Different photosynthetic responses to night chilling among twelve populations of *Jatropha curcas*

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Abstract

Jatropha curcas, one of the most important energy plant resources, is vulnerable to chilling. To evaluate the effects of chilling on photosynthesis of *J. curcas* and intraspecific differences in chilling tolerance, seedlings of twelve populations were treated with the temperature of 4–6°C for five consecutive nights with normal environmental temperature during the day. Night chilling treatment decreased light-saturated photosynthetic rate (P_{max}) significantly for all populations. Stomatal limitation could not explain the decreased P_{max} because intracellular CO_2 concentration was not significantly reduced by night chilling in all populations (with only one exception). The decreased soluble-protein content, which may be related to the increased malondialdehyde (MDA) content, contributed to the decreased P_{max}. The increased MDA content indicated that oxidative stress occurred after night chilling, which was associated with the larger decrease in P_{max} compared with the decrease in actual photochemical efficiency of photosystem II, and the slight increase in thermal dissipation of excessive energy. After five-day recovery, MDA (with two exceptions) and P_{max} still did not recover to the levels as those before night chilling treatment for all populations, indicating that *J. curcas* was vulnerable to chilling. Chilling tolerance was significantly different among populations. Populations originating from high elevations had greater chilling-tolerant abilities than populations originating from low elevations, showing a local adaptation to environmental temperatures of origins. Our study shed light on the possibility to find or breed chilling-tolerant genotypes of *J. curcas*.

Additional key words: chlorophyll fluorescence; *Jatropha curcas*; malondialdehyde; night chilling; photoinhibition; photosynthesis; populations; soluble protein.

Introduction

Low-temperature stress is one of the most important factors that limit survival, growth, reproduction, and distribution of plant species in fields (Boyer 1982, Annicchiarico *et al*. 2001). In tropical and subtropical areas, most plants are relatively vulnerable to low temperature because they grow the whole year in a relatively warm climate (Crawford 1989, Greer 1990). Crawford (1989) indicated that temperatures between 6–10°C could cause injury or even mortality to typically tropical plants. Low-temperature stress can impact a number of plant physiological processes (Xin and Browse 2000, Karimzadeh *et al*. 2005, Liang *et al*. 2007).

Photosynthesis is one of the processes that are sensitive to low temperature (Huner *et al*. 1998, Feng and Cao 2005, Ensminger *et al*. 2006). When plants are exposed to chilling stress, photosynthetic enzymes may be inactivated or degraded and photodamage to photosystem (PS) II may happen, reducing photosynthesis (Flexas 1999, Feng and Cao 2005, Dai *et al*. 2007). Degradations of photosynthetic enzymes such as Rubisco may cause reduced soluble protein content, as Rubisco accounts for approximately half of soluble proteins (Miller and Huffaker 1982, Pell *et al*. 1994). The reduced photosynthesis may lead to accumulation of excess energy especially at high irradiance and consequently to photoinhibition (Hovenden and Warren 1998, Feng and

Cao 2005). There are several ways for plants to dissipate the surplus energy, such as xanthophyll cycle and reversible inactivation of PSII reaction centres (Feng *et al.* 2002, Rapacz 2008). If the excess energy is not dissipated safely, plants will produce reactive oxygen species (ROS) such as $O_2^{\cdot-}$, $^{\cdot}OH$, and H_2O_2 through various processes, which may cause peroxidation of membrane lipids and destruction of the photosynthetic apparatus (Foyer *et al.* 1994). Malondialdehyde (MDA), the product of membrane lipid peroxidation, is also toxic to the photosynthetic apparatus.

Chlorophyll (Chl) fluorescence technique has been widely used as a rapid and non-destructive tool to detect the functional changes in the photosynthetic apparatus. The maximum photochemical efficiency of PSII (F_v/F_m), the actual photochemical efficiency of PSII in the light (Φ_{PSII}) and nonphotochemical quenching (NPQ) are the widely used variables to measure the effects of abiotic or biotic stress on photosynthesis (Feng and Cao 2005, Dai *et al.* 2007, Liang *et al.* 2007).

