DOI: 10.1007/s11099-013-0009-2 PHOTOSYNTHETICA 51 (1): 127-138, 2013

Interactive effects of temperature and light intensity on photosynthesis and antioxidant enzyme activity in *Zizania latifolia* Turcz. plants

N. YAN[*], X.-F. XU[*], Z.-D. WANG[*], J.-Z. HUANG[**], and D.-P. GUO[*,+]

Department of Horticulture, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China[*]
Institute of Nuclear-Agricultural Sciences, Zhejiang University, Hangzhou 310029, P.R. China[**]

Abstract

We compared the interactive effects of temperature and light intensity on growth, photosynthetic performance, and antioxidant enzyme activity in *Zizania latifolia* Turcz. plants in this study. Plants were grown under field (average air temperature 9.6–25°C and average light intensity 177–375 W m^{-2}) or greenhouse (20–32°C and 106–225 W m^{-2}) conditions from the spring to the early summer. The results indicated that greenhouse-grown plants (GGP) had significantly higher plant height, leaf length, and leaf width, but lower leaf thickness and total shoot mass per cluster compared with field-grown plants (FGP). Tiller emergence was almost completely suppressed in GGP. Significantly higher chlorophyll (Chl) content and lower Chl *a*/*b* ratio were observed in GGP than in FGP. From 4 to 8 weeks after treatment (WAT), net photosynthetic rate (P_N) was significantly lower in FGP than in GGP. However, from 9 to 12 WAT, P_N was lower in GGP, accompanied by a decrease in stomatal conductance (g_s) and electron transport rate (ETR) compared with FGP. Suppressed P_N in GGP under high temperature combined with low light was also indicated by photosynthetic photon flux density (PPFD) response curve and its diurnal fluctuation 10 WAT. Meanwhile, ETR in GGP was also lower than in FGP according to the ETR - photosynthetically active radiation (PAR) curve. The results also revealed that GGP had a lower light saturation point (LSP) and a higher light compensation point (LCP). From 4 to 8 WAT, effective quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching (q_P), and ETR were slightly lower in FGP than in GGP. The activities of ascorbate peroxidase (APX), guaiacol peroxidase (POD), glutathione reductase (GR), superoxide dismutase (SOD), and malondialdehyde (MDA) content were significantly higher from 4 to 8 WAT, but lower from 10 to 12 WAT in FGP. However, catalase (CAT) activity was significantly lower in FGP from 4 to 8 WAT. Our results indicated that the growth and photosynthetic performance of *Z. latifolia* plants were substantially influenced by temperature, as well as light intensity. This is helpful to understand the physiological basis for a protected cultivation of this crop.

Additional key words: antioxidant enzymes; chlorophyll *a* fluorescence; chlorophyll content; photosynthetic gas exchange; temperature; *Zizania latifolia*.

Introduction

Temperature is a key parameter for plant growth and development. Under natural conditions, both high and low temperatures usually have damaging impacts on plant performance and productivity (Zinn *et al*. 2010), they significantly reduce yields and quality, and they can cease a production (Ruelland and Zachowski 2010).

Received 23 August 2011, *accepted* 8 November 2012.

[+] Corresponding author; tel: 86+571-88982796, fax: 86+571-88982796, e-mail: dpguo@zju.edu.cn

Abbreviations: APX – ascorbate peroxidase; AsA – ascorbic acid; C_i – intercellular CO_2 concentration; CAT – catalase; Chl – chlorophyll; DM – dry mass; *E* – transpiration rate; ETR – electron transport rate; FGP – field-grown plants; FM – fresh mass; F_0 – minimal fluorescence yield of the dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; GGP – greenhouse-grown plants; GR – glutathione reductase; g_s – stomatal conductance; LCP – light-compensation point; LSP – light-saturation point; MDA – malondialdehyde; NPQ – nonphotochemical quenching; PAR – photosynthetically active radiation; P_{Nmax} – light-saturated net photosynthetic rate; P_N – net photosynthetic rate; POD – guaiacol peroxidase; PPFD – photosynthetic photon flux density; PSII – photosystem II; q_P – photochemical quenching; ROS – reactive oxygen species; SOD – superoxide dismutase; WAT – weeks after treatment; Φ_{PSII} – effective quantum yield of PSII photochemistry.

Acknowledgements: This research was supported by the Special Fund for Agro-scientific Research in the Public Interest of China (No: 200903017-03).

Photosynthetic process appears to be one of the most temperature-sensitive processes in plants, and numerous changes in a structure and function of the photosynthetic apparatus can be caused by high or low temperature (Wahid *et al.* 2007). At high temperatures, photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplasts have been reported to be the primary sites of an injury (Berry and Björkman 1980, Wise *et al.* 2004), and photosynthetic activity can be inhibited by the inactivation of PSII thereby reducing ETR (Yamori *et al.* 2008). In addition, high temperatures also significantly decrease the activity of Rubisco, a key enzyme in the Calvin cycle (Weis 1981). Therefore, high temperature-induced deleterious effects are manifested by reduced metabolism, photosynthetic capacity and photochemical efficiency (Percival 2005, Guo *et al.* 2006). As a consequence, the plant growth is also affected due to reduced photosynthesis and carbon gain. Under field conditions, low temperatures are commonly experienced by plants during the growth in the early spring (Berry and Björkman 1980), which can greatly reduce their growth due to a decrease in photosynthetic capacity accompanied by reduced ETR and decreased rates of enzymatic reactions (Groom and Baker 1992, Allen and Ort 2001). The negative effect of low temperature on photochemical efficiency is more serious when combined with light stress that leads to photoinhibition (Groom and Baker 1992). For a plant, low temperatures affect the rate of the growth by weakening the uptake of water and nutrients, and consequently, the rates of photochemical processes need to adjust to the reduced metabolic sink capacity. Thus, the effects of low temperatures on photosynthesis and assimilates eventually determine a productivity and a growth of plants (Farage and Long 1991).

The light intensity is another important environmental factor affecting plant photosynthesis. Under conditions of reduced light, plants exhibit relatively lower P_N, and reduced light-saturated net photosynthetic rate (P_{Nmax}), Φ_{PSII}, and ETR (Zheng *et al.* 2011). However, high light usually causes an imbalance between an energy supply and energy consumption, which generally leads to the photoinhibition (Demmig-Adams and Adams 1992).

Reactive oxygen species (ROS) are believed to be the major free radicals leading to cell damage in plants (Laloi *et al.* 2004). They are able to initiate a range of metabolic changes, such as reduced enzyme activities and a decrease in the photosynthetic rate (Dizengremel *et al.* 2008). ROS are formed in many cellular processes in a response to a variety of stress factors, such as, *e.g.* temperature stress (Perelman *et al.* 2006, Wahid *et al.* 2007). ROS induce an oxidative damage at the molecular and cellular level; they can be detoxified or removed by several antioxidant enzymes, such as APX, CAT, POD, and SOD. Under low temperatures, some antioxidant enzyme activities, such as APX, POD, GR, and SOD are observed to increase (Lee and Lee 2000, Turan and Ekmekçi 2011). Thus, the improvement of a temperature stress tolerance is often regarded as being related to the enhanced activities of antioxidant enzymes in plants (Almeselmani *et al.* 2006). In plant, MDA is the indicator of a lipid peroxidation and plant oxidative stress (Salin 1988, Turan and Ekmekçi 2011).

In China, a perennial plant of Graminaceae family, *Z. latifolia*, forms after the infection by *Ustilago esculenta* the swollen culm that has been used as a vegetable for several centuries (Zhang *et al.* 2012). The growth period of this crop usually lasts from early February to December in Hangzhou, and the yield of this crop as a vegetable is determined to a great extent by the number of tillers forming swollen culms. However, under paddy field conditions, some of the culms of plants (tillers) are unable to swell because of the relatively short growth period. Therefore, an early and vigorous plant growth is obviously important for the formation of culms capable of swelling during a cultivation. In order to increase the earliness and higher profitability of this crop, a plastic tunnel cultivation is adopted and becomes one of the efficient methods to promote the growth of overwintering buds and subsequent culm swelling in summer-harvest variety in China.

