

Linear Relationships between Photosynthetic Rate and Photochemical Energy Expressed by $PAR \times F_v/F_m$

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Abstract

Photosynthetic rate (P_n) of plants is simultaneously affected by photosynthetically active radiation (PAR) and maximum yield of primary photochemistry (F_{ν}/F_{m}) . In order to explore the quantitative relationship between P_{n} , *PAR* and F_{v}/F_{m} , those parameters were simultaneously measured for different plant species (maize, sunflower, daylily and alfalfa), growth stages and irrigation treatments. Results indicated that the diurnal variation of P_n had no significant correlation with that of F_v/F_m . Mean diurnal values of P_n were linearly correlated with those of F_{ν}/F_{m} among the different irrigation treatments of alfalfa (p < 0.05), but this linear correlation was not observed among the different species. There was a positive relationship between P_n and F_v/F_m only at midday (12:00 and 14:00) (p < 0.01). A significant linear relationship was observed between the diurnal variation of P_n and $PAR \times$ F_{v}/F_{m} (p < 0.05), this law was suitable for the different species, and the different growth stages and the different irrigation treatments of the same species. This study confirms that P_n is significantly related to the photochemical energy $(PAR \times F_v/F_m)$, the light energy directly used in photochemical reactions of plants.

Keywords

Net Photosynthetic Rate, *PAR*, F_v/F_m , Relationship

1. Introduction

The power driving photosynthesis in plants is light which mainly comes from solar radiation. Many studies have documented a positive relation between the

net photosynthetic rate (P_n) and photosynthetically active radiation (PAR) [1] [2] [3] [4] [5], which only presents an overall trend in P_n increasing with *PAR*, or a linear relationship at low light intensity. In general, P_n initially increases as the solar radiation increases, and levels off and reaches light saturation at high radiation, and the response curve of P_n to *PAR* is a logarithmic function [6] [7] [8]. However, high light can inhibit photosynthesis [9] [10]. When plants are exposed to more light than they can utilize, a phenomenon called photoinhibition appears [9] [11] and the photosynthetic rate decreases so that the relationship between P_n and *PAR* is a quadratic function, particularly under high temperature [12] or drought stress [13] [14] [15].

The rate of photosynthesis of plants is not only related with the intensity of *PAR*, but also affected by the efficiency of light quantum chemistry [16]. Maximum quantum efficiency of PSII photochemistry (F_r/F_m) is the most frequently used parameter [17] [18]. P_n of *Leymus chinensis* among different levels of drought stresses was significantly correlated with F_r/F_m [19], but P_n had no correlation with F_r/F_m among broad-leaved trees [20]. The diurnal variation of P_n of alfalfa in different irrigation treatments was no significant correlation with that of F_r/F_m [21], and similar result was obtained in the studies of arid sandy shrub [5] [22].

Actually, P_n of plants is simultaneously affected by *PAR* and F_r/F_{nr} . Our study found a positive correlation between P_n of alfalfa and the product of *PAR* and F_r/F_m (*PAR* × F_r/F_m) [21], which means the maximum light energy directly used in photochemistry reactions of plants. In order to further explore the universality of this law, P_m , *PAR* and the chlorophyll fluorescence parameters for different plant species, growth stages and irrigation treatments of the same plant species were examined simultaneously.

2. Materials and Methods

This study was conducted at Jiazhuang, a village of Hunyuan County, Shanxi Province (39°53'N and 113°32'E). The site is located in the northeast of Loess Plateau. The altitude is 1091.9 m above sea level. It is a temperate continental semi-arid monsoon climate with mean annual temperature of 6.2° C, precipitation of 436.2 mm, water evaporation of 1828 mm, sunshine hours of 2700 h and frost-free period of 110 ~ 140 days. The soil type is kastanozems rich in fine sand. The top soil at 0 ~ 20 cm depth contained 11.2 g/kg of organic matter, 8.1 of pH, 24 mg/kg of available P and 101.1 mg/kg of exchangeable K.

2.1. Plants and Dates Selected

Maize (*Zea mays L.*), sunflower (*Helianthus annulus L.*), daylily (*Hemerocallis fulva L.*) and alfalfa (*Medicago sativa L.*) were selected for this study. The local cultivated maize variety *Yongfeng* 1^{\sharp} and alfalfa variety *Ameristand* 210+Z introduced from US were selected. Sunflower and daylily were planted by local farmers. Alfalfa was sown in July 2003 with seeding rate 15 kg·ha⁻¹, and applied

nitrogen 13.8 kg·N·ha⁻¹·year⁻¹, phosphorus 105 kg·P₂O₅·ha⁻¹·year⁻¹. Maize was sown in May 2004 with density of 55000 plants·ha⁻¹ and chemical fertilizer application was 300 kg·N·ha⁻¹ and 90 kg·P₂O₅·ha⁻¹. Sunny days were selected to observe for this work. The days selected are shown in **Table 1**.

2.2. Design of Irrigation

There were 4 levels for alfalfa irrigation procedures including irrigated 0 time, 1 time, 2 times and 3 times for each harvest expressed by W_0 , W_1 , W_2 and W_3 , respectively. The irrigation quota for each time was 75 mm controlled by water meter. Border irrigation method was employed. The irrigation scheme is shown in **Table 2**.

2.3. Measurements of *P_n* and *PAR*

 P_n and *PAR* were measured with Li-6400 portable photosynthetic system using the natural light source. Three typical plants sampling for each treatment were selected for the measurements. Maize, sunflower and daylily were determined on the middle of the first fully expanded leaf on the top of the plants, and alfalfa was determined on the middle leaflet of the first three fully expanded leaves on the top of plants. The measurements were operated in 2 h interval from 6:00 to 18:00. The light saturation point was determined by PAR corresponding to the maximum photosynthetic rate.

2.4. Measurements of Chlorophyll Fluorescence Parameters

The chlorophyll fluorescence parameters were observed with Fim-1500 portable chlorophyll fluorescence meters. The leaves were subjected to darkness for 20 - 30 minutes prior to each measurement, and then the initial fluorescence (F_0) was measured. A saturating flash light was used to determine the maximal fluorescence (F_m). The variable fluorescence (F_v) and maximum quantum efficiency of PSII photochemistry ($F_v/F_m = (F_m - F_0)/F_m$) were calculated according to Kitajima and Buter [23]. The chlorophyll fluorescence parameters and P_n were simultaneously measured. Another three typical plants sampling for each treatment were selected for measuring chlorophyll fluorescence parameters. The method of the sampling leaves selected was the same as that for measuring P_n .

Table 1. Date of determination and	the growth	period of plants
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Date	Growth period of plants				
	Maize	Sunflower	Daylily	Alfalfa	
2005-06-09	Seedling stage				
2005-06-22	Jointing stage	Budding stage	Budding stage	Renewable period after the first harvest	
2005-07-23	Huge bellbottom stage			Beginning of flowering	

Date of irrigation	Irrigation scheme of the first crop		Date of Irrigation	Irrigation scheme of the first crop			
2005-04-26	W_1	W_2	W_3	2005-06-12	W_1	W_2	W ₃
2005-05-13			W_3	2005-06-27			W_3
2005-05-23		W_2		2005-07-04		W_2	
2005-05-26			W ₃	2005-7-12			W ₃

Table 2. Irrigation scheme for alfalfa. W_0 , W_1 , W_2 and W_3 represent 0 time, 1 time, 2 times and 3 times irrigations for each harvest respectively.

2.5. Measurements of Soil Water

The soil water content was measured with a time-domain-reflectometry (TDR) system [24]. Observations were performed at intervals of 20 cm to a depth of 0 - 280 cm every 10 days with three duplicates for each treatment. The soil water content was measured only for alfalfa and maize in the experiment station, not for sunflower and daylily in the farmer land.

2.6. Statistical Analysis

Significance test and correlation analysis were carried out through SAS statistical software.

3. Results

3.1. The Relationship between *P_n* and *PAR*

Under non-irrigation condition in the semi-arid region, P_n of maize, sunflower, daylily and alfalfa to changes in *PAR* had a similar response pattern, which presented an initially rapid rise as the increase of *PAR*, then a slow rise and a pronounced decline at high light (**Figure 1**). The relationship between P_n and *PAR* was a significantly quadratic function with the determination coefficient (\mathbb{R}^2) of 0.72 - 0.94 (p < 0.01).

Different crop species possessed different maximum P_n and light saturation point. The maximum P_n was ranked maize (25.7 µmol·m⁻²·s⁻¹) > daylily (23.9 µmol·m⁻²·s⁻¹) > sunflower (23.5 µmol·m⁻²·s⁻¹) > alfalfa (10.1 µmol·m⁻²·s⁻¹), and the light saturation point was ranked as the same order as P_n , *i.e.* maize (1539 µmol·m⁻²·s⁻¹) > daylily (1356 µmol·m⁻²·s⁻¹) > sunflower (1238 µmol·m⁻²·s⁻¹) > alfalfa (984 µmol·m⁻²·s⁻¹) (**Figure 1**). The difference of P_n and light saturation of the plant species may be due to different soil moisture.

The response curves of P_n to *PAR* were different for different growth stages of maize (**Figure 2**). At the seedling stage, P_n increased with rise of *PAR* and no light saturation was observed, which showed the relationship between P_n and *PAR* was a logarithmic function with R² of 0.97 (p < 0.01). At the elongation and huge bellbottom stages, P_n increased initially and then decreased as the increase of *PAR*, *i.e.* the light saturation occurred, which showed the relationship between P_n and *PAR* was a quadratic function with R² of 0.92 and 0.94, respectively



Figure 1. Relationships between diurnal variation of net photosynthetic rate (P_n) and photosynthetic active radiation (PAR) for different plant species (2005-06-22).



Figure 2. Relationships between diurnal variation of net photosynthetic rate (P_n) and photosynthetic active radiation (PAR) for maize at different growth stages.

(p < 0.01). The occurrence of the light saturation of maize was related to drought stress because the leaves wilted due to lower soil moisture at the elongation and huge bellbottom stages. Light saturation point of maize decreased with drought stress intensifying. The light saturation point of maize was 1539 µmol·m⁻²·s⁻¹ at the elongation stage with soil water content of 16.8%, and reduced to 1343 µmol·m⁻²·s⁻¹ at the huge bellbottom stage with soil water content of 15.1% comparing to that of 17.1% at the seedling stage.

Water is a very important factor influencing P_n of plants. Relationships between P_n of alfalfa and *PAR* showed marked differences for different irrigation treatments (**Figure 3**). Under low soil water conditions (W_0 and W_1) which meant alfalfa might be at risk of drought stress, P_n increased initially and then fell with increasing of *PAR*, *i.e.* the light saturation occurred, which demonstrated a quadratic function relationship between P_n and *PAR* with R^2 of 0.74 and 0.88, respectively (p < 0.01). Under suitable soil water conditions (W_2 and W_3) which meant there might be no drought stress to alfalfa, P_n increased with rise of *PAR*, which presented the relationship between P_n and *PAR* was a logarithmic function with R^2 of 0.88 (p < 0.01) (**Figure 3**). The aggravation of drought stress to alfalfa significantly lowered the light saturation point. The light saturation point was 984 µmol·m⁻²·s⁻¹ and 1431 µmol·m⁻²·s⁻¹ for W_0 and W_1 , respectively, and there were no light saturations observed for W_2 and W_3 .



Figure 3. Relationships between diurnal variation of net photosynthetic rate (P_n) and photosynthetic active radiation (PAR) for alfalfa among different irrigation treatments (2005-07-23).

3.2. The Relationship between P_n and F_v/F_m

For different plant species (maize, sunflowers, daylily and alfalfa), maize at different growth stages and alfalfa under different irrigation treatments, the diurnal variation of P_n had no significant correlation with that of F_v/F_m (data not shown).

At the different observation moments of daytime, however, there were different relationships between P_n and F_r/F_m among the different species (**Figure 4**) or the different irrigation treatments of alfalfa (**Figure 5**). P_n was significantly correlated with F_r/F_m only at 12:00 and 14:00 with R² of 0.63 ~ 0.84 (p < 0.01), but P_n was not significantly correlated with F_r/F_m at the other observation moments, *i.e.* at 6:00, 8:00 and 10:00 in the morning and at 16:00 and 18:00 in the afternoon.

Mean diurnal values of P_n among different species were no correlation with those of F_r/F_m (**Figure 4**), but mean diurnal values of alfalfa among different irrigation treatments were significantly positive correlation with F_r/F_m with R² of 0.84 (p < 0.01) (**Figure 5**).

3.3. The Relationship between P_n and $PAR \times F_v/F_m$

For the different species, maize at the different growth stages and alfalfa under different irrigation treatments, the diurnal variation of P_n was significantly correlated with the product of F_r/F_m and $PAR(PAR \times F_r/F_m)$ with R^2 of 0.62 ~ 0.91 (p < 0.01 or p < 0.05) (Figures 6-8). The linear functions obtained for the different species highlighted different slopes, which of alfalfa was the smallest due to the low soil moisture (Figure 6). The slopes and intercepts of the linear functions obtained for alfalfa also increased with irrigation times (Figure 8) which indicated that the slope of the linear function can reflect the extent of drought stress to plants.

At the different observation moments of the daytime, P_n among the different species had a significant positive correlation with $PAR \times F_v/F_m$ (p < 0.01) (**Figure 9**), and P_n of alfalfa among different irrigation treatments also showed the same correlation (p < 0.01 or p < 0.05) (**Figure 10**).



Figure 4. Relationships between net photosynthetic rate (P_n) and maximum quantum efficiency of PSII photochemistry (F_n/F_m) among different plant species (maize, sunflowers, day lily and alfalfa) at the different observation moments of daytime (2005-06-22).



Figure 5. Relationships between net photosynthetic rate (P_n) and maximum quantum efficiency of PSII photochemistry (F_r/F_m) among different irrigation treatments at the different observation moments of daytime (2005-07-23).







Figure 7. Correlation of diurnal variation of net photosynthetic rate (P_n) and $PAR \times F_v/F_m$ for maize at different growth stages.



Figure 8. Correlation of diurnal variation of net photosynthetic rate (P_n) and $PAR \times F_n/F_m$ for alfalfa among different irrigation treatments.



Figure 9. Correlation of photosynthetic rate (P_n) and $PAR \times F_v/F_m$ among different species at the different observation moments of daytime (2005-06-22).

Mean diurnal values of P_n were a significant positive correlation with those of $PAR \times F_v/F_m$ among the different species and different irrigation treatments of alfalfa, respectively (p < 0.01). The slopes of the linear functions obtained at 10:00 - 16:00 were lower which indicated that drought stress was even more pronounced at this period, especially at 12:00 and 14:00 (**Figure 9** and **Figure 10**).



Figure 10. Correlation of net photosynthetic rate (P_n) and $PAR \times F_n/F_m$ among different irrigation treatments of alfalfa at the different observation moments of daytime (2005-07-23).

4. Discussion

The quantitative relationships between P_n of plants and *PAR* were unfixed in the fields condition. Under drought stress, P_n and *PAR* showed a quadratic function which result was in good accordance with some studies [8] [13]. Under proper water conditions for plants, however, P_n and *PAR* had a logarithmic function which was also in consistent with many studies [7] [25] [26].

Photosynthetic response curves to light were different with artificial light source (red and blue light) and natural light source. A logarithmic curve of P_n was usually obtained with the artificial light, and no reduction of P_n was observed even with very high light intensity. However, the results determined with natural light sources revealed that obvious midday depression of photosynthesis occurred [2] [15] [26] [27]. This was because P_n -light response curves measured with the artificial light source were usually conducted from 9:00 to 11:00 when high temperature or drought stress to the plants had not occurred yet.

Several studies revealed that P_n -light response curves simulated were a rectangular hyperbola [28] [29] or a non-rectangular hyperbola [30] [31] [32] [33]. However, both the rectangular hyperbola and non-rectangular hyperbola could neither be used to directly estimate the light saturation point, nor explain the decline of P_n caused by the photoinhibition of plants [28] [34] [35] [36].