Jatropha curcas L. (Euphorbiaceae), a deciduous perennial shrub with Central America origin, is now widely cultivated in tropics and subtropics worldwide (Deore and Johonson 2008). Seed oil content of this plant is about 40%, higher than the typical oil crops such as soybean and rape (Gubitz *et al.* 1999, Deore and Johonson 2008). The oil can be used in diesel engines after simple processing because it is similar to diesel oil in characteristics, being a potential substitute for fossil fuel and a renewable energy (Berchmans and Hirata 2008, Deore and Johonson 2008). Thus, *J. curcas* has been considered as a strategic plant resource in many countries (Carvalho *et al.* 2008). In recent years, Chinese government also pays much attention to this plant, which has been grown at some mountain areas in several southern provinces. However, *J. curcas* is relatively vulnerable to low temperatures especially at the seedling stage (Liang *et al.* 2007), limiting its cultivation in cold areas such as high mountains. Therefore, it is important to select chilling-tolerant genotypes for expanding its cultivation area and breeding chilling-tolerant varieties. It has been documented that chilling tolerance is different among populations in many plant species (Harris *et al.* 2001, Annicchiarico *et al.* 2001, Bravo *et al.* 2007, Zhang *et al.* 2009). Our preliminary study showed that low semilethal temperature is significantly different among populations of *J. curcas* (Yang-Ping Li *et al.*, unpublished data). In this study, we compared the differences among 12 populations of *J. curcas* in photosynthetic responses to chilling. The main purposes of this study were to detect the impact of low-temperature stress on photosynthesis and the potential differences among populations in chilling tolerance.

Materials and methods

Plants and chilling treatment: This study was carried out at Xishuangbanna Tropical Botanical Garden (21°56' N, 101°15' E) of Chinese Academy of Sciences, located in Mengla County, Yunnan Province, southwest China. The mean annual temperature is 21.7°C, with a mean of 25.3°C in the hottest month (July) and 15.6°C in the coolest month (January); the mean annual precipitation is 1,557 mm (Feng *et al.* 2002). In this area, chilling temperature usually occurs at night, it is still warm during the day (Feng and Cao 2005). Therefore, chilling treatment was only applied at night in this study.

In 2005, seeds of *J. curcas* were collected in 12 populations located at different latitude (21°41′ N–24°52′ N), longitude (97°52′ E–105°40′ E), and altitude (420–1427 m a.s.l.) in south Yunnan Province (Table 1). In each population, seeds were collected from 10–15 plants, mixed, dried at a room temperature and stored in paper bags at 4°C until used. The seeds were sowed in a seedbed in November 2007 and in late December, when the seedlings were approximately 15 cm tall. The seedlings were singly transplanted into 15 dm³ pottery pots. The pots were filled with equal proportions of river sand

Table 1. Information on the 12 sample populations of *Jatropha curcas*.

Code	Site	Longitude (E)	Latitude (N)	Elevation [m]
A	Binghanqiao, Yingjiang county	97°52′	24°52′	883
B	Daheishan, Lüchun county	101°53′	22°45′	462
C	Heyun, Ruili county	97°54′	24°02′	772
D	Menglun, Mengla county	101°25′	21°41′	870
E	Zhongaiqiao, Mojiang county	101°30′	23°20′	803
F	Zhongaiqiao, Mojiang county	101°20′	23°28′	916
G	Sinanjiang, Mojiang county	101°45′	23°07′	530
H	Tongguan, Mojiang county	101°23′	23°17′	1068
I	Bajiaoqing, Mojiang county	101°04′	23°08′	1427
J	Mengla farm, Jinping county	105°40′	22°30′	420
K	Yijia, Jinping county	103°13′	22°47′	850
L	Mangfu, Lancang county	100°01′	22°43′	1363

and topsoil of forest. The seedlings were grown at an open site with full sunshine and were watered when necessary.

In April 2008, when the seedlings were approximately 60 cm tall, similarly sized individuals were moved into a dark low-temperature house (4–6°C) for 12 h (19:00–07:00) per day for five consecutive nights. During the day, the night-chilling-treated seedlings were put back at their original open site. After five nights of the chilling treatment, the seedlings were grown for another five days at the open site. Before and after the five-night chilling treatment, and after the five-day recovery, measurements of photosynthesis and Chl fluorescence were taken at the open site on the youngest fully expanded leaves of five individuals per population. Afterwards, the sample leaves were collected for determining the contents of MDA and soluble proteins. For most of the sample plants, one leaf was big enough for all measurements. In this case, the same leaf of each sample plant was used for the measurements. In this way, the influences on relationships among variables of the potential differences among leaves of the same plant could be avoided. But for few sample plants with small leaves, we had to select two similar leaves to measure the variables.

Gas exchange: In the morning, when the studied plant could achieve the daily highest photosynthetic rate, light-saturated photosynthetic rate (P_{max}), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured using a *Li-6400 Portable Photosynthesis System* (*Li-Cor*, Lincoln, NE, USA) under 2000 µmol m^{-2} s^{-1} photosynthetic photon flux density. The saturating light was provided by the *6400-02B* red and blue light source of the equipment. Relative humidity and CO_2 concentration of the air in the reference chamber and leaf temperature were controlled automatically by the equipment at 75%, 380 µmol mol^{-1} and 25°C, respectively. Before the measurement, each sample leaf was illuminated with the saturating light for about 10 min to achieve full photosynthetic induction.