One of the most important features of such a protected cultivation is a high temperature, which is often prevailing in the late spring. It was found that the temperature increase over the range of 10–25°C stimulated the production of leaves and tillers in wheat, which was attributable to the increased assimilate supply (Friend 1965). Higher temperatures, however, can reduce the tiller number (Ryle 1964), especially, when combined with low light intensities due to decreased assimilate supply and utilization (Hunt and Thomas 1985). Previous study also showed that temperature beyond optimum may decrease photosynthesis, and in turn, reduce plant growth and biomass (Qaderi and Reid 2009). Although the physiological effects of temperatures are fairly well understood (Wahid *et al.* 2007, Ruelland and Zachowski 2010), the effects of temperature on the growth and photosynthesis of *Z. latifolia* are scarcely reported (Zhang 1991a,b). It is unclear how the temperature-dependent growth of *Z. latifolia* plants changes under the greenhouse conditions and how photosynthesis is affected. These basic physiological data could contribute to the greenhouse cultivation of this crop for early harvest and high yield.

The aim of this experiment was to investigate the interacting effects of temperature and light on the plant growth, photosynthesis, and antioxidant enzyme activity of *Z. latifolia.* For this purpose, the growth parameters, Chl content, photosynthetic gas exchange, Chl *a* fluorescence, and antioxidant enzyme activities of GGP- and FGP were measured.

Materials and methods

Plant materials and growth conditions: Sixteen clusters of *Z. latifolia* (cv. Zhejiao No.2, a double-harvest variety from the Experimental Station of Zhejiang University), each having 10 tillers and a height of 10–15 cm, were transplanted into 16 plastic containers (about 15 L) filled with a nursery soil mixture, and then they were placed in the field on February 13. The same number of the plants in plastic containers were placed in a neighbouring greenhouse. These plants were regularly watered to keep a 5–10 cm layer of water above the soil. Greenhouse climate was monitored and controlled by a *Priva-Integro Control System* (*P721*, *Priva*, The Netherlands). The temperature and light intensity in the field and in the greenhouse are presented in Table 1. Measurements were made in 2 experimental sets of plants, grown in the spring of 2011 and 2012.

Table 1. Temperature and light intensity (means) in field and greenhouse recorded in the experiment. Air temperature averages were weekly averages of the day and night temperatures, respectively.

			Week after treatment								
			4	5	6	7	8	9	10	11	12
Air temperature [°C]	Field	Day	12	15	15	15	18	25	22	21	24
		Night	9.6	12	12	12	14	20	19	19	21
	Greenhouse	Day	25	25	25	25	26	32	28	26	27
		Night	21	21	21	21	20	23	22	22	22
Light intensity [W m^{-2}]	Field		245	180	177	189	261	375	258	179	258
	Greenhouse		147	108	106	113	157	225	155	108	155

Morphological index: The plant height, number of leaves, leaf length, leaf width of the third fully expanded leaf from the top and tiller number were measured weekly from 4 WAT and thereafter until the end of the experiment. Leaf thickness, fresh mass (FM) per tiller, FM per cluster, dry mass (DM) per tiller and DM per cluster were measured 12 WAT. DM was determined after drying of plant material at 80°C for 96 h.

Chl content: About 1 g of the third fully-expanded leaves from different plants was extracted in 80% acetone after grounding. Chl *a* and *b* were estimated with a spectrophotometer (*Shimadzu UV-2410*, Kyoto, Japan) by the procedure described by Lichtenthaler (1987).

Gas-exchange measurements: P_N, g_s, intercellular CO_2 concentration (C_i), and transpiration rate (E) in the third fully expanded leaves were measured with a portable photosynthesis system (*LI-6400*, *LI-COR*, Lincoln, USA) at 25°C under artificial light of 1,200 μmol m^{-2} s^{-1}, relative humidity of 45%, and CO_2 concentration of 350 ppm. Measurements were carried out at 09:00–11:00 h or 15:00–17:00 h on sunny days.

Light-response curves for the third fully expanded leaves were obtained by varying the photosynthetic photon flux densities (PPFD) from 2,000 μmol m^{-2} s^{-1} to zero and a leaf equilibration in a measuring chamber for 3 min. The light-response curves were then adjusted according to the equation of Prado and de Moraes (1997): $P_N = P_{Nmax}\ [1 - e^{k(Qc-Q)}]$, where Qc is the LCP, Q is the PPFD, and k is the constant of adjustment. LSP at 90% P_{Nmax} was also obtained from the equation above.

Chl fluorescence: Chl *a* fluorescence parameters of the third fully expanded leaves were measured with *Chl Fluorescence System M-Series Imaging-PAM* (*Walz*, Effeltrich, Germany) after the leaves were dark-adapted at room temperature (25°C) for 30 min. After dark adaptation, the plants were successively illuminated at an intensity of 0.5 μmol m^{-2} s^{-1} for the measurement of the minimal fluorescence yield of dark-adapted state (F_0), with a saturating pulse of intensity 2,800 μmol m^{-2} s^{-1} for the measurement of the maximal fluorescence yield of dark-adapted state (F_m), followed by the calculation of variable fluorescence $F_v = F_m - F_0$ and maximal quantum yield of PSII photochemistry $F_v/F_m = (F_m - F_0)/F_m$ (Krause and Weis 1991). Φ_{PSII}, q_P, ETR, and nonphotochemical quenching (NPQ) were followed after the cessation of the actinic light of 146 μmol m^{-2} s^{-1}, using saturating pulses added periodically for 5 min. Φ_{PSII}, NPQ, q_P, and ETR were exported by the software *Imaging-WIN*. The $q_P = (F_m' - F_s)/(F_m' - F_0')$ and $NPQ = 1 - (F_m' - F_0')/(F_m - F_0)$ were calculated according to Van Kooten and Snel (1990), where F_m' is maximal fluorescence yield of the light-adapted state and F_0' is minimal fluorescence yield of light-adapted state. The $\Phi_{PSII} = (F_m' - F_s)/F_m'$ was calculated as defined by Genty *et al.* (1989) and ETR was calculated as follows: $ETR = (F_m' - F_s)/F_m' \times PAR \times 0.5 \times 0.84$, where F_s is steady-state fluorescence yield. The response curves of ETR *vs.* PAR were obtained by varying PAR from 700 μmol m^{-2} s^{-1} to zero, because photosynthesis of the two experimental plants was saturated below 700 μmol m^{-2} s^{-1}. The ETR-PAR curves were adjusted by applying the equation: $ETR = ETR_{max}\ (1 - e^{-kQ})$, where ETR_{max} is the maximal ETR .

Antioxidant enzyme activity: For the enzyme assays, 0.15 g of the third fully-expanded leaves were ground with 1.5 mL of ice-cold 50 mM HEPES buffer (pH 7.8) containing 0.2 mM EDTA, 2 mM ascorbic acid (AsA), and 2% PVP (w/v). The homogenates were centrifuged at 4°C for 20 min at 12,000 × *g*, and the resulting supernatants were used for the spectrophotometric determination of enzymatic activity. APX (EC 1.11.1.11) activity was measured at 290 nm according to the method of Nakano and Asada (1981). CAT (EC 1.11.1.6) activity was determined at 240 nm by using the method of Patra *et al.* (1978). POD (EC 1.11.1.7) activity was assayed at 470 nm by using the method of Lee and Lee (2000). GR (EC 1.6.4.2) activity was measured at 340 nm according to Foyer and Halliwell (1976). SOD（EC 1.15.1.1）activity was assayed at 560 nm following the method of Stewart and Bewley (1980). All spectrophotometric analyses were conducted on a spectrophotometer *UV-2410* (*Shimadzu*, Kyoto, Japan).

Lipid peroxidation: Oxidative damage to lipids was estimated by measuring the content of MDA in leaf homogenates, prepared with 10% TCA. Samples were mixed with 10% TCA containing 0.65% 2-thiobarbituric acid (TBA) and heated at 95°C for 25 min, as described by Stewart and Bewley (1980).

Statistical analyses were performed with *SPSS software*. All the data were subjected to analysis of variance (*ANOVA*) and the significance of *Tukey*'s test was determined at 5% level.

Results

Plant growth: Influence of temperature and light intensity on plant growth was reflected by the changes of plant height, leaf growth, and tiller number (Fig. 1*A*). The plant height increased in GGP compared with FGP. In early March, the plant height (21/25°C) was 327% higher than that of FGP (9.6/12°C) 4 WAT. Afterwards, the plant height increased with the further growth of plant and the temperature rise, and only 54.4% increase in plant height was observed in GGP 12 WAT(Fig. 1*A*).

