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Dynamics of photosynthesis in *Eichhornia crassipes* Solms of Jiangsu of China and their influencing factors

Li Xia*, Zheng Jianchu, Yan Shaohua, Ren Chenggang, Wang Man, Cong Wei, Sheng Jing and Zhu Puping

Jiangsu Academy of Agricultural Sciences, Nanjing 210014, China.

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With LI-6400 portable photosynthesis system, the photosynthetic characteristics of artificially cultured *Eichhornia crassipes* in Jiangsu, China, were monitored from June 1 to November 14, 2009. Both the net photosynthetic rate (Pn) in different positions and light and temperature-response curves of the top fourth leaf were measured in an open-circuit gas channel system in June, July, and August, respectively. The top third to sixth leaves matured with a high Pn in August, 2009. The values of the maximum net photosynthesis (Pmax), light component point (LCP) and apparent quantum efficiency (AQE) of the top fourth leaf of *E. crassipes* were 34.5 ± 0.72 and $20.25 \pm 3.6 \mu\text{mol m}^{-2}\text{s}^{-1}$ as well as 0.0532 ± 0.0014 , respectively, significantly higher than those in rice and maize. The light-saturation point (LSP) of leaves of *E. crassipes* was $2358 \pm 69 \mu\text{mol m}^{-2}\text{s}^{-1}$, significantly higher than that in rice and much close to that in maize. The natural light intensity and temperatures in Jiangsu are suitable for *E. crassipes* to rapidly grow but not good enough for it to show the maximum internal photosynthetic capacity from the perspective of photosynthetic physiology, thus resulting in its low biomass in this region.

Key words: *Eichhornia crassipes*, photosynthetic characteristics, environmental influencing factors.

INTRODUCTION

Eichhornia crassipes Solms, commonly known as water hyacinth, is an aquatic plant with a bundle. Because of its well developed root system, strong reproductive ability, and ultra strong absorbency, it is widely used for sewage purification (Hu et al., 2007; Qi et al., 1999). Introduced to China as a feed, it has recently been applied to a medium composition for edible fungus and methane fermentation and has become one of the important resources in modern low-carbon eco-agriculture (Zhou et al., 2005).

Known as one of the fastest-growing plants, *E. crassipes* is native to the Amazon basin, including such countries

such as Brazil, Argentina and Peru, but is now found through most areas between 32.3° north and south latitudes (An and Li, 2007). At 25 ~ 35°C, it grows at an alarming rate and can reach 10 to 60 million trees in 8 months. Conditions permitting, a single plant may produce 140 million trees per year, covering a water surface of 140 hm² with a fresh weight of 28 000 t, a testimony to its reproductive ability and diffusivity (Wang and Wu, 2004).

There are eight species of *E. crassipes*, but only the one with little genetic differences is currently found in China as indicated by the cytological and molecular genetic analysis. Since it was introduced from Brazil (Wang and Wang, 1988; Ren et al., 2005), its high biomass might be more related to its habitat that enjoys high light intensity and temperatures. In terms of sewage purification, it is exceedingly difficult for *E. crassipes* to achieve the maximum biomass for large-scale use if artificially planted and bred, particularly in the open Taihu Lake (Dou et al., 1995). Therefore, how to maximize its dry matter accumulation at Taihu would become a hot topic for modern low-carbon eco-agriculture (Chen et al.,

*Corresponding author. E-mail: jspplx@jaas.ac.cn. Tel: 00862584390361. Fax: 00862584390322.

Abbreviations: PAR, Photosynthetic active radiation; P, photosynthetic rate; Pmax, maximum photosynthesis; AQE, apparent quantum efficiency; Pn, net photosynthetic rate; LCP, light component point; LSP, light saturation point.

2008).

Photosynthesis refers to the process in which inorganic substance is converted into organic substance and, simultaneously, solar energy is fixed into plant energy *in vivo*, which is the basis of dry matter production in green plants. It was said in an early report that the biomass of *E. crassipes* was influenced by certain environmental conditions (Wang and Zhang, 1996). For example, compared with alligator alternanthera, *E. crassipes* has a higher leaf area index and chlorophyll content, but it is sensitive to low temperatures (Li et al., 1995). Further results showed that its growth speed and adaptability were related more with external environmental conditions (Li and Wang, 2007). However, the characteristics of its photosynthesis in terms of photosynthetic active radiation (PAR) and temperatures in Taihu Lake remain rarely studied. In this study, with the leaves of *E. crassipes* grown in Jiangsu as the materials, the photosynthetic characteristics, including the changes over the year and at different stages of its growth, were investigated.

Furthermore, when *E. crassipes* reached the maximum photosynthetic rate in the year (in August, 2009), its photosynthetic characteristics in response to essential environmental factors, such as light intensity, temperature and humidity, were systemically measured, and the indexes of the photosynthetic characteristics were thoroughly analyzed. The above mentioned study revealed the physiological mechanism of its fastest growth by its photosynthetic characteristics and found out key environmental factors that influenced its photosynthetic production and dry material accumulation in Jiangsu, which might help enhance its local artificial stocking and provide reference for its efficient, large-scale use for pollution control in the Taihu Lake Basin.