Chl fluorescence was measured using a portable fluorometer *(PAM-2100, Walz*, Effeltrich, Germany). At dawn, when the studied plant could achieve the daily highest F_v/F_m, the minimum fluorescence yield (F_o) was measured on each dark-adapted leaf (adaxial side) under a weak modulated red beam, then the maximum fluorescence yield (F_m) was determined by irradiating the sample leaf with a saturating white pulse (5000 µmol m^{-2} s^{-1}, 0.8 s), and F_v/F_m was calculated as (F_m–F_o)/F_m. At midday, the steady state fluorescence yield (F_s) was determined under white actinic light of 500 µmol m^{-2} s^{-1}.

The maximum light-adapted fluorescence yield (F_m') was determined by irradiating the sample leaf with the saturating pulse. Finally, the minimum light-adapted fluorescence yield (F_o') was recorded after keeping the sample leaf in dark for 10 s, in second half of which the leaf was irradiated by far-red beams. The lights used in the measurements were provided automatically by the equipment. Φ_{PSII} and NPQ were calculated as ($F_m' - F_s$)/F_m' and ($F_m - F_m'$)/F_m', respectively. The value of NPQ measured at midday represents the potential ability of thermal dissipation and the decrease in F_v/F_m measured at dawn indicates long-term photoinhibition or even photodamage (Feng *et al.* 2002).

Contents of MDA and soluble proteins were determined spectrophotometrically. MDA was extracted using 10% trichloroacetic acid and detected using 2-thiobarbituric acid (Wang *et al.* 1986). Soluble proteins were extracted using phosphate buffer and detected using Coomassie brilliant blue G-250 (Wang *et al.* 1986).

Calculation of a relative value: The value of each variable may be different among the 12 sample populations before the night chilling treatment. Thus, the differences among populations in an absolute value (measured directly) of each variable after night chilling and recovery treatments may not reflect the intraspecific differences in susceptibility to night chilling. To evaluate intraspecific differences in chilling tolerance, relative values of each variable after chilling and recovery treatments were calculated as the ratios of the absolute values to the value measured before chilling treatment, respectively.

Statistical analyses: The effects of population, treatment and their interaction on variables measured in this study were evaluated using a two-way *ANOVA*. The differences among populations at the same treatment, and the differences among treatments for the same population were tested using a one-way *ANOVA*. The differences between chilling treatment and recovery in correlations between relative P_{max} and relative values of other variables were tested using a one-way *ANOVA*. Treatment (chilling *vs*. recovery) was used as a fixed factor; P_{max} as a dependent variable; and variables indicated by x-axes in the figures as covariate, respectively. If the difference had been significant, we tested the significance of correlations (Pearson correlation, two-tailed) for chilling and recovery treatments separately; otherwise, we pooled data from two treatments to test for the significance of correlations. All analyses were carried out using *SPSS 12.0* (*SPSS Inc*., Chicago, IL, USA).