A number of leaves was apparently higher in GGP than in FGP ($p>0.05$) (Fig. 1*B*). Although the number of leaves was different, there was no difference in a new leaf development rate between both two treatments. For example, the number of leaves was 3.6, 4.0 at 4 WAT, respectively, and it was 8.75 and 9.45 in FGP and GGP at 12 WAT, respectively.

The leaf length and leaf width significantly increased in GGP compared with FGP (Fig. 1*C*,*D*). At 12 WAT, the leaf length and leaf width exhibited an enhancement of 56.7% and 31.9%, respectively, but the leaf thickness was reduced by 49.1% in GGP. Meantime, the FM and DM per cluster were reduced by 14.2% and 12.0% in GGP compared with FGP (Table 2).

Table 2. Fresh mass (FM) and dry mass (DM) per tiller, FM and DM per cluster, and leaf thickness of *Zizania latifolia* plants grown in field and greenhouse 12 week after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$.

	12 weeks after treatment Field	 Greenhouse
FM [g tiller^{-1}]	25.71 ± 3.34*	48.94 ± 9.52
DM [g tiller^{-1}]	4.03± 0.51*	12.92 ± 2.64
Leaf thickness [mm]	0.55 ± 0.08	0.28 ± 0.04*
FM [g cluster^{-1}]	325.04 ± 10.10	279.8 ± 9.21*
DM [g cluster^{-1}]	56.21 ± 2.98	49.53± 2.41*

A tiller number was the most significantly affected by the greenhouse cultivation. Tillering was almost completely suppressed in GGP (under the average night temperature higher than 20°C) compared with FGP (Fig. 1*E*). The tiller number in GGP increased from 10 at 4 WAT to 10.2 at 12 WAT, while it reached 25.4 at 12 WAT in FGP.

Photosynthetic gas exchange: As the leaf extension proceeded and the temperature rose from 4 to 11 WAT, P_N and g_s increased in FGP, while those parameters were relatively stable in GGP throughout the period of our experiment except for a decrease 9 WAT (Fig. 2*A*,*B*). From 4 to 8 WAT, P_N, g_s, and E were higher, but C_i was lower in GGP than in FGP. However, from 9 to 12 WAT, P_N and g_s were lower, but C_i was higher in GGP (Fig. 2*A*,*B*,*C*).

The light response curve obtained 10 WAT, showed that P_{Nmax} was much lower in GGP than in FGP, *i.e.* 16.8 *vs.* 22.9 μmol(CO$_2$) m^{-2} s^{-1}. Moreover, LSP was 970 and 1,210 μmol m^{-2} s^{-1} for GGP and FGP, respectively. However, LCP was higher in GGP compared with FGP, *i.e.* 55.4 *vs.* 34.5 μmol m^{-2} s^{-1} (Fig. 3).

Diurnal variation in gas-exchange parameters indicated that P_N, g_s and E were significantly lower in GGP than in FGP (Fig. 4*A*,*B*,*D*). By contrast, the plants had higher C_i when grown in the greenhouse (Fig. 4*C*).

The relationship between P_N and g_s, as well as between P_N and E in both types of plants was estimated (Fig. 5). A close correlation between P_N and g_s was found for GGP ($P_N = 37.2\ g_s + 2.82$, $r^2 = 0.895$, $p<0.001$) and FGP ($P_N = 38.8\ g_s + 1.87$, $r^2 = 0.969$, $p<0.001$) (Fig. 5*A*). At the same time, there was also a close correlation between P_N and E in GGP ($P_N = 1.90\ E + 6.43$, $r^2 = 0.658$, $p<0.001$) and FGP ($P_N = 2.74\ E + 1.78$, $r^2 = 0.940$, $p<0.001$) (Fig. 5*B*).

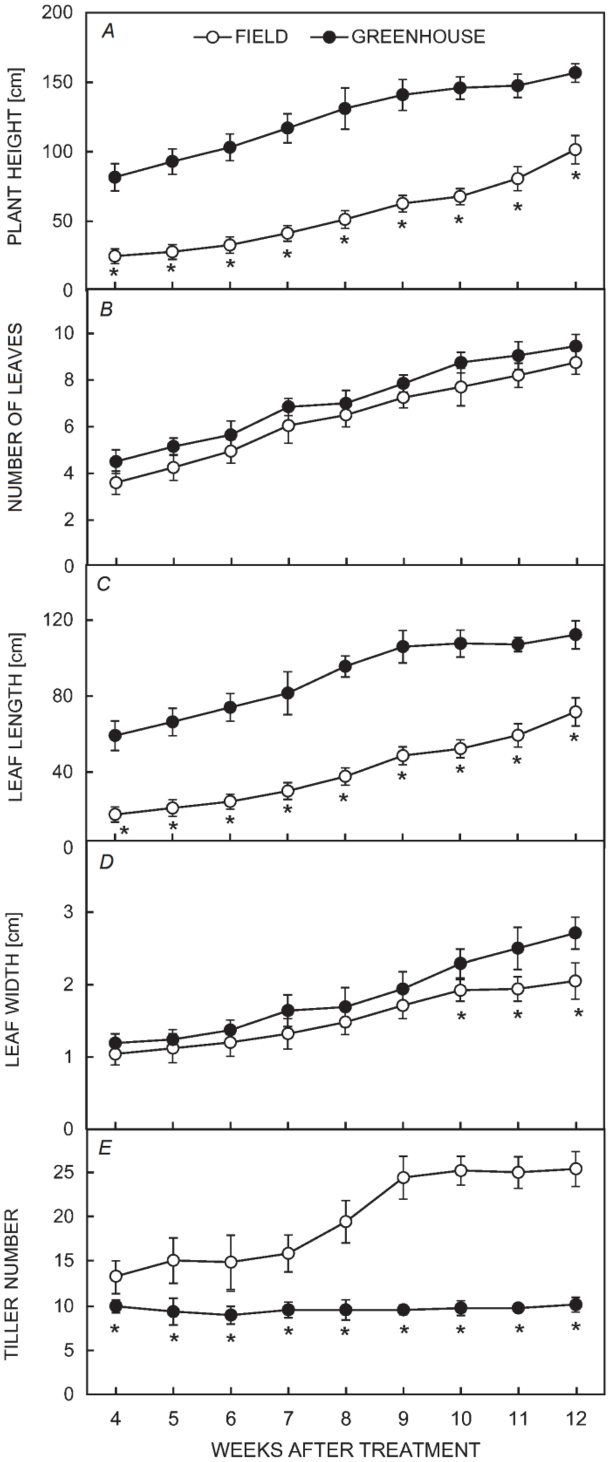

Fig. 1. Plant height (*A*), number of leaves (*B*), leaf length (*C*), leaf width (*D*), and tiller number (*E*) of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) from 4 to 12 weeks after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$.

Chl content and Chl fluorescence: Chl *a* and *b* were higher, but Chl *a/b* ratio was lower in leaves of GGP compared with FGP from 4 to 12 WAT (Table 3).