MATERIALS AND METHODS

Materials

E. crassipes plants were collected between June 1 and November 14, 2009, from ponds in Jiangsu Academy of Agricultural Sciences. The plants grew at the initial stocking volume of 2 kg per m² in a 2 m² plot surrounded with bamboo fences. When the biomass reached 25 kg per m², the uniform plants (a robust single-branch, 7 ± 3 leaves, the top second leaf's petiole length of 20 ± 5.2 cm, and white fibrous roots) were selected to measure the photosynthesis indexes twice per month with 10 repetitions for each measurement.

The seeds were provided by Jiangsu Academy of Agricultural Sciences. The japonica rice cultivar was Kitaake (*Oryza sativa* L.), and the corn cultivar was Nongda 108 (*Zea mays* L), both selected as materials in Nanjing, Jiangsu in 2009. Before being sown, the seeds were sterilized in 5% H₂O₂ for 5 min, soaked in water for 24 h, and incubated at 35°C for 48 h. Seedlings at similar stages of development were transplanted into pots (5 hills per pot, 1 seedling per hill) and grown in an outdoor net-room. A completely randomized design with five replicates was employed. The temperature averaged from 21 to 27°C, with a daily difference of 7.1 to 8.7°C. Chemical fertilizer (2.0 g N, 1.6 g P₂O₅, and 1.4 g K₂O) was applied per plot as the basal dressing and 1.0 g N as the top dressing at tillering and booting stages, respectively. The soil was

paddy soil.

Methods

Fluctuations in air temperature

The tested plants were measured between June 1st and November 14th, 2009, in Nanjing. The air temperature, including the highest, lowest, and average temperature, during that period was recorded systematically.

Photosynthetic rate (P) measurement

The P of intact rice leaves to varying irradiances was monitored with a Li-Cor 6400 (Lincoln, Nebraska, USA) at 25°C according to the method proposed by Li et al. (2002). The gas source was compressed air (a CO₂ concentration of 350 μmol mol⁻¹), and the light source was the halogen light source. Varying irradiances to the leaf surface were obtained by adjusting the distance between the light source and the leaf chamber. A layer of circulating water between leaves and the light source was maintained for heat insulation (25°C and relative humidity of 60%). The P to varying irradiances (0, 50, 100, 150, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 2000, 2200, 2400, 2600 and 2800 μmol.m⁻² s) was measured, respectively. The photosynthetic rate at each PAR was surveyed with 4 to 6 repetitions. The curves of photosynthetic light response were obtained by measuring the steady rates under different PARs.

According to the method proposed by Li et al. (2006a), the curves of photosynthetic temperature response were obtained by measuring the steady rates at different temperatures (15, 20, 25, 30, 35, 40 and 45°C). According to the method proposed by Li et al. (2006b), the photosynthetic humidity response curves were obtained by measuring the steady rates at the relative humidity between 0 and 60% in the atmosphere.

Statistical analysis

All results reported here are the mean values of replicates. Data were subjected to the analysis of variance (ANOVA) with the Statistical Package for the Social Sciences (SPSS) 17.0 (Statistical Graphics Corp., Princeton, NJ)

RESULTS

Photosynthetic characteristics of *E. crassipes* during 2009 in Jiangsu, China

The daily air temperature, including the highest, lowest and average temperature, during the experiment was recorded systematically (Figure 1A). Annual photosynthetic characteristics of *E. crassipes* in Jiangsu took on the "bell-shaped" characteristics (Figure 1B); the maximum photosynthesis (P_{max}) was low in June, increased in July, peaked in August, fell in September, and then dropped drastically in October and November, which were same to the apparent quantum efficiency (AQE), an index reflecting the plant's ability to use light energy during 0-200 μmolm⁻²s⁻¹.

Furthermore, their light saturation point and compensation point in July and early October (Figure 1C) were