Results

Effects of chilling treatment: Treatment and population (except for g_s and C_i) significantly affected all the variables evaluated in this study (data not shown). Five-night chilling treatment decreased P_{max}, Φ_{PSII}, and soluble protein content but increased MDA (except for population L) significantly for all studied populations
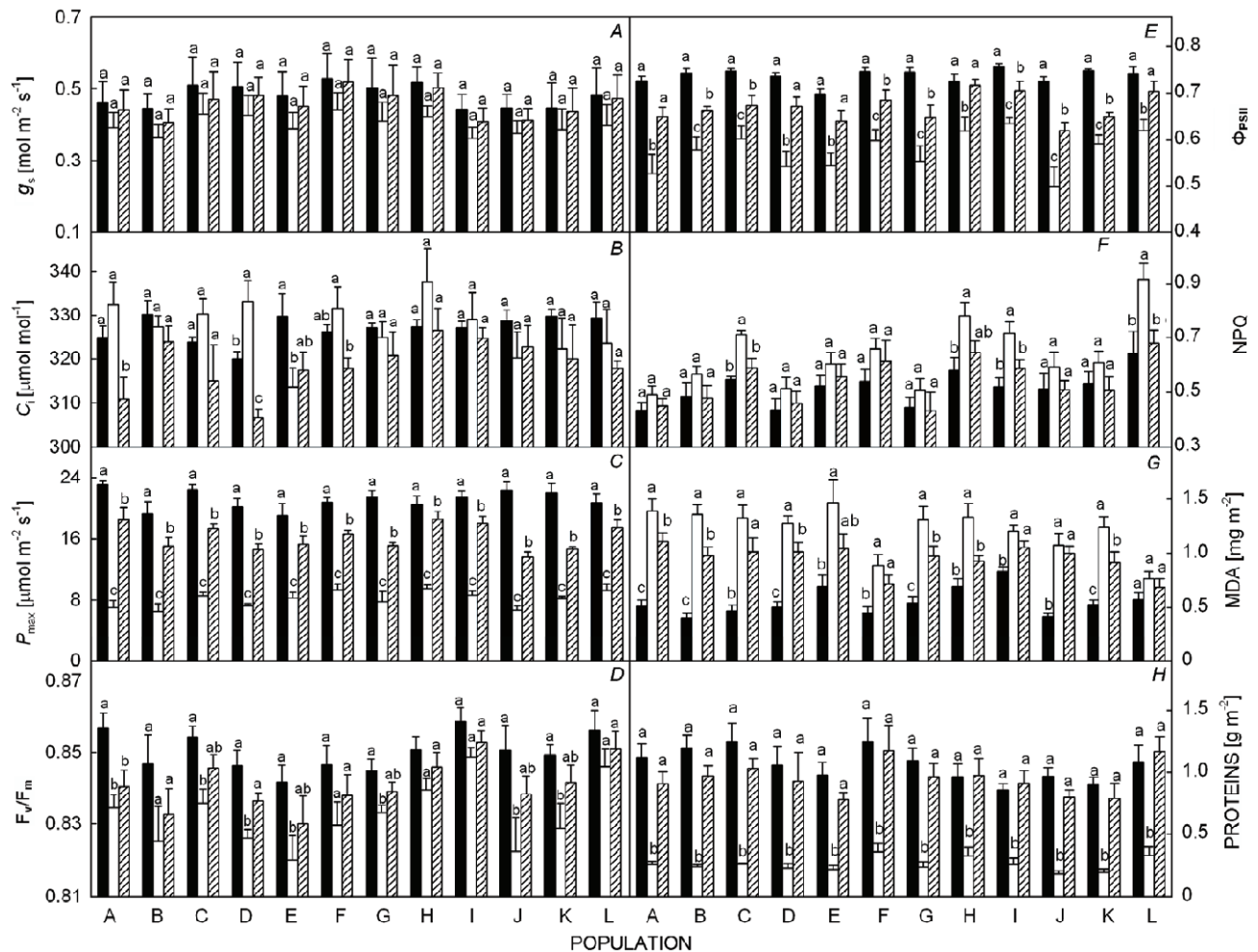

Fig. 1. *A*: Stomatal conductance (g_s), *B*: intercellular CO_2 concentration (C_i), *C*: light-saturated photosynthetic rate (P_{max}), *D*: maximum photochemical efficiency of PSII (F_v/F_m), *E*: actual photochemical efficiency of PSII (Φ_{PSII}), *F*: nonphotochemical quenching (NPQ), *G*: malondialdehyde content (MDA), and *H*: soluble protein content in different populations of *Jatropha curcas* before (*black bars*) and after (*open bars*) five-night chilling treatment, and after five-day recovery (*hatched bars*). Mean ± SE (*n* = 5). Different letters indicate significant differences among treatments for the same population (*p*< 0.05).

(Figs. 1*C,E,G,H*). Similarly, night chilling treatment decreased g_s and F_v/F_m but increased NPQ although the changes were not significant for some populations (Figs. 1*A,D,F*). Night chilling treatment significantly increased C_i for population D but decreased C_i for population E, whereas its effect on C_i was not significant for other populations (Fig. 1*B*). In contrast, five-day recovery treatment increased g_s, P_{max}, F_v/F_m, Φ_{PSII}, and soluble protein content but decreased C_i (except for populations E and J), NPQ, and MDA for all studied populations (Fig. 1). After five-day recovery from chilling treatment, g_s and soluble protein content increased and NPQ decreased to the values as those before night chilling treatment for all studied populations, and C_i and F_v/F_m also recovered completely for most of the 12 populations (Fig. 1*A,B,D, F,H*). However, P_{max} and MDA (except of populations H, L) did not recover completely from night chilling treatment for all studied populations, and Φ_{PSII} also did not recover for seven of the 12 populations (Fig. 1*C,E,G*).

Intraspecific differences in chilling tolerance: Among populations, F_v/F_m, Φ_{PSII}, NPQ, and MDA were significantly different after night chilling treatment and P_{max},

Table 2. The F-values of one-way *ANOVA* expressing the differences among populations of *Jatropha curcas*. Relative values of each variable after chilling and recovery treatