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

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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 ($F_v/F_m$). 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 $F_v/F_m$ 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 \( (F_v/F_m) \) is the most frequently used parameter \[17\] \[18\]. \( P_n \) of \( Leymus chinensis \) among different levels of drought stresses was significantly correlated with \( F_v/F_m \) \[19\], but \( P_n \) had no correlation with \( F_v/F_m \) among broad-leaved trees \[20\]. The diurnal variation of \( P_n \) of alfalfa in different irrigation treatments was no significant correlation with that of \( F_v/F_m \) \[21\], 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 \( F_v/F_m \). Our study found a positive correlation between \( P_n \) of alfalfa and the product of \( PAR \) and \( F_v/F_m \) \( (PAR \times F_v/F_m) \) \[21\], which means the maximum light energy directly used in photochemistry reactions of plants. In order to further explore the universality of this law, \( P_n \), \( PAR \) 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 \( Yongfeng 1^e \) 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 W₀, W₁, W₂ and W₃, 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.

<table>
<thead>
<tr>
<th>Date</th>
<th>Growth period of plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Maize</td>
</tr>
<tr>
<td>2005-06-09</td>
<td>Seedling stage</td>
</tr>
<tr>
<td>2005-06-22</td>
<td>Jointing stage</td>
</tr>
<tr>
<td>2005-07-23</td>
<td>Huge bellbottom stage</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Date of irrigation</th>
<th>Irrigation scheme of the first crop</th>
<th>Date of irrigation</th>
<th>Irrigation scheme of the first crop</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005-04-26</td>
<td>( W_1 ) ( W_2 ) ( W_3 )</td>
<td>2005-06-12</td>
<td>( W_1 ) ( W_2 ) ( W_3 )</td>
</tr>
<tr>
<td>2005-05-13</td>
<td>( W_3 )</td>
<td>2005-06-27</td>
<td>( W_3 )</td>
</tr>
<tr>
<td>2005-05-23</td>
<td>( W_2 )</td>
<td>2005-07-04</td>
<td>( W_2 )</td>
</tr>
<tr>
<td>2005-05-26</td>
<td>( W_3 )</td>
<td>2005-07-12</td>
<td>( W_3 )</td>
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</tbody>
</table>

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 (\( R^2 \)) 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 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > daylily (23.9 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > sunflower (23.5 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > alfalfa (10.1 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)), and the light saturation point was ranked as the same order as \( P_n \), i.e. maize (1539 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > daylily (1356 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > sunflower (1238 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) > alfalfa (984 \( \mu \text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \)) (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 \( R^2 \) 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 \( R^2 \) 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 $W_3$. 

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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 $F_v/F_m$ among the different species (Figure 4) or the different irrigation treatments of alfalfa (Figure 5). $P_n$ was significantly correlated with $F_v/F_m$ only at 12:00 and 14:00 with $R^2$ of 0.63 - 0.84 ($p < 0.01$), but $P_n$ was not significantly correlated with $F_v/F_m$ 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 $F_v/F_m$ (Figure 4), but mean diurnal values of alfalfa among different irrigation treatments were significantly positive correlation with $F_v/F_m$ with $R^2$ 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 $F_v/F_m$ and $PAR \times F_v/F_m$ 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 ($F_v/F_m$) 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 ($F_v/F_m$) among different irrigation treatments at the different observation moments of daytime (2005-07-23).

Figure 6. Correlation of diurnal variation of net photosynthetic rate ($P_n$) and $PAR \times F_v/F_m$ for different plant species (2005-06-22).
Mean diurnal values of $P_n$ were a significant positive correlation with those of $PAR \times Fv/Fm$ 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).
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-
between 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 irradiation 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 $F_v/F_m$ and $PAR (PAR \times F_v/F_m)$. 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 $F_v/F_m$ 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 $F_v/F_m$ (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 (Pn), maximum yield of primary photochemistry (Fv/Fm), photosynthetic active radiation (PAR) and PAR × Fv/Fm 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 Pn of plants was significantly correlated with the product (ΔF/Fm') (PFD × ΔF/Fm') (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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