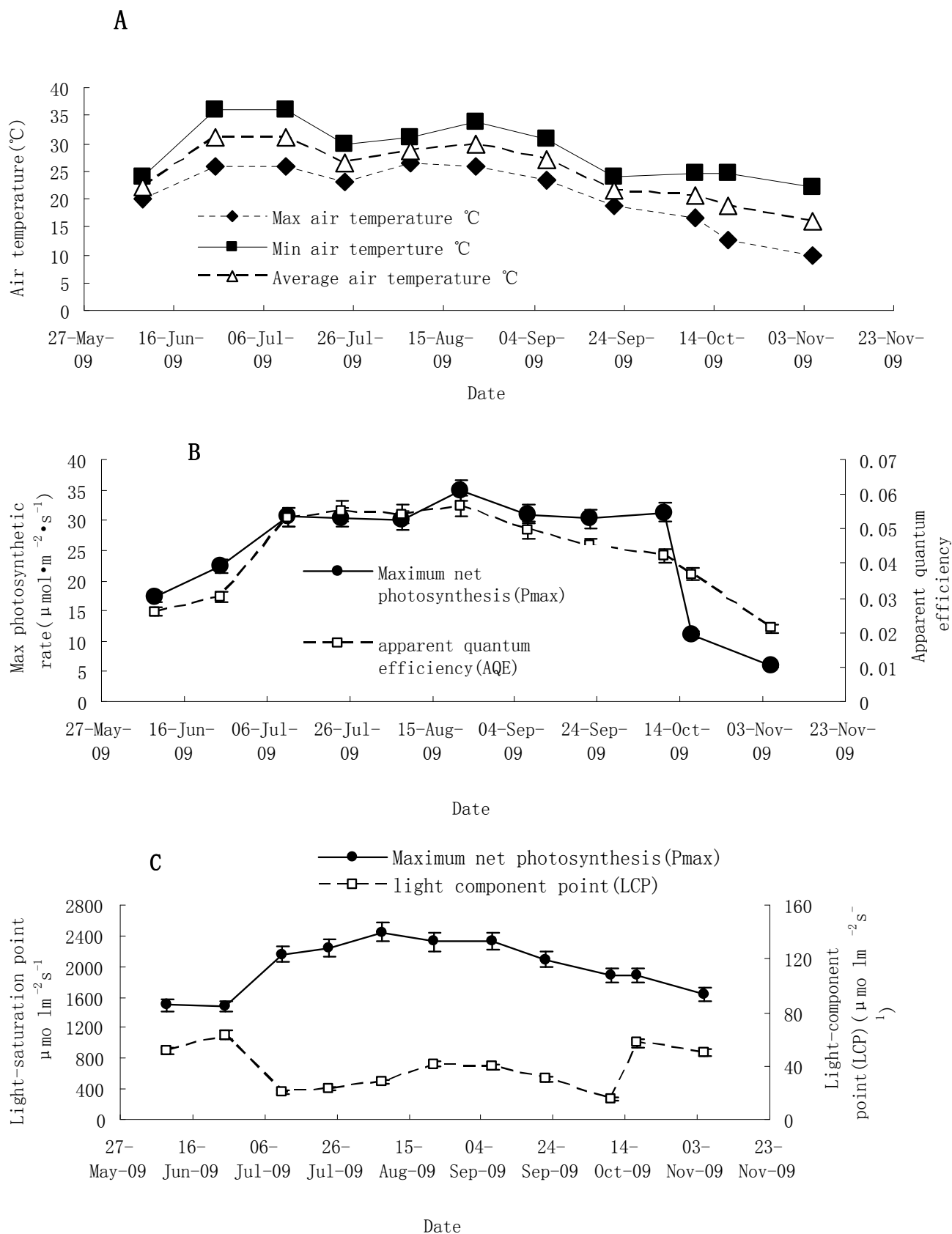


Figure 1. The changes in the maximum net photosynthesis (Pmax), light component point (LCP), apparent quantum efficiency (AQE) and light-saturation point (LSP) of leaves in *E. crassipes* and the air temperature of this period in natural conditions.

Table 1. Comparison of photosynthetic parameters of leaves among *E. crassipes*, typical C₃ plants, rice (*Oryza sativa* L.) and typical C₄ plants, maize (*Zea mays* L.) in Jiangsu Province.

Parameter	<i>E. crassipes</i>	Rice	Maize
Light-saturation point [$\mu\text{mol m}^{-2}\text{s}^{-1}$]	2358±69.00	1641±32.00	2550±37.00
The maximum photosynthesis rates [$\mu\text{mol m}^{-2}\text{s}^{-1}$]	34.50±0.72	19.56±0.62	30.36±0.42
Light compensation point [$\mu\text{mol m}^{-2}\text{s}^{-1}$]	20.25±2.60	38.56±3.60	29.75±2.80
Apparent quantum efficiency	0.0522±0.0014	0.0269±0.0011	0.0427±0.0012

found to be more suitable to show a high photosynthetic productivity for higher P_{max} and a wider range of luminous intensity use. Their photosynthetic characteristics and local air temperatures, especially the lowest ones, in 2009 were closely correlated. From mid-October to November, when the air temperature became lower than 15°C, both the P_{max} and the AQE fell obviously.

Net photosynthetic rate (P_n) of *E. crassipes* at different stages of leaf development in Jiangsu

As shown in Figure 2, from July to September, the P_n of *E. crassipes* at different stages of leaf development grew in the youngest central leaf, but it was low in the outermost leaf. Among them, the P_n of the youngest central leaf became lower, but it was the lowest in the outermost leaf due to senescence, because the flowering season of *E. crassipes* in Jiangsu is between July and August. Interestingly, it could be seen that the P_n of the leaf nearest to the flower in the flowering season was higher than that of the youngest central leaf, but obviously lower than those of other mature ones, thus, suggesting that some photosynthetic matter might be used partially in blossoming and seed breeding.

Therefore, the photosynthetic ability of its leaf was determined more by the intrinsic stages of the leaf's growth. But the number of the leaves that performed the photosynthetic function and the P_n of the leaves were a bit different in different months: 4-6 leaves in July, 3-8 leaves in August, 2-8 leaves in September, which were actually closely related with the air temperature.

Photosynthesis characteristics of the functional leaf in *E. crassipes*

The light curve of photosynthesis of leaves in *E. crassipes*

PAR was one of the dominant environmental factors for photosynthesis. The curve of photosynthetic rate to PAR could reflect the plant's ability to use light energy. According to the curve of photosynthetic rate to PAR in *E. crassipes*, many indexes, such as the LCP, LSP, AQE,

and P_{max}, could be determined. As shown in Figure 3A, function in response to light intensity was a typical parabolic graph, which expressed the equation:

$$y = -7 \times 10^{-6}x^2 + 0.0304x + 1.2869, R^2 = 0.977^*$$

Furthermore, during the range of weak light intensity (0-200 $\mu\text{mol m}^{-2}\text{s}^{-1}$), its AQE was 0.0522 (Figure 3B), indicating its strong ability to use light when there was a low light intensity. When light intensity grew, the photosynthetic rate also increased to its peak accordingly. Its LSP was up to 2458±69 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and the light-saturated photosynthetic rate was 34.50±0.72 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Moreover, it did not fall until 2800 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Therefore, it was easy to see that *E. crassipes* could not only adapt itself to a wide range of light intensity but also exhibit higher photosynthetic capability at a high light intensity.

The photosynthesis of *E. crassipes* in response to temperature

The growth and purifying function of *E. crassipes* are largely subject to the influence of temperatures. As shown in temperature curves of its leaves' photosynthesis (Figure 4), at the atmospheric CO₂ concentration, the change of its photosynthesis in response to temperatures was in a bell-shaped graph, and the optimum temperature was between 30-35°C. Its photosynthetic rate decreased when the temperature was beyond the range at 15°C, while the photosynthetic rate was 28.5% at 30 and 45°C, 57.1% at 30°C. Obviously, these results showed that its photosynthesis was better adapted to high temperatures, which was also an important physiological basis to determine the temperature range for the natural growth of *E. crassipes*.

The photosynthesis of *E. crassipes* in response to humidity

In Figure 5, the photosynthetic rate was negatively correlated with the absolute value of relative humidity in both the leaf chamber (Figure 5A) and the atmosphere (Figure 5B), and there was a significantly positive cor-

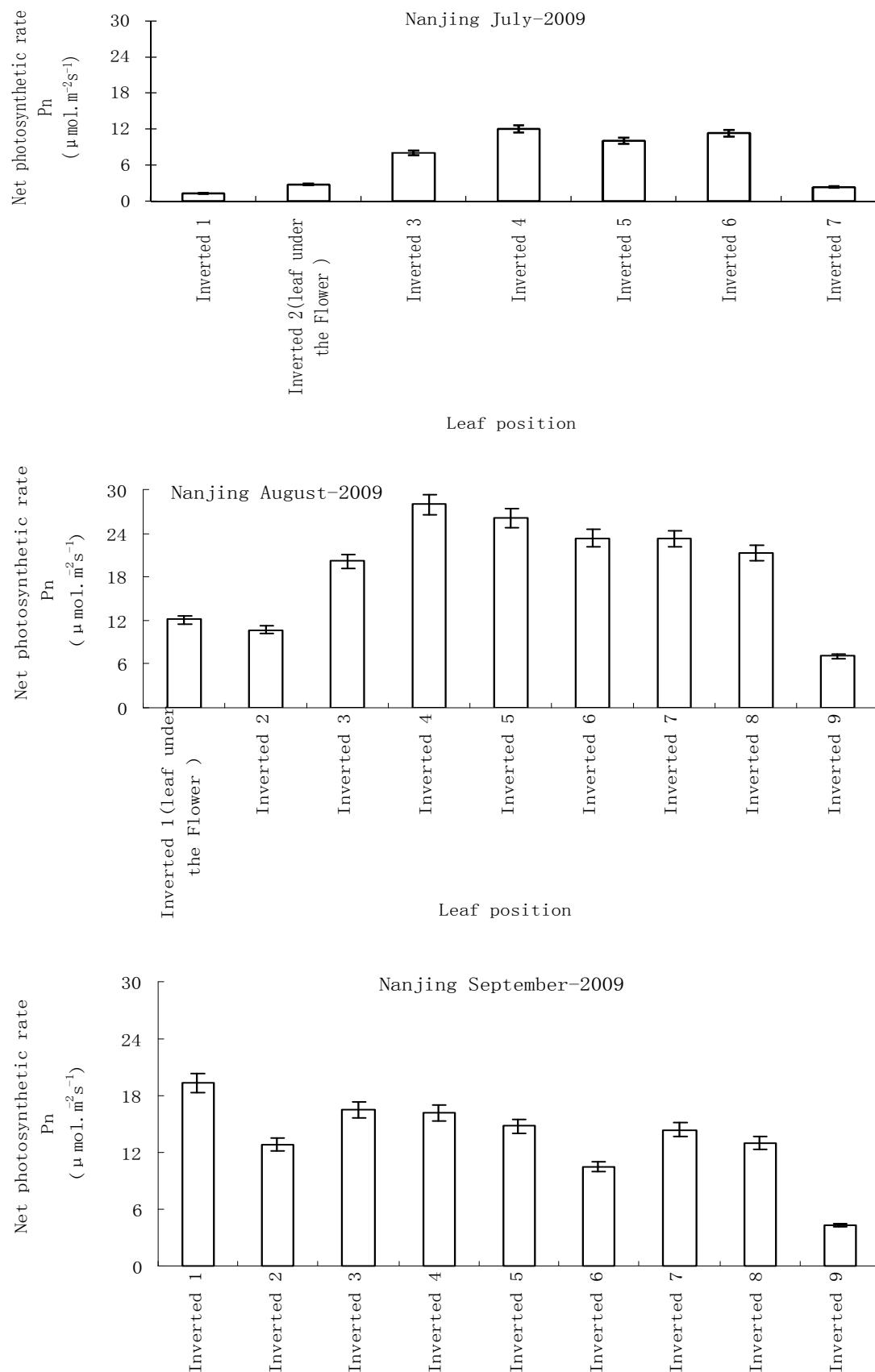


Figure 2. The changes in net photosynthetic rate of leaves at different positions from July to September, 2009.

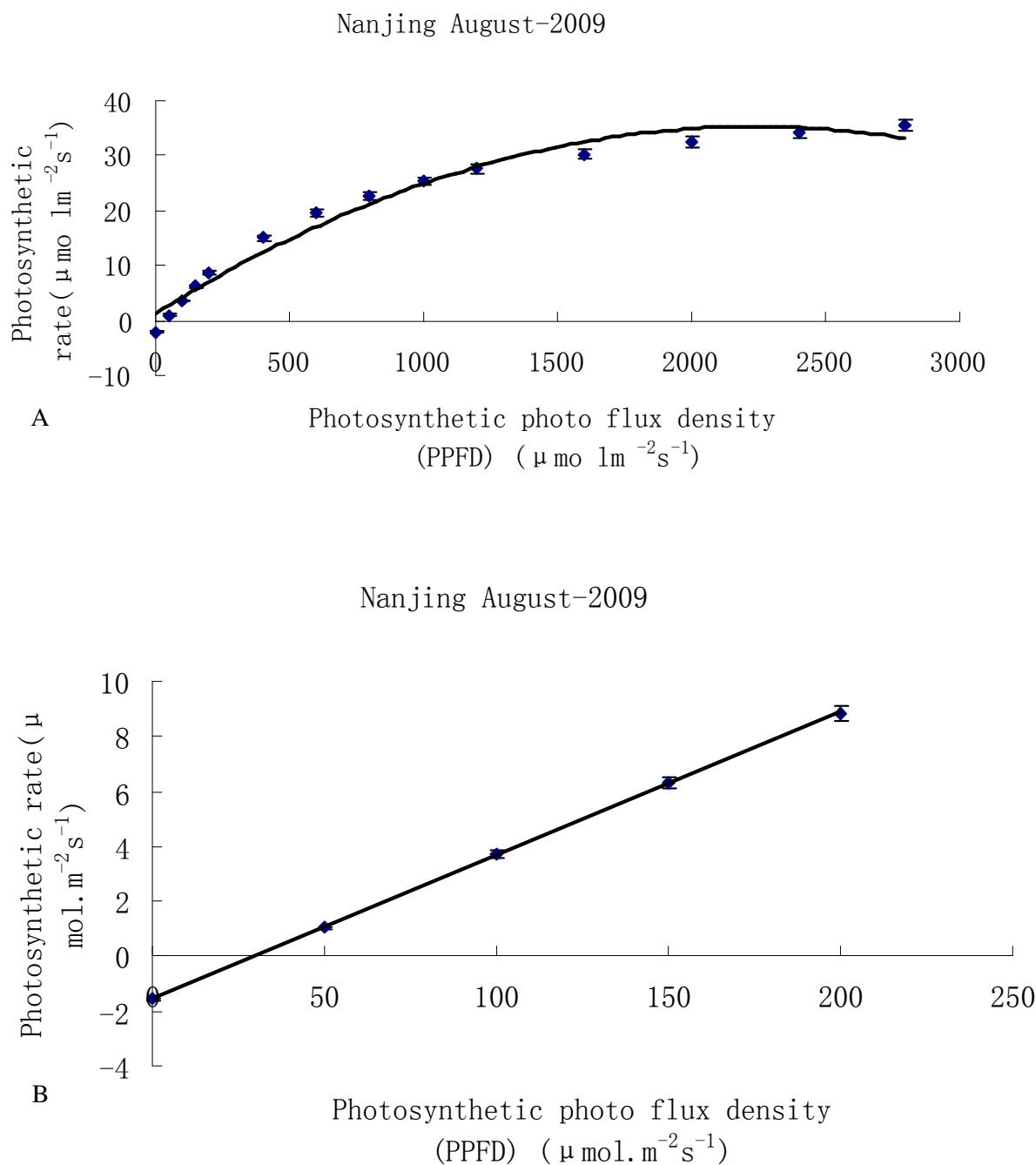


Figure 3. The response curve of PPFD for photosynthesis of the leaves in *Eichhornia crassipes*

relation between the changes in relative humidity in the leaf chamber and those in the atmosphere (Figure 5C). Furthermore, as indicated in Figure 5D, the coefficient of correlation between the stomata conductance and the relative humidity was even higher. It showed that the larger the relative humidity difference between inside and outside the leaf chamber, the more conducive it was to stomata opening, leading to more atmospheric photosynthetic substrates, such as CO_2 and H_2O , into the leaf and consequently a higher photosynthetic capacity.

Comparison of photosynthetic indexes among *E. crassipes*, the C_3 plant, rice, and the C_4 plant, maize

In order to facilitate the visual assessment of the photosynthetic capacity of *E. crassipes*, the light-photosynthesis curve is shown in Figure 6 by simultaneous determination of photosynthesis of leaves of the C_3 plant, rice, and the C_4 plant, maize in the region. Through EXCEL mapping, a series of photosynthetic indexes were obtained and shown in Table 1. It could be seen that

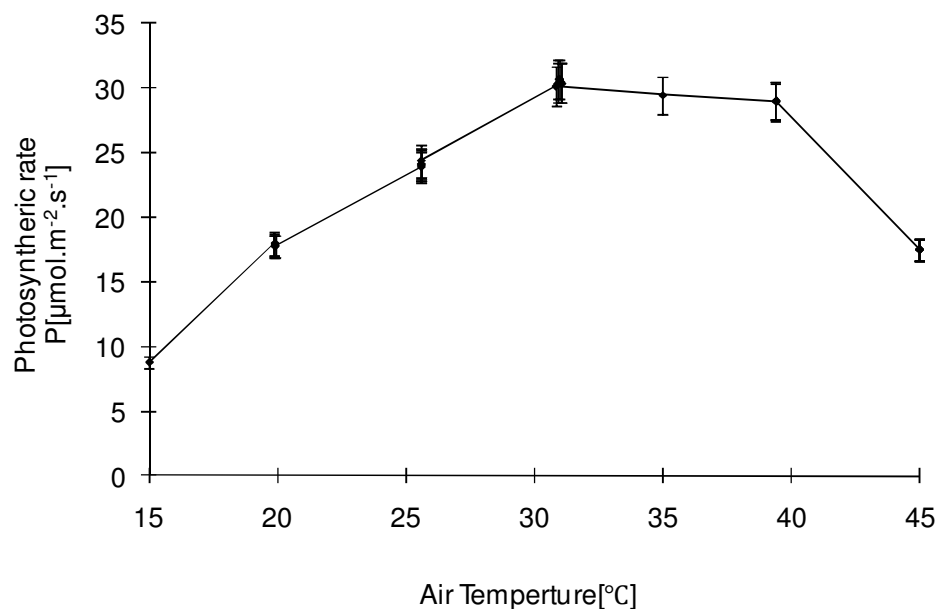


Figure 4. The response curve of temperature for photosynthesis of the leaves in *E. crassipes*.

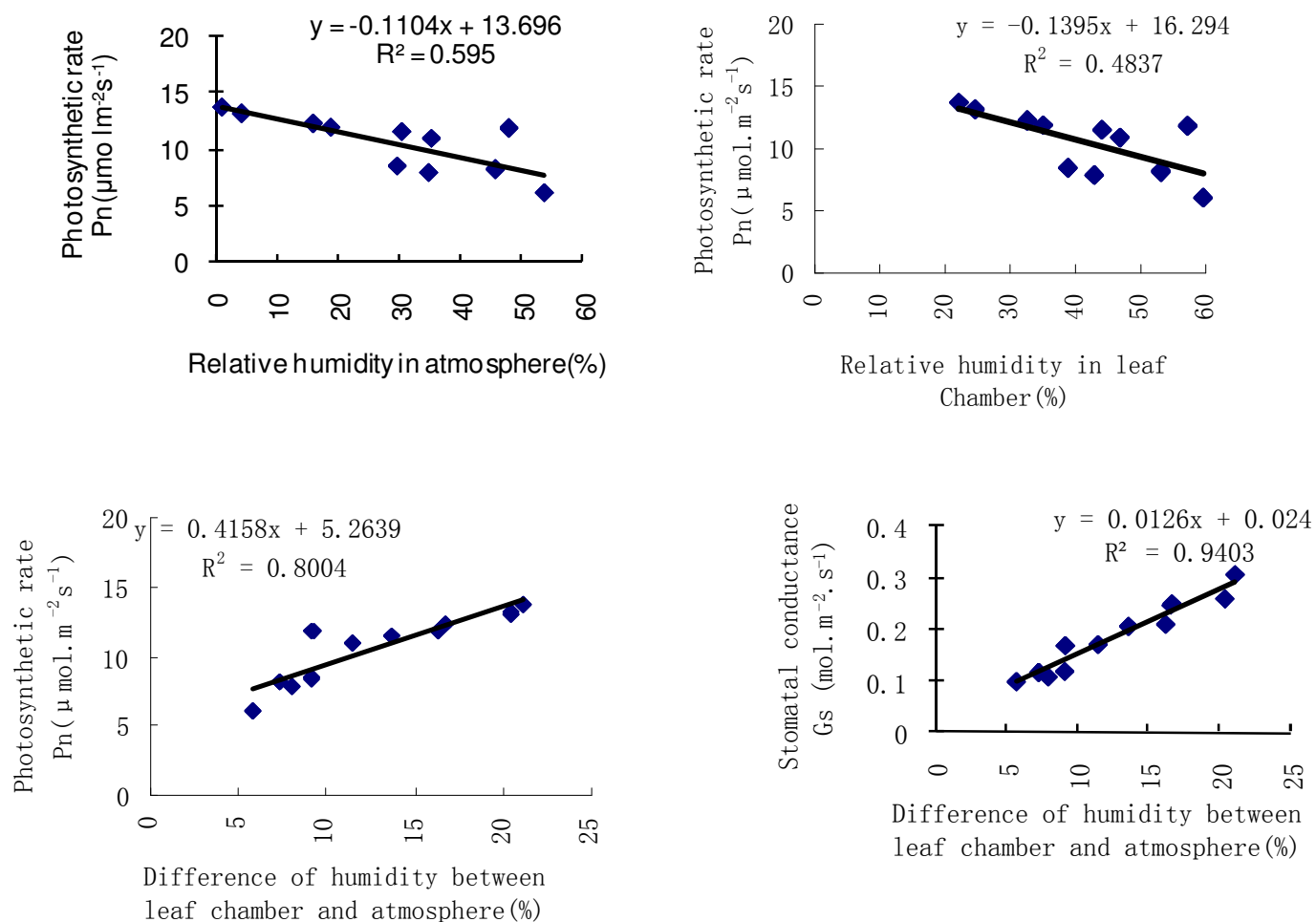


Figure 5. The response curve of humidity for photosynthesis of the leaves in *Eichhornia crassipes*.

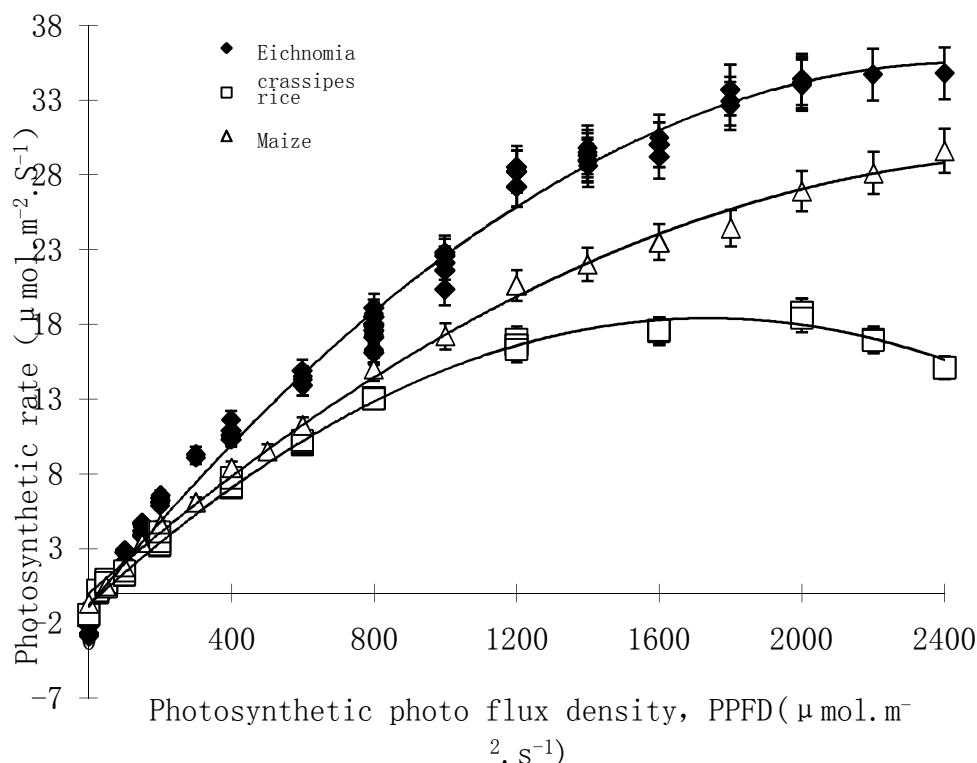


Figure 6. Then response curves of PPFD for the 1eaves among *Eichhornia crassipes* ,typical C₃ plants, rice (*Oryza sativa* L.) and typical C₄ plants maize (*Zea mays* L) in Jiangsu Province.

although *E. crassipes* was a C₃ plant, it showed a Pmax and light saturation points higher than those of the typical C₃ plant, rice, and similar to those of the typical C₄ plant maize.

Furthermore, the AQE in *E. crassipes* was higher than that in maize. These results suggested that *E. crassipes* had not only a high photosynthetic capacity but also a wide range of photosynthetic ecology (20.25 ± 3.6 - $2358 \pm 69 \mu\text{molm}^{-2}\text{s}^{-1}$).

DISCUSSION

Mechanism of the high photosynthetic capacity of *E. crassipes* in Jiangsu

Photosynthesis in plants would change along with the environment, including illumination, air temperature, CO₂ concentration, and the relative moisture. It is one of the physiological processes most sensitive to internal and external factors (Wu et al., 2009). Therefore, the changes of the photosynthetic indexes can represent the responses of most plants to environmental factors, thus directly reflecting the differences in their patterns of physiological and ecological adaptation to the environmental factors. The LSP and LCP of the leaves would indicate that the requirements of plants for

photosynthesis are within the range of the highest and lowest light intensity. For example, most sun plants have a LSP as high as 1500-2000 $\mu\text{molm}^{-2}\text{s}^{-1}$, and a light compensation point around 50-100 $\mu\text{molm}^{-2}\text{s}^{-1}$, but shade plants usually have a lower LSP, and a LCP as low as 20 $\mu\text{molm}^{-2}\text{s}^{-1}$ (Jiang et al., 2004). In this study, the results show that *E. crassipes* in Jiangsu is a typical sun plant that has photosynthetic characteristics of tropical plants (Jiang and He, 1999).

Most interestingly, the LCP of *E. crassipes* in Jiangsu has been found to be much lower compared with that of rice and maize, and its LSP is higher than that of rice and close to that of maize. There is obviously a broad ecological niche of photosynthesis of *E. crassipes* in this region, showing that it has the good adaptability to different light environments by enhancing its light use efficiency in case of the low light intensity and increasing the Pmax in case of the high light intensity. These unique photosynthetic characteristics could promote the maximal use of sunlight to synthesize organic substances and the rapid accumulation of dry matter, thus, bringing about a faster growth and a higher accumulation of dry matter than the C₄ plant sugarcane (Yan et al., 1994).

At the same time, it leaves also has a broad scope of photosynthetic responses to temperatures, which is also between 30-35°C. Thus, it is helpful to bring into playing the photosynthetic capacity at different air temperatures.

Structurally, *E. crassipes* in Jiangsu has a short stem, with leaves and the root nearly attached to each other. It has a high transpiration rate, indicating a short photosynthate distance between the leaves and the root (An and Li, 2007). As for the aquatic environment, a higher relative humidity is also helpful to the stomatal opening, bringing more photosynthetic substrates, CO₂ and H₂O, into the photosynthetic apparatus.

On the whole, for *E. crassipes* in Jiangsu, these internal and external factors are undoubtedly the important physiological basis of its higher photosynthetic capability than the typical C₃ plant paddy rice and the typical C₄ plant maize. The intrinsic mechanism of the high photosynthetic capacity, especially under high light intensity of *E. crassipes* in this region is yet to be studied thoroughly on either the ultra-structural or the biochemical level.

Analysis of main environment factors for the growth of *E. crassipes* in Jiangsu

With a favorable environment, *E. crassipes* would reproduce extremely fast. The mother plant can produce a new generation of plants through the stolon within 5 days (Harward and Harley, 1998). Under the temperatures in this study, the light saturation point of the mature leaves in *E. crassipes* reached up to 2358 $\mu\text{molm}^{-2}\text{s}^{-1}$, but the light intensity was not good enough for them to show the maximum photosynthetic capacity despite this region boasts of the rather favorable sunlight and temperature conditions. In summer, however, the climate in Jiangsu would be subjected to the influence of land, sea and the monsoon, which often brings high winds or torrential rains, and it is therefore more cloudy or rainy with low light intensity. Therefore, even if the solar radiation reaches the peak in this region, usually in July or August, the maximum light intensity at the sunny noon would not be higher than 1400 $\mu\text{molm}^{-2}\text{s}^{-1}$ (Li, 1990). The comparison of the light and temperature conditions required for its higher photosynthetic ability and the limited solar radiation in Jiangsu showed that the key factor restricting *E. crassipes* growth in the region has always been the photosynthetic limitation (such as stomatal limitation), which may be the main reason that impedes its intrinsic high photosynthetic capacity and finally affects its dry matter accumulation.

Temperature is also a key environmental factor that determines its growth and physiological states. Studies have shown that *E. crassipes* can usually live at temperatures not lower than 5°C. If the water temperature drops to the freezing point, it will die within a few hours. If the air temperature is not lower than 7°C, it can survive the winter. 39-40°C are the highest air temperatures for its growth. But when the water temperature is above 35°C for 5 - 6 h, its growth would be severely inhibited, resulting in yellow or wilted leaves (An et al., 2007). The results in this paper further show that the optimal tempe-

rate for its photosynthesis is between 30-35°C, indicating a high consistency between the temperature for its most vigorous growth and that for its maximal photosynthetic ability. In fact, *E. crassipes* grows in Jiangsu from early April to mid-October, at which time, the average air temperature is between 21.5-23.5°C. It can be seen that the air temperature in this region is suitable for its rapid growth, but not good enough for its maximal photosynthesis, so it limits its largest dry matter accumulation to a certain extent.

In conclusion, the natural light intensity and temperature conditions in Jiangsu are suitable for *E. crassipes* to rapidly grow, but not high enough for it to reach the maximal intrinsic photosynthetic capacity, resulting in its low biomass in this region. In future, when *E. crassipes* is bred with the extensive adaptability to light and temperature conditions, it would be beneficial for it to make good use of the local light and temperature to achieve the maximum photosynthetic capacity, which is one of the decisive issues for its high-yield cultivation in the region.

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