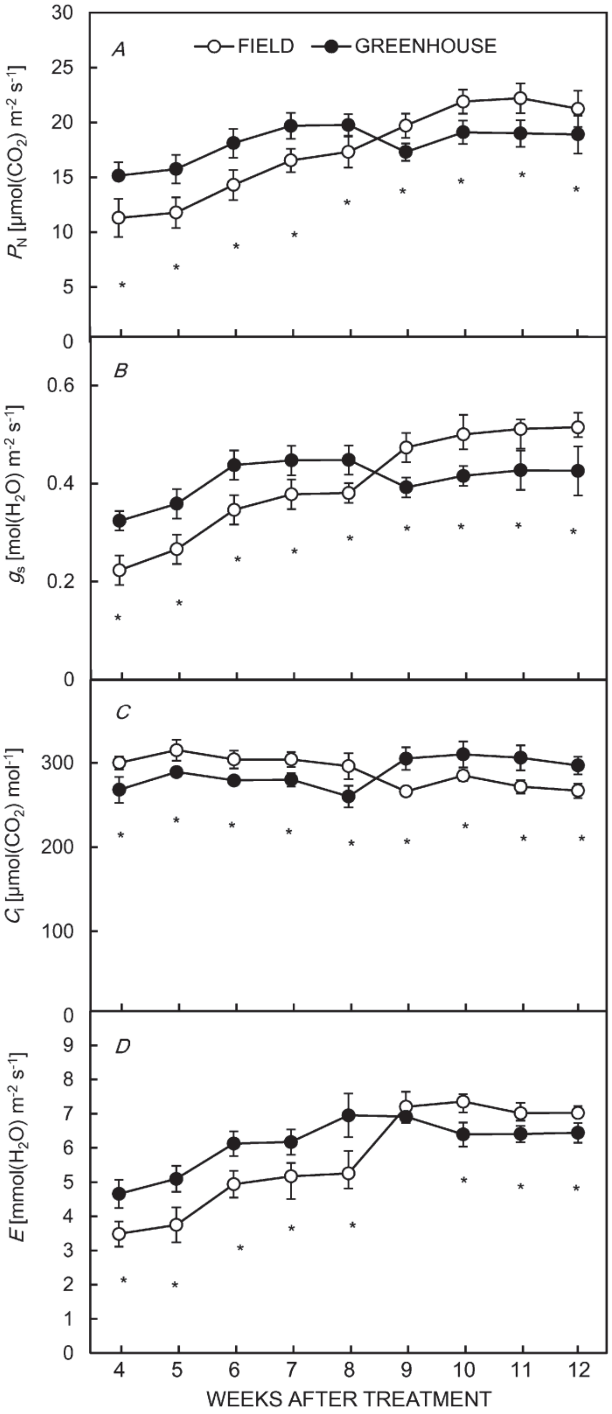

Fig. 2. Net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*), intercellular CO$_2$ concentration (C_i) (*C*), and transpiration rate (*E*) (*D*) in leaves of *Zizania latifolia* plants grown in the field (*open circle*) and in the greenhouse (*closed circle*) from 4 to 12 weeks after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$.

From 4 to 8 WAT, F_v/F_m was significantly lower in FGP than in GGP (Fig. 6*A*). As the temperature rose during the growth of plants, F_v/F_m also increased in FGP,

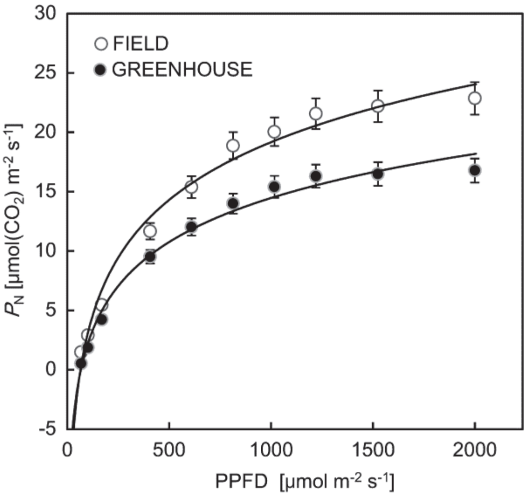

Fig. 3. Photosynthetic photon flux density (PPFD) response curve of net photosynthetic rate (P_N) in leaves of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) 10 weeks after treatment. Values are means ± SE ($n = 6$). Measurements were made at 25°C under relative humidity of 45%, CO_2 concentration of 350 ppm and from 0 to 2,000 μmol m^{-2} s^{-1} PPFD.

and a difference in F_v/F_m between both treatments became indistinguishable from 9 to 12 WAT (Fig. 6*A*). Φ_{PSII}, q_P, and ETR were slightly higher from 4 to 8 WAT, but they were moderately lower from 10 to 12 WAT in GGP (Fig. 6*B*,*D*,*E*). By contrast, NPQ showed a different trend; it was slightly lower from 4 to 8 WAT, but higher from 10 to 12 WAT in GGP (Fig. 6*C*).

The saturations of ETR required about 480 and 590 μmol m^{-2} s^{-1} PAR at 10 WAT for GGP and FGP, respectively (Fig. 7). When PAR ranged from 0 to 146 μmol m^{-2} s^{-1}, there was no significant difference in ETR between GGP and FGP. However, the significant difference between both treatments was observed in ETR when PAR ranged from 200 to 700 μmol m^{-2} s^{-1}.

Antioxidant enzyme activity and lipid peroxidation: From 4 to 8 WAT, the activities of APX, POD, GR, and SOD were higher, but CAT activity was lower in FGP compared with GGP ($p<0.05$). However, GGP exhibited higher activities of APX, CAT, POD, GR, and SOD ($p>0.05$) 10 and 12 WAT (Fig. 8*A*–*E*).

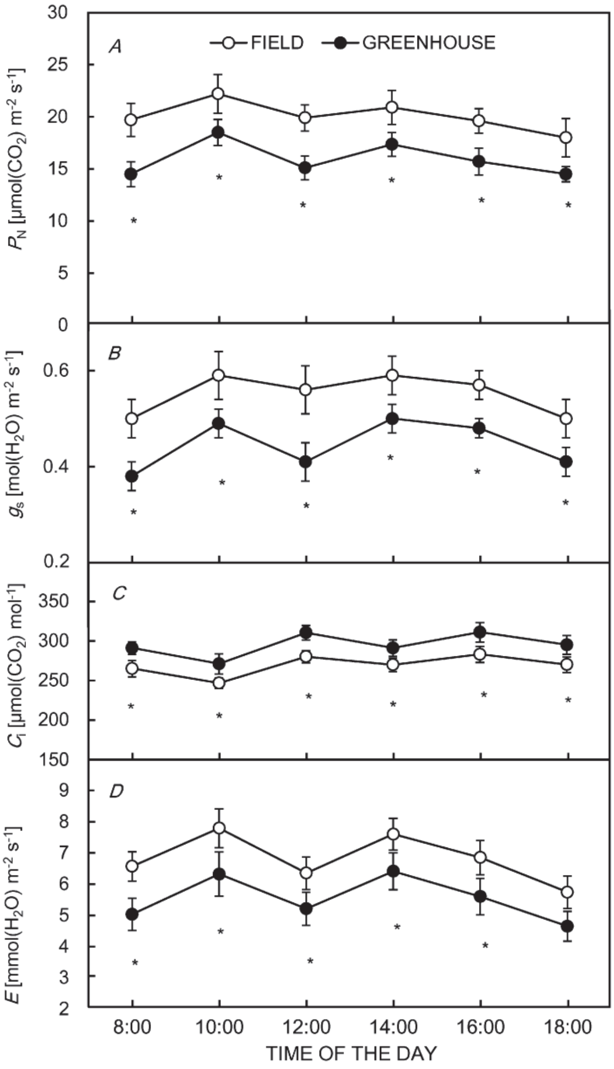

Fig. 4. Diurnal fluctuation in net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*), intercellular CO_2 concentration (C_i) (*C*), and transpiration rate (E) (*D*) in leaves of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) 10 weeks after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$.

From 4 to 8 WAT, MDA content was lower in GGP than in FGP, while, from 10 to 12 WAT, there was no great difference in MDA content between both types of the plants (Fig. 8*F*).

Discussion

Plant growth: Low-temperature treatments and/or large average temperature differences, especially combined with a low light, inhibited typically the plant growth. Our temperature data showed that FGP were exposed to low temperatures and wide diurnal temperature ranges (Table 1). There is no surprise that the growth of plants was found to respond directly to changes of temperature and light intensity. Such a growth response has been well characterized for other crop species including wheat (Bos and Neuteboom 1998), ryegrass (Hunt and Thomas1985), and stem mustard (Guo *et al.* 1994). In the present study, temperature combined with a light intensity significantly affected morphological characteristics of *Z. latifolia*, such as the number of leaves, the plant height, the leaf length

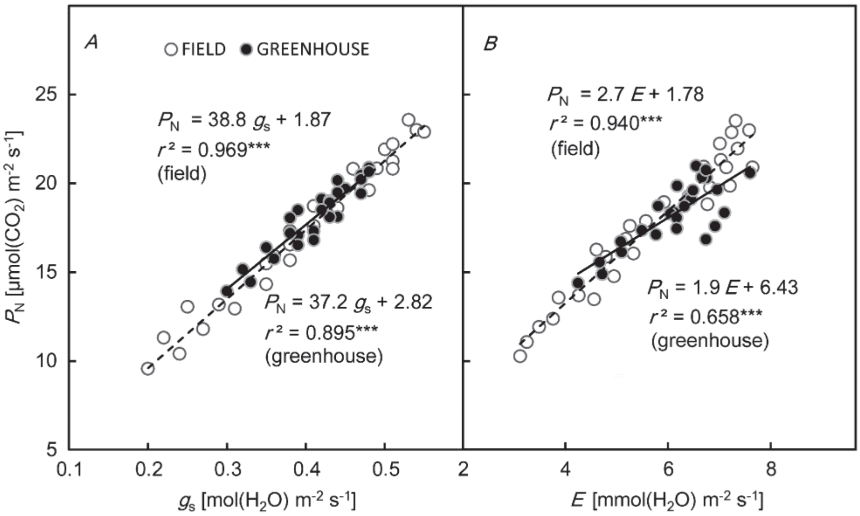

Fig. 5. The relationships between net photosynthetic rate (P_N) and stomatal conductance (g_s) (*A*), and between P_N and transpiration rate (E) (*B*) in leaves of *Zizania latifolia* plants grown in field (*open circle*, *dashed line*) and greenhouse (*closed circle*, *solid line*). *** – $p<0.001$.

Table 3. Chlorophyll (Chl) *a*, Chl *b*, total Chl content, and Chl *a/b* ratio in leaves *of Zizania latifolia* plants grown in field and greenhouse from 4 to 12 weeks after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$. FM – fresh mass.

Week after treatment	Chl *a* [mg g^{-1}(FM)] Field	Greenhouse	Chl *b* [mg g^{-1}(FM)] Field	Greenhouse	Total Chl [mg g^{-1}(FM)] Field	Greenhouse	Chl *a/b* Field	Greenhouse
4	1.29 ± 0.05*	2.59 ± 0.05	0.44 ± 0.02*	0.95 ± 0.02	1.73 ± 0.07*	3.54 ± 0.07	2.91 ± 0.05	2.72 ± 0.03*
5	1.40 ± 0.16*	2.65 ± 0.02	0.49 ± 0.05*	0.98 ± 0.02	1.89 ± 0.21*	3.63 ± 0.04	2.87 ± 0.06	2.70 ± 0.03*
6	1.35 ± 0.12*	2.69 ± 0.14	0.46 ± 0.06*	0.97 ± 0.04	1.81 ± 0.18*	3.66 ± 0.18	2.95 ± 0.06	2.76 ± 0.05*
7	1.38 ± 0.12*	2.86 ± 0.14	0.46 ± 0.06*	1.04 ± 0.04	1.85 ± 0.18*	3.91 ± 0.18	2.99 ± 0.06	2.76 ± 0.09*
8	1.44 ± 0.18*	2.84 ± 0.28	0.48 ± 0.07*	1.05 ± 0.10	1.93 ± 0.25*	3.89 ± 0.38	2.99 ± 0.04	2.70 ± 0.03*
9	1.84 ± 0.05*	2.83 ± 0.23	0.65 ± 0.06*	1.06 ± 0.08	2.49 ± 0.11*	3.89 ± 0.31	2.83 ± 0.04	2.66 ± 0.06*
10	1.94 ± 0.18*	2.74 ± 0.28	0.65 ± 0.07*	1.02 ± 0.10	2.59 ± 0.25*	3.76 ± 0.38	2.98 ± 0.06	2.69 ± 0.05*
11	2.17 ± 0.08*	2.65 ± 0.26	0.75 ± 0.04*	0.99 ± 0.08	2.94 ± 0.12*	3.65 ± 0.34	2.91 ± 0.05	2.67 ± 0.04*
12	2.11 ± 0.20*	2.66 ± 0.17	0.72 ± 0.08*	1.02 ± 0.07	2.83 ± 0.28*	3.68 ± 0.24	2.93 ± 0.10	2.62 ± 0.03*

the leaf width, and especially the tiller number (Fig. 1). In a previous study, it has been reported that under field conditions, the overwintering axillary buds of *Z. latifolia* broke dormancy, when the average air temperature rose above 5°C, and then it might grow into a tiller (Ding *et al.* 1993). The results of the present study indicated that the tiller emerged mainly in FGP during the period of 7 to 8 WAT, when the average air temperature approached 18°C, while the emergence of new tillers was almost completely suppressed under the greenhouse conditions, where the average day temperature was generally above 25°C, in spite of the increased growth in terms of plant growth characteristics compared with the plants grown in the field (Fig. 1, Table 1). These observations coincided with the reports by Zhang (1991a,b) that tillering was suppressed, when average temperature was over 28°C in a field. In this study, the reduced tiller number in GGP might be caused, at least partially, by a reduced endogenous cytokinin content, especially, of free cytokinins, in plant tissues, which could result from a high temperature exposure (Guo *et al.* 1994, Chou *et al.* 2000). In addition, lower light in the greenhouse could be another causal factor for reduced number of tillers since a high temperature together with a low irradiation suppressed the tiller number in wheat (Bos and Neuteboom 1998). Therefore, it is crucial to maintain a proper temperature, *ca.* 5–25°C, for tiller outgrowth during protected cultivation of *Z. latifolia*.

The FM and DM per cluster, which represent the whole above-ground plant biomass, were much lower in GGP than in FGP (Table 2). This was clearly due to much fewer tillers and thinner leaves in GGP (Fig.1, Table 2). Although a single leaf photosynthesis seemed to be higher in GGP during the early stages, the overall canopy photosynthesis appeared to be lower due to fewer tillers, leading to a reduced overall biomass. In this experiment, the reduced leaf thickness and prolonged leaf length were also an phenomenon usually observed under greenhouse

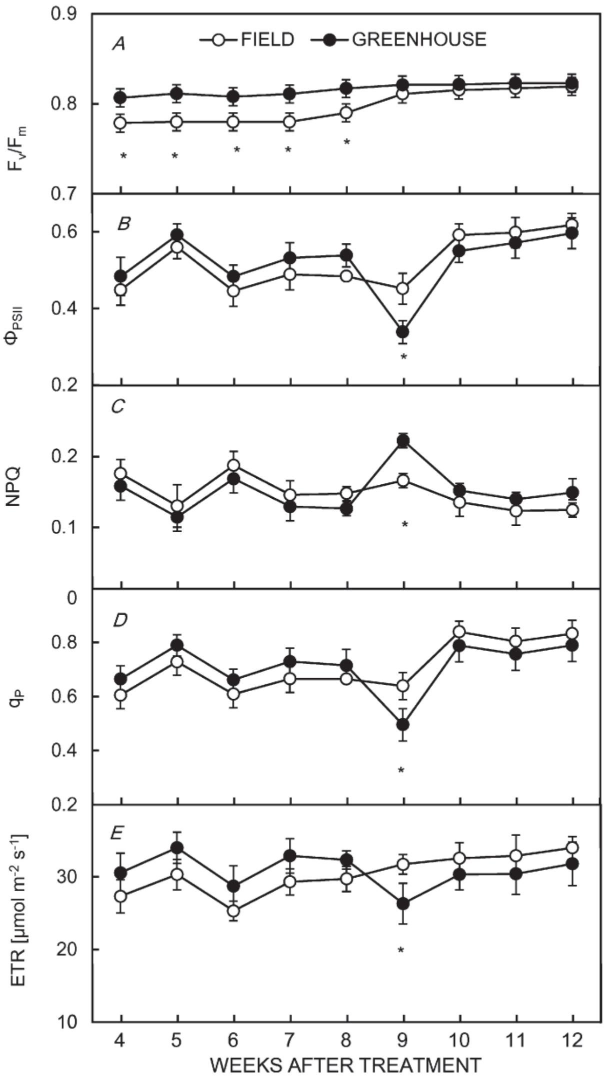

Fig. 6. Maximal quantum yield of PSII photochemistry (F_v/F_m) (*A*), effective quantum yield of PSII photochemistry (Φ_{PSII}) (*B*), nonphotochemical quenching (NPQ) (*C*), photochemical quenching (q_P) (*D*), and electron transport rate (ETR) (*E*) in leaves of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) from 4 to 12 weeks after treatment. Values are means ± SE ($n = 6$). * – $p<0.05$.

conditions with a higher temperature and lower light intensity (Ballantine and Forde 1970, Hunt and Thomas 1985, Korner and Diemer 1987).

Temperature is the primary factor controlling the leaf appearance rate, with a number of leaves, often linearly related to accumulated thermal units (McMaster *et al.* 2003). In this study, unexpectedly, the leaf appearance rate was not higher in GGP than in FGP except for 4 WAT, when GGP had relatively more rapid leaf appearance. Since the leaf extension in GGP was clearly enhanced (Fig. 1, Table 2), the apparent insensitive response of a leaf emergence to temperature seemed to be attributed to a weak light under the greenhouse conditions (Bos and Neuteboom 1998).

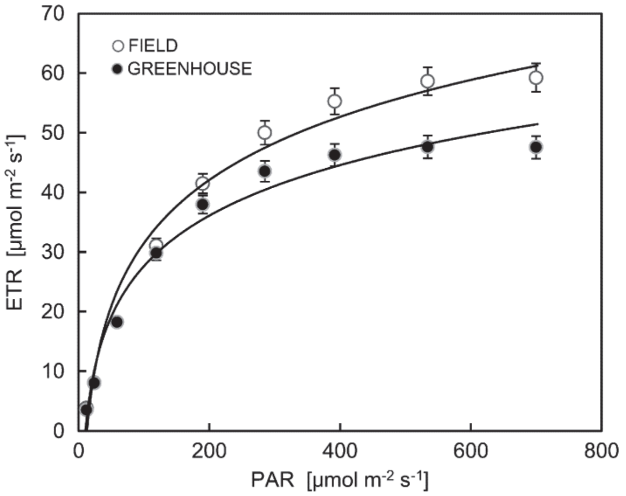

Fig. 7. Photosynthetically active radiation (PAR) response curves of electron transport rate (ETR) in leaves of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) 10 weeks after treatment. Values are means ± SE ($n = 6$). Measurements were made under 25°C and from 0 to 700 μmol m^{-2} s^{-1} PAR.

Photosynthetic gas exchange: In plants, photosynthetic response to changes of the temperature depends on various aspects (Silim *et al.* 2010). At low temperatures, plants usually showed a decrease in photosynthesis (Martin *et al.* 1981). However, high temperature generally caused a limitation to the carbon assimilation, especially at temperatures over 40°C (Pastenes and Horton 1996). In this study, from 4 to 8 WAT, P_N, g_s, and E were higher in GGP compared with FGP (Fig. 2). It is clear that higher P_N (Table 1) was directly related to the higher temperature under the greenhouse conditions (Yamasaki *et al.* 2002), while lower P_N in FGP during this period was due to the low temperature, which induced a decrease in g_s and E (Fig. 2) (Islam *et al.* 2011). Moreover, higher C_i in FGP suggested that g_s was not responsible for decreased CO_2 uptake (Fig. 2*C*), implying that the capacity of the mesophyll to assimilate CO_2 was impaired. This observation is consistent with the results reported by Mooney *et al.* (1978) that low temperature increased C_i. From 9 to 12 WAT, P_N in GGP decreased significantly, when the average day temperature rose above 26°C (Table 1, Fig. 2*A*). Although g_s decreased in parallel to a high temperature, the decreased P_N at high temperature might not be caused by g_s (Fig. 2*B*), but it was possibly induced by reduced ETR and a decreased ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Weis 1981, Salvucci *et al.* 2001, Wise *et al.* 2004, Silim *et al.* 2010).

We found that P_{Nmax} was much lower in GGP compared with FGP 10 WAT, as shown by light-response curve (Fig. 3). This might be in part due to thinner leaves, which had a reduced light capture capacity (Table 2) (Berry and Björkman 1980). However, GGP had higher

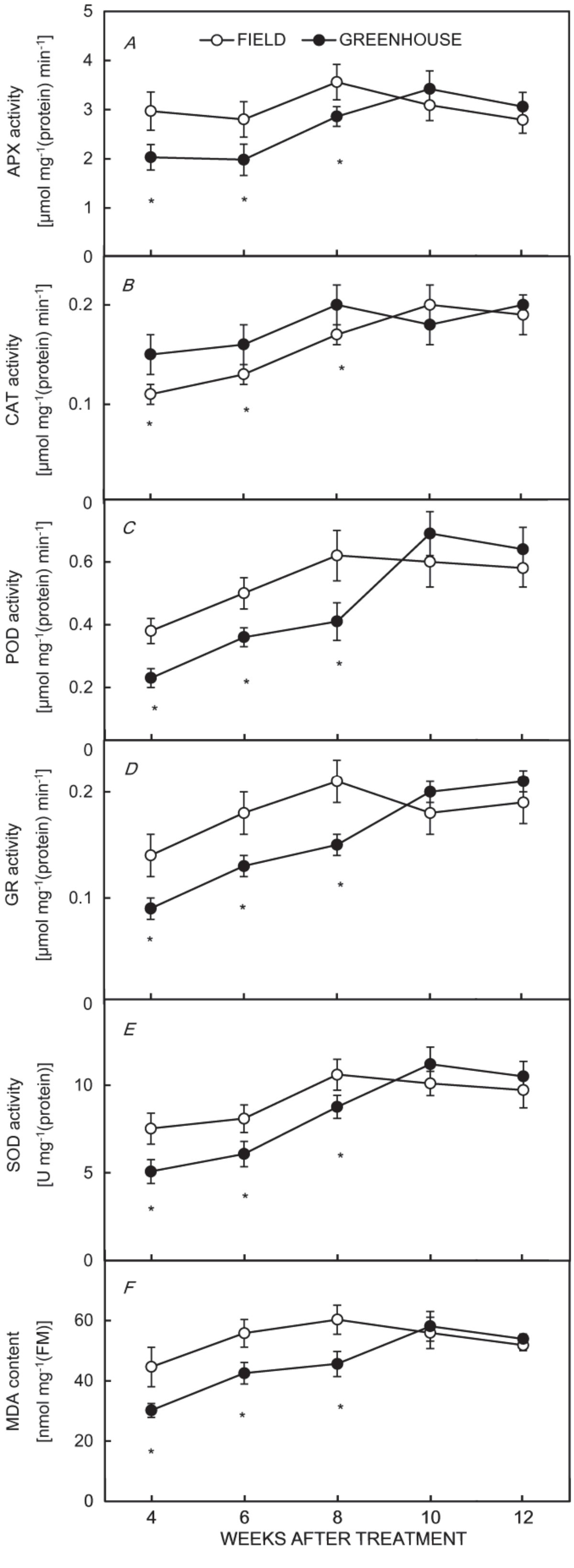

Fig. 8. Activities of ascorbate peroxidase (APX) (*A*), catalase (CAT) (*B*), guaiacol peroxidase (POD) (*C*), glutathione reductase (GR) (*D*), superoxide dismutase (SOD) (*E*), and malondialdehyde (MDA) content (*F*) in leaves of *Zizania latifolia* plants grown in field (*open circle*) and greenhouse (*closed circle*) from 4 to 12 weeks after treatment. Values are means ± SE (n = 6). FM – fresh mass. * – $p<0.05$.

LCP, implying that they were capable of using energy of a lower light compared with FGP (Fig. 3). Similar phenomenon was also reported by Zheng *et al.* (2011). The plants grown under 60% of solar irradiance had lower P_N compared with plants grown under 100% irradiance. Meanwhile, in this study, higher temperature might be another factor causing a significant reduction in P_N from 9 to 12 WAT; this inhibition of photosynthesis by high temperature was also observed by Guo *et al.* (2006). Therefore, decreased P_N from 9 to 12 WAT was not only caused by the high temperature, but also related to the low light intensity.

We observed that there was a small midday depression of P_N in GGP and FGP (Fig. 4*A*); such a phenomenon was also reported in rice (Ishihara and Saitoh 1987). Moreover, a midday decrease in g_s occurred also in our plants (Fig. 4*B*). However, our results indicated that a limitation of CO_2 availability by stomata closure was unlikely to be the cause of the midday depression of P_N, since C_i remained in plants relatively higher at noon (Fig. 4*C*). The results suggested that a decrease in ribulose-1,5-bisphosphate (RuBP) content caused by a high temperature may be the major factor responsible for the midday depression of P_N (Tenhunen *et al.* 1984).

Chl content and Chl fluorescence: Chl content was proportional to the temperature and inversely related to the light intensity (Ballantine and Forde 1970). In this study, we observed that GGP had much higher Chl content under conditions of high temperature and relatively lower light intensity (Tables 1,3). Furthermore, the reduction in Chl *a*/*b* ratio found in these plants might be attributed to a lower light (Tables 1,3), because it decreased typically, when plants were subjected to a low light intensity (Zheng *et al.* 2011). Meanwhile, Chl *a*/*b* ratio was relatively steady in GGP, indicating that the plants were acclimated to the light conditions.

In this study, from 4 to 8 WAT, F_v/F_m in FGP was lower compared with GGP (Fig. 6*A*). It suggests that photoinhibition of photosynthesis in these plants occurred due to low temperatures and the high light (Groom and Baker 1992, Zheng *et al.* 2011). The ratio of F_v/F_m in GGP sustained between 0.80 and 0.82 from 4 to 12 WAT, indicating that a suitable high temperature did not damage the primary photochemical reactions of photosynthetic apparatus (Govindachary *et al.* 2004). In this study, there was no decrease in F_v/F_m in response to high temperature (Fig. 6*A*), although the temperature was high in the greenhouse from 9 to 12 WAT (Table 1). This may be due to a low light intensity in the greenhouse that might alleviate a damage of photochemical process caused by high temperature. Meanwhile, Φ_{PSII}, q_P, and ETR in FGP were slightly lower than in GGP from 4 to 8 WAT (Fig. 6*B*,*D*,*E*); this was consistent with the reports that low temperature caused a decrease of the photochemical efficiency (Groom and Baker 1992).

However, from 9 to 12 WAT, Φ_{PSII}, q_P, and ETR were lower in GGP compared with FGP (Fig. 6*B*,*D*,*E*), which could be due to relatively lower light intensity in the greenhouse (Zheng *et al.* 2011). Moreover, the decreased ETR was also related to high temperatures in the greenhouse (Fig. 7, Table 1) (Yamasaki *et al.* 2002, Yamori *et al.* 2008). Therefore, significant decreases of Φ_{PSII}, q_P, and ETR in GGP were induced by the high temperature combined with the low light intensity under the greenhouse conditions 9 WAT (Fig. 6*B*,*D*,*E*). High temperature suppressing ETR was also shown by ETR-PAR response curve, and it was observed that maximum of ETR was much lower in GGP 10 WAT, and a difference in ETR between two groups of plants became pronounced, when PAR ranged from 200 to 700 μmol m^{-2} s^{-1}(Fig. 7).

NPQ was significantly higher in GGP than in FGP 9 WAT, (Fig. 6*C*). It was apparently caused by high temperature extremes during daytime, with 3 d and about total 10 h exceeding 39°C under the greenhouse conditions (data not shown), indicating that high temperature in the greenhouse increased thermal de-excitation of PSII and kept less energy for photochemical reaction (Fig. 6*C*) (Gilmore 1997). Therefore, P_N in GGP showed a sudden decrease 9 WAT (Fig. 2*A*).

Antioxidant enzyme activity and lipid peroxidation: There are many processes affecting P_N performance in plants, including increased photorespiration, damage to the CO_2 fixed reaction mechanism, as well as an occurrence of ROS. The generation of ROS, particularly under environmental constrains, is damaging to cellular components and leads to the accumulation of lipid peroxides (Lidon and Henriques 1993). Accumulation of cytotoxic ROS is antagonized by antioxidant defence system in plants that is pivotal for the maintenance of membrane integrity, which, in turn, allows plants to remain functioning for a longer time under environmental stress. In this study, from 4 to 8 WAT, higher MDA content was observed in FGP (Fig. 8*F*), indicating that peroxidation of membrane lipids by ROS accumulation occurred at a low temperature stress (Salin 1988). Previous studies (Lee and Lee 2000, Perelman *et al.* 2006, Islam *at al.* 2011) demonstrated an increase in the antioxidant enzyme activity in plants subjected to different low temperatures. Similarly, in our study, there was a marked stimulation in the activities of APX, POD, GR, and SOD in FGP in a response to low temperatures (Fig. 8*A*,*C*,*D*,*E*). However, there was a decrease in CAT activity (Fig. 8*B*). Our observations were consistent with the results of Lee and Lee (2000) that reported a decreased activity of CAT under low temperature. In addition, increased antioxidant enzyme activity in FGP appeared to be related to a high irradiance (Špundová *et al.* 2005). Therefore, the low temperature combined with the high light intensity in the field was responsible for the increased activities of APX, POD, GR, and SOD from 4 to 8 WAT.

There was no significant difference in MDA content between GGP and FGP 10 and 12 WAT (Fig. 8*F*) and no significant differences in activities of APX, CAT, POD, GR, and SOD were found between both groups of the plants (Fig. 8*A–E*). Our results were different from the reports that high temperature stress in plants resulted in an increase of antioxidant enzyme activities (Almeselmani *et al.* 2006). This might be related to findings that shading conditions weaken the antioxidative protection and the oxidative stress symptoms at high temperatures (Špundová *et al.* 2005). In our experiment, there was no significant difference in F_v/F_m between both groups of the plants 10 and 12 WAT, which suggested that the high temperature in the greenhouse seemed not to be a stressful for photochemical processes in PSII of *Z. latifolia* plants (Fig. 6*A*).

Conclusions: The study demonstrated that in the early spring, under the greenhouse conditions, higher temperatures favored plant growth but retarded new tiller emergence of *Z. latifolia* compared with the field conditions. However, from 10 to 12 WAT, due to the high temperature (>26°C) and the low light intensity, P_N decreased in GGP, which subsequently affected their growth. Therefore, a manipulation of the aerial environment by decreasing the temperature would be necessary for *Z. latifolia* if grown in a plastic-house in temperate zones during the hot season. Our results also indicated that *Z. latifolia* FGP showed a significant decrease in P_N under low temperatures and saturating irradiance in the early spring (from 4 to 8 WAT) compared with GGP, where the average day temperature was higher than 25°C. Moreover, FGP exhibited higher activities of APX, POD, GR, and SOD as a protection against the low temperature. At low temperatures, it was also observed that reduced P_N was in parallel to a decrease of photochemical activity, with a lower ETR and F_v/F_m. No limitation of photosynthesis due to g_s was observed.

References

Allen, D.J., Ort, D.R.: Impacts of chilling temperatures on photosynthesis in warm-climate plants. – Trends Plant Sci. **6**: 36-42, 2001.

Almeselmani, M., Deshmukh, P.S., Sairam, R.K., Kushwaha, S.R., Singh, T.P.: Protective role of antioxidant enzymes under high temperature stress. – Plant Sci. **171**: 382-388, 2006.

Ballantine, J.E.M., Forde, B.J.: The effect of light intensity and temperature on plant growth and chloroplast ultrastructure in soybean. – Amer. J. Bot. **57**: 1150-1159, 1970.

Berry, J., Björkman, O.: Photosynthetic response and adaptation to temperature in higher plants. – Annu. Rev. Plant Physiol. **31**: 491-543, 1980.

Bos, H.J., Neuteboom, J.H.: Morphological analysis and tiller number dynamics of wheat (*Triticum aestivum* L.): responses to temperature and light intensity. – Ann. Bot. **81**: 131-139, 1998.

Chou, C.C., Chen, W.S., Huang, K.L. *et al*.: Changes in cytokinin levels of *Phalaenopsis* leaves at high temperature. – Plant Physiol. Biochem. **38**: 309-314, 2000.

Demmig-Adams, B., Adams, W.W., III: Photoprotection and other responses of plants to high light stress. – Annu. Rev. Plant Physiol. Plant Mol. Biol. **43**: 599-626, 1992.

Ding, X., Shi, G., Chen, W., Xu, X.: [Morphological studies on the development and cold resistance of the winter buds of *Zizania caduciflora* Hand.-Mazz.] – J. Wuhan Bot. Res. **11**: 104-110, 1993. [In Chin.]

Dizengremel, P., Le Thiec, D., Bagard, M., Jolivet, Y.: Ozone risk assessment for plants: central role of metabolism-dependent changes in reducing power. – Environ. Pollut. **156**: 11-15, 2008.

Farage, P.K., Long, S.P.: The occurrence of photoinhibition in an over-wintering crop of oil-seed rape (*Brassica napus* L.) and its correlation with changes in crop growth. – Planta **185**: 279-286, 1991.

Foyer, C.H., Halliwell, B.: The presence of glutathione and glutathione reductase in chloroplasts: a proposed role in ascorbic acid metabolism. – Planta **133**: 21-25, 1976.

Friend, D.J.C.: Tillering and leaf production in wheat as affected by temperature and light intensity. – Can. J. Bot. **43**: 1063-1076, 1965.

Genty, B., Briantais, J.M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Gilmore, A.M.: Mechanistic aspects of xanthophylls cycle-dependent photoprotection in higher plant chloroplasts and leaves. – Physiol. Plant. **99**: 197-209, 1997.

Govindachary, S., Bukhov, N.G., Joly, D., Carpentier, R.: Photosystem II inhibition by moderate light under low temperature in intact leaves of chilling-sensitive and -tolerant plants. – Physiol. Plant. **121**: 322-333, 2004.

Groom, Q.J., Baker, N.R.: Analysis of light-induced depressions of photosynthesis in leaves of a wheat crop during the winter. – Plant Physiol. **100**: 1217-1223, 1992.

Guo, D.P., Jiang, Y.T., Zeng, G.W., Shah, G.A.: Stem swelling of stem mustard, as affected by temperature and growth regulators. – Sci. Hort. **60**: 153-160, 1994.

Guo, Y.P., Zhou, H.F., Zhang, L.C.: Photosynthetic characteristics and protective mechanisms against photooxidation during high temperature stress in two citrus species. – Sci. Hort. **108**: 260-267, 2006.

Hunt, W., Thomas, V.: Growth and developmental responses of perennial ryegrass grown at constant temperature. II. Influence of light and temperature on leaf, tiller and root appearance. – Funct. Plant Biol. **12**: 69-76, 1985.

Ishihara, K., Saitoh, K.: Diurnal courses of photosynthesis, transpiration, and diffusive conductance in the single-leaf of the rice plants grown in the paddy field under submerged condition. – Jpn. J. Crop Sci. **56**: 8-17, 1987.

Islam, S., Izekor, E., Garner, J.O.: Effect of chilling stress on the chlorophyll fluorescence, peroxidase activity and other physiological activities in *Ipomoea batatas* L. genotypes. – Am. J. Plant Physiol. **6**: 72-82, 2011.

Korner, C., Diemer, M.: *In situ* photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. – Funct. Ecol. **1**: 179-194, 1987.

Krause, G.H., Weis, E.: Chlorophyll fluorescence and photosynthesis–the basics. – Annu. Rev. Plant Physiol. Plant Mol. Biol. **42**: 313-349, 1991.

Laloi, C., Apel, K., Danon, A.: Reactive oxygen signaling: the latest news. – Curr. Opin. Plant Biol. **7**: 323-328, 2004.

Lee, D.H., Lee, C.B.: Chilling stress-induced changes of antioxidant enzymes in the leaves of cucumber: in gel enzyme activity assays. – Plant Sci. **159**: 75-85, 2000.

Lichtenthaler, H.K.: Chlorophylls and carotenoids: Pigments of photosynthetic membranes. – Methods Enzymol. **148**: 350-382, 1987.

Lidon, F.C., Henriques, F.S.: Oxygen metabolism in higher plant chloroplasts. – Photosynthetica **29**: 249-279, 1993.

Martin, B., Ort, D.R., Boyer, J.S.: Impairment of photosynthesis by chilling-temperatures in tomato. – Plant Physiol. **68**: 329-334, 1981.

McMaster, G.S., Wilhelm, W.W., Palic, D.B. *et al*.: Spring wheat leaf appearance and temperature: Extending the paradigm? – Ann. Bot. **91**: 697-705, 2003.

Mooney, H.A., Björkman, O., Collatz, G.J.: Photosynthetic acclimation to temperature in desert shrub, *Larrea divaricata*.1. Carbon-dioxide exchange characteristics of intact leaves. – Plant Physiol. **61**: 406-410, 1978.

Nakano, Y., Asada, K.: Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. – Plant Cell Physiol. **22**: 867-880, 1981.

Pastenes, C., Horton, P.: Effect of high temperature on photosynthesis in beans II. CO_2 assimilation and metabolite contents. – Plant Physiol. **112**: 1253-1260, 1996.

Patra, H.K., Kar, M., Mishra, D.: Catalase activity in leaves and cotyledons during plant development and senescence. – Biochem. Physiol. Pflanz. **172**: 385-390, 1978.

Percival, G.C.: The use of chlorophyll fluorescence to identify chemical and environmental stress in leaf tissue of three oak (*Quercus*) species. – J. Arbor. **31**: 215-227, 2005.

Perelman, A., Dubinsky, Z., Martínez, R.: Temperature dependence of superoxide dismutase activity in plankton. – J. Exp. Mar. Bio. Ecol. **334**: 229-235, 2006.

Prado, C.H.B.A., De Moraes, J.A.P.V.: Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field conditions. – Photosynthetica **33**: 103-112, 1997.

Qaderi, M.M., Reid, D.M.: Crop responses to elevated carbon dioxide and temperature. In: Singh, S.N. (ed.), Climate Change and Crops. – Springer-Verlag, Berlin Heidelberg, 1-18, 2009.

Ruelland, E., Zachowski, A.: How plants sense temperature. – Environ. Exp. Bot. **69**: 225-232, 2010.

Ryle, G.J.A.: A comparison of leaf and tiller growth in seven perennial grasses as influenced by nitrogen and temperature. – Grass Forage Sci. **19**: 281-290, 1964.

Salin, M.L.: Toxic oxygen species and protective systems of the chloroplast. – Physiol. Plant. **72**: 681-689, 1988.

Salvucci, M.E., Osteryoung, K.W., Crafts-Brandner, S.J., Vierling, E.: Exceptional sensitivity of Rubisco activase to thermal denaturation *in vitro* and *in vivo*. – Plant Physiol. **127**:

1053-1064, 2001.

Silim, S.N., Ryan, N., Kubien, D.S.: Temperature responses of photosynthesis and respiration in *Populus balsamifera* L.: acclimation versus adaptation. – Photosynth. Res. **104**: 19-30, 2010.

Špundová, M., Slouková, K., Hunková, M., Nauš, J.: Plant shading increases lipid peroxidation and intensifies senescence-induced changes in photosynthesis and activities of ascorbate peroxidase and glutathione reductase in wheat. – Photosynthetica **43**: 403-409, 2005.

Stewart, R.R.C., Bewley, J.D.: Lipid peroxidation associated with accelerated aging of soybean axes. – Plant Physiol. **65**: 245-248, 1980.

Tenhunen, J.D., Lange, O.L., Gebel, J., Beyschlag, W., Weber, J.A.: Changes in photosynthetic capacity, carboxylation efficiency, and CO_2 compensation point associated with midday stomatal closure and midday depression of net CO_2 exchange of leaves of *Quercus suber*. – Planta **162**: 193-203, 1984.

Turan, Ö., Ekmekçi, Y.: Activities of photosystem II and antioxidant enzymes in chickpea (*Cicer arietinum* L.) cultivars exposed to chilling temperatures. – Acta Physiol. Plant. **33**: 67-68, 2011.

Van Kooten, O., Snel, J.: The use of chlorophyll fluorescence nomenclature in plant stress physiology. – Photosynth. Res. **25**: 147-150, 1990.

Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R.: Heat tolerance in plants: an overview. – Environ. Exp. Bot. **61**: 199-223, 2007.

Weis, E.: Reversible heat-inactivation of the Calvin cycle: A possible mechanism of the temperature regulation of photosynthesis. – Planta **151**: 33-39, 1981.

Wise, R.R., Olson, A.J., Schrader, S.M., Sharkey, T.D.: Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. – Plant Cell Environ. **27**: 717-724, 2004.

Yamasaki, T., Yamakawa, T., Yamane, Y. *et al.*: Temperature acclimation of photosynthesis and related changes in photosystem II electron transport in winter wheat. – Plant Physiol. **128**: 1087-1097, 2002.

Yamori, W., Noguchi, K., Kashino, Y., Terashima, I.: The role of electron transport in determining the temperature dependence of the photosynthetic rate in spinach leaves grown at contrasting temperatures. – Plant Cell Physiol. **49**: 583-591, 2008.

Zhang, F.L.: [Preliminary study on growth dynamics of double-harvest *Zizania latifolia*: I. Autumn-harvest variety.] – Chin. Veg. **2**: 31-33, 1991a. [In Chin.]

Zhang, F.L.: [Preliminary study on growth dynamics of double-harvest *Zizania latifolia*: I. Summer-harvest variety.] – Chin. Veg. **3**: 28-30, 1991b. [In Chin.]

Zhang, J.Z., Chu, F.Q., Guo, D.P. *et al.*: Cytology and ultrastructure of interactions between *Ustilago esculenta* and *Zizania latifolia*. – Mycol. Prog. **11**: 499-508, 2012.

Zheng, Y., Mai, B., Wu, R. *et al.*: Acclimation of winter wheat (*Triticum aestivum*, cv. Yangmai 13) to low levels of solar irradiance. – Photosynthetica **49**: 426-434, 2011.

Zinn, K.E., Tunc-Ozdemir, M., Harper, J.F.: Temperature stress and plant sexual reproduction: uncovering the weakest links. – J. Exp. Bot. **61**: 1959-1968, 2010.