were measured. Slope of linear part of light response curve was used to determine α_A. The relationship between α_A and intercellular CO_2 concentration in 25℃ of temperature was analyzed and compared with the result of Farquhar et al.[1].

2 Result

2.1 Comparison of α_A on Tibetan Plateau with those in low elevation areas

The values of α_A in the flowering period of winter wheat on the Tibetan Plateau are shown in fig. 1. The values of α_A varied with different temperatures. The average values of α_A, their standard deviation and apparent quantum requirement are listed in table 1. In 30℃ of leaf temperature and 65.4 kPa of atmospheric pressure, the value of α_A was 0.0476 ± 0.0038 for winter wheat on the Tibetan Plateau. In contrast with low elevation area with the same temperature and 100 kPa of atmospheric pressure, the α_A value of the Tibetan Plateau is approximate to low elevation level, 0.0524[3]. The discrepancy of the α_A value is not significant. Although the discrepancy of atmosphere pressure is about 30%, the difference of α_A is less than 10%. The measured values of α_A were much higher than those measured in Xining, 0.023[7] and in Lhasa, 0.034[8]. If converting the α_A into the number of quantum requirement for assimilating 1 molecular of CO_2, the number of present study is 21 quanta. It is only 2 quanta higher than the measurement in the low elevation area by Ehleringer et al.[3]. It is far less than those measured in Xining, 43 quanta[7] and in Lhasa, 29 quanta[8] in the past on the Tibetan Plateau.

2.2 Dependence of α_A of winter wheat on temperature on the Tibetan Plateau

In general, α_A decreased linearly with leaf tem-

1) The local time in Lhasa is ca. 2 hours later than that in Beijing.

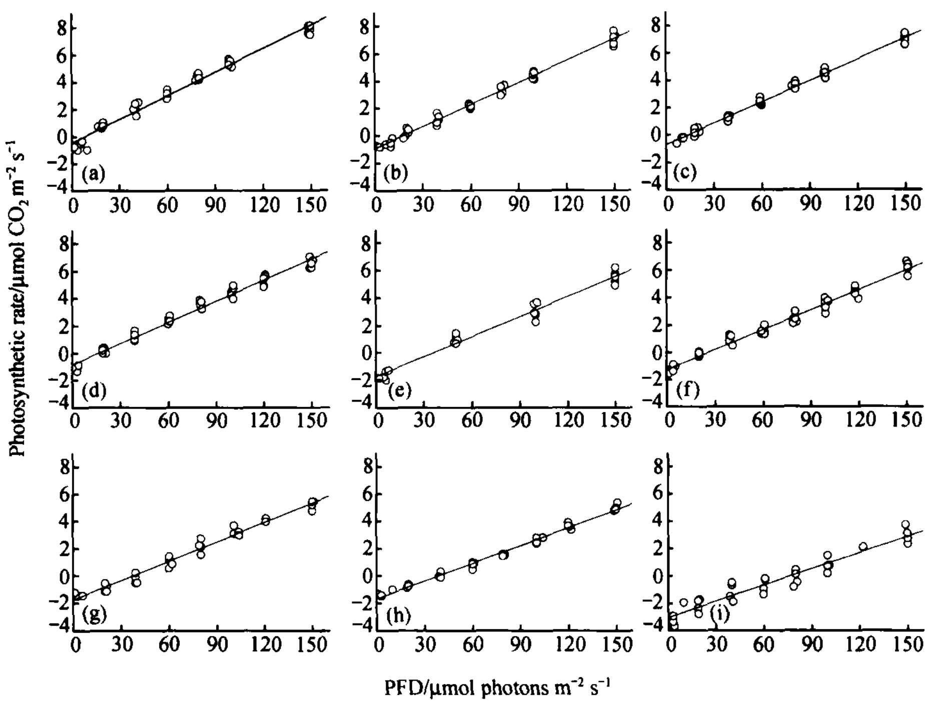

Fig. 1. Linear parts of light response curves of winter wheat in different temperatures. (a)—(i) represent the light response curves in temperature from 15 to 35℃ with interval of 2.5℃.

Table 1 Apparent quantum yield and quantum requirement of winter wheat in different temperatures

Leaf temperature/℃	Apparent quantum yield	Standard deviation	Quantum requirement
15.0	0.0570	0.0022	18
17.5	0.0531	0.0024	19
20.0	0.0518	0.0026	19
22.5	0.0515	0.0023	19
25.0	0.0487	0.0025	21
27.5	0.0483	0.0060	21
30.0	0.0476	0.0032	21
32.5	0.0435	0.0038	23
35.0	0.0398	0.0033	25

perature increase (r^2 = 0.937, $p < 0.001$). α_A decreased by 0.0007 when leaf temperature decreased by 1℃ (fig. 2). However, the dependence of α_A on temperature varied with temperature. Fig. 2 shows that α_A decreased slower in lower leaf temperature than in higher leaf temperature. In particular, α_A decreased more rapidly when leaf temperature was over 30℃.

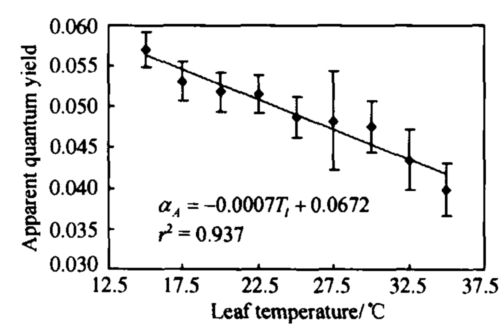

Fig. 2. Dependence of apparent quantum yield of winter wheat on leaf temperature.

2.3 Dependence of α_A of winter wheat on intercellular CO_2 concentration

The dependence of α_A on C_i presented a hyperbolic curve (fig. 3). Similar to CO_2 response curve of photosynthesis, α_A of winter wheat increased sharply with C_i when CO_2 is less than 200 μmol mol^{-1}, and increased slowly when CO_2 concentration is higher, and then tended to be steady in a value of 0.07.

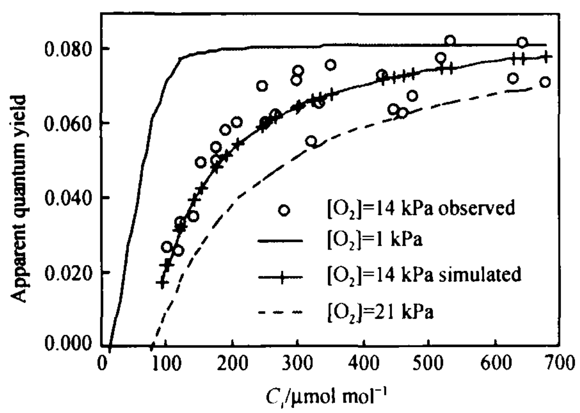

Fig. 3. Dependence of α_A on intercellular CO_2 concentration at 25℃ of leaf temperature. The data of $[O_2]$ in 1 and 21kPa are from Farquhar[1], data of 14 kPa of $[O_2]$ were the observed data on the Tibetan Plateau.

In the low elevation areas with near 1 standard atmospheric pressure, O_2 partial pressure ($[O_2]$) is about 21 kPa. While it decreases to ca. 14 kPa on the Tibetan Plateau with an elevation of 3688 m, it is about 2/3 of that in the low elevation areas. We compared the result of present study with that of Farquhar et al.[1] because they are C_3 plants. Fig. 3 shows that the response curve of α_A with intercellular CO_2 concentration on the Tibetan plateau is between the curves of 1 kPa (optimal condition in laboratory) and 21 kPa (in low elevation areas with near 1 standard atmospheric pressure) of O_2 partial pressure. In the same C_i, the value of α_A on the Tibetan Plateau is higher than those in the low elevation areas but lower than that of the optimal condition of laboratory with O_2 partial pressure of 1 kPa. It suggested that O_2 partial pressure is one of important factors to influence the change of α_A. The lower the $[O_2]$, the more sensitive α_A response to C_i.

3 Discussion

3.1 The value of α_A and impact of O_2 partial pressure

The α_A of winter wheat on the Tibetan Plateau measured in 30℃ of leaf temperature is 0.0476 ± 0.0038. The discrepancy with the low elevation area is not much. It showed that the α_A of C_3 plants on the plateau is not significantly lower than that of C_3 plants in lower elevation areas. In fact, the key factors to influence α_A of C_3 plants in its optimal environment is $[CO_2]/[O_2]$ and leaf temperature[5]. There were many reports that when $[O_2]$ is constant, increase of CO_2 concentration will increase the ratio of RuBP carboxylase to oxygenase and therefore the carboxylation process was enhanced and, so α_A increased. On the contrary, increase of temperature will increase the ratio of RuBP oxygenase and as a result, respiration was enhanced, and therefore α_A decreased[1,10,11]. CO_2 enrichment experiment also provided the evidence[5]. Although $[CO_2]$ is lower than and only 2/3 of those in low elevation areas, $[O_2]$ is also lower than and 2/3 of those in the low elevation areas. Lower $[O_2]$ undoubtedly reduced oxygenase of RuBP and therefore the tendency of α_A decrease was slow down due to the reduction of respiration. As a result, the ratio of $[CO_2]/[O_2]$ is constant at any elevations. Under a certain temperature, α_A on the Tibetan Plateau is not too much lower than those in the low elevation areas. The measured values of α_A for wheat[7,8] in Lhasa and Xining on the plateau may be too low.

Some research in the past argued that the value of α_A decreased with the reduction of partial pressure of CO_2 ($[CO_2]$) in proportion. The authors explained that α_A might be 2/3 of that in the low elevation areas because $[CO_2]$ is 2/3 of that in the low elevation areas[8]. Firstly, this explanation neglected the fact that $[O_2]$ is also low. Secondly, the lower measured values of α_A might be due to the error of measuring instrument and data processing methods. The instrument for measurement in the past including CID-301 photosynthesis system could not control light and leaf temperature. The weak light condition (0—150 μmol m^{-2}s^{-1}) could not be available for automatic measurement of net photosynthetic rates. PFD into transparent leaf chamber in daytime is very strong. Even in the early morning and near night, the weak light condition for measuring α_A is not ensured. Because measured light response curve had few data in the low light area, simulation of α_A using rectangular hyperbolic function would undoubtedly reduce the slope of linear part of light response curve. This would reduce the value of

α_A[12]. Furthermore, temperature varied in the daytime when the daily photosynthetic rates were used for simulation because leaf temperature cannot be controlled. The simulated α_A was not sure in which temperature and cannot be used for comparison with α_A values of other researches. Rectangular hyperbolic curve is a function to simulate light response curve of photosynthesis. The function has a hypothesis that the steepness is 1. However, a lot of data are suitable for simulation by using nonrectangular hyperbolic function. The steepness of the light response curve varied with different environment. So the simulations from rectangular or nonrectangular hyperbolic functions are difficult to compare and consequently result in error. And therefore, the linear part of light response curve in the weak light area (0—150 μmol $m^{-2}s^{-1}$), according to the definition of α_A[1] can be more reliable[12].

3.2 Dependence of α_A on temperature

There were some reports that α_A was linearly correlated with temperature between 15—35℃. For example, the values of *Encelia californica* decreased 0.024 from 0.068 to 0.044[3]. *Triticum aestivum* L. decreased 0.013 from 0.061 to 0.048[13]. *Avena sativa* decreased 0.030 from 0.074 to 0.044[14]. *Lolium perenne* decreased 0.017 from 0.060 to 0.043[15]. *Pinus sylvestris* decreased 0.014 from 0.072 to 0.058[16]. The average values of above C_3 species decreased 0.0009 in every 1℃ increase from 15 to 35℃. The α_A of present study decreased from 0.057 to 0.040 from 15 to 35℃. On average, α_A decreased 0.0007 in every increase of temperature. The decrease tendency of α_A is similar to C_3 plants in low elevation areas. But the decrease rate is slower than those of the low elevation areas. This indicated that the value of α_A is lower than those of C_3 plants in the low elevation areas, but decreases with temperature slowly.

There were some reports that there was no decrease of α_A in *Glycine max* with temperature even when temperature rose to 25℃[17]. However, in some species intolerant of coldness were subjected to injuring below 15℃ and resulted in decrease of α_A because of low temperature stress and damage to cell membrane[16]. The major reason for the decrease with temperature rise is that more NADPH and ATP produced by electronic transferring were used for respiration[1,3]. The present study presented the same tendency although the value of α_A deceased more rapidly when temperature was above 30℃.

3.3 Dependence of α_A on intercellular CO_2 concentration

Peisker argued that the values of α_A of C_3 plants were determined by α_0 ([O_2] was close to 0) and [CO_2]/[O_2]. When [O_2] was in a certain value, light respiration was restrained with increase of [CO_2] and the value of α_A increased[18]. Farquhar[1] showed that when [O_2] is near 1 kPa, α_0 increased linearly with intercellular CO_2 concentration from 0 to 50 ppm, increased slowly when C_i is from 50 to 200 ppm, and α_0 tends to be a static value of 0.077. Comparing the response of α_A on C_i on the Tibetan Plateau and low elevation areas, it showed that in a certain intercellular CO_2 concentration α_A decreased with increase of [O_2]. This indicated that the ratio of [CO_2]/[O_2] is a major determinant of α_A. And it also indicated that winter wheat on the Tibetan Plateau is more sensitive to increase of CO_2 concentration. The exact reason for sensitive response of α_A on increase of CO_2 concentration is due to lower [O_2] on the plateau. RuBP carboxylase activity took advantage and the ratio of carboxylase to oxygenase was enhanced. And therefore the value of α_A increased. In addition, the simulation from a biochemistry model of photosynthesis from Cannell and Thornley[19] also showed that α_A decreased more slowly with the increase of temperature when CO_2 concentration was enriched. If it is the case, the photosynthetic rate will be enhanced in the future scenario of global warming and CO_2 enrichment on the lower atmospheric pressure on the Tibetan Plateau. But the photosynthesis and production on canopy level is still unknown because they are influenced by more factors.

4 Conclusion

The value of α_A is generally lower than those in the low elevation areas because it is influenced by low atmospheric pressure. At 30℃, the average value of

α_A is 0.0476±0.0038. It is not quite different from the values in the low elevation areas. α_A is influenced both by temperature and by the ratio of $[CO_2]/[O_2]$. Although $[CO_2]$ and $[O_2]$ are both lower than those in the low elevation areas, the ratio between them is constant. So the α_A value on the Tibetan Plateau is not much lower than those in the low elevation areas. The measured values in the previous studies were much lower. This might be due to systematic errors from instrument and data processing methods. The values of α_A decreased linearly with temperature with a slope of −0.0007. The decrease slope is similar to those researches in the past. While $[O_2]$ is constant, α_A increases with C_i with a hyperbolic relationship. In comparison with the low elevation areas, the α_A on the Tibetan Plateau is more sensitive to increase of CO_2.

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