There was no linear correlation between diurnal variation of P_n and that of F_v/F_m of plants. This was because the diurnal changes of P_n and F_v/F_m were not synchronous with rise of *PAR*. In low light conditions, P_n rapidly increased while F_v/F_m slowly reduced with increase of *PAR*. In high light conditions, P_n slowly increased while F_v/F_m rapidly dropped with increase of PAR [21]. At the different observation monuments in the morning (6:00, 8:00 and 10:00) and in the afternoon (16:00 and 18:00), P_n of plants had no correlation with F_v/F_m among the different species and the different irrigation treatments of alfalfa, respectively. Zheng & Shangguan (2006) also found that there was no correlation between P_n and F_v/F_m among various broad-leaved trees at the observation moments be-

tween 9:00 and 10:30 [20]. At midday (12:00 and 14:00), however, there was a positive relationship between P_n and F_v/F_m among the different species and the different irrigation treatments of alfalfa. That is to say, the substantial decline of F_v/F_m due to severe environmental stresses from high light intensity and high temperature at midday made significant difference of F_v/F_m could be only observed among the different species and the different soil moisture conditions, respectively, because the difference of F_v/F_m among the different treatments was very small in the morning and in the afternoon.

Mean diurnal values of P_n among different irrigation treatments of alfalfa were linearly correlated with those of F_v/F_m , but this linear correlation was not observed among different plant species. This finding further confirmed that soil moisture was critical to the photosynthesis, as our previous study had proved that both P_n and F_v/F_m of alfalfa had significant positive correlation with soil moisture content [21]. Under proper moisture conditions, plants may absorb and utilize most light energy, and keep the primary photochemical efficiency higher in order to maintain the photosynthesis higher.

A significant linear relationship was observed between the diurnal variation of P_n of plants and the product of F_r/F_m and PAR (PAR $\times F_r/F_m$). This law was suitable for the different species, and the different growth stages and the different soil water conditions of the same species. This is because P_n is not only related to PAR and F_{ν}/F_{m} , but also more importantly to the light energy directly used in photochemical reactions of plants, i.e. photochemical energy. The product of PAR and F_v/F_m (PAR $\times F_v/F_m$) can reflect the maximum photochemical energy consumed in photosynthesis. When light intensity is low, majority of solar radiation energy is absorbed and used for the photochemical reaction in plants, which reveals the photochemical efficiency is high, but the total energy used for the photochemical reactions is actually small, so that P_n is relatively low. When the light intensity is increasing, more and more solar radiation is used for fluorescence emission and heat dissipation of plants themselves, so that the proportion of light energy being absorbed and used for the photochemical reactions is relatively fall, which makes F_v/F_m (the photochemical efficiency) relatively lower, but the increase of light intensity can compensate the reduction of the photochemical efficiency in PSII, so that the total amount of energy used for photochemical reactions is still increasing, so P_n of plants is also rising as a result. When light intensity at midday is enough strong and exceeds the capability of light energy utilization of plants, the photosynthesis of plants may be inhibited, majority of the solar radiation is not used for the photosynthesis but for the fluorescence emission and heat dissipation of plants themselves, which makes F_{u}/F_{m} (the photochemical efficiency) dramatically drop, so the total energy used for the photochemical reactions declines which leads to the reduction of P_n . This phenomenon was particularly true when the plants are exposed to the environmental stresses [36] [37] [38]. On the whole, the diurnal pattern of P_n of plants was in consistent with that of $PAR \times F_v/F_m$ (Figure 11). Similar researches had demonstrated that P_n of plants was significantly correlated with the product



Figure 11. Diurnal variation of photosynthetic rate (P_n) , maximum yield of primary photochemistry (F_v/F_m) , photosynthetic active radiation (PAR) and $PAR \times F_v/F_m$ for different species (2005-06-22).

of photosynthetic flux density (*PFD*) and the effective quantum yield of PSII in the illuminated leaf had demonstrated that P_n of plants was significantly correlated with the product ($\Delta F/F_m$ ') ($PFD \times \Delta F/F_m$ ') (p < 0.01) [39] [40] [41], but this linear relationship was obtained without the environmental stresses to plants [42] [43], and had been reported to become non-linear when plants were subject to the environmental stresses [18] [42] [43] such as strong solar radiation [44] and drought [45] [46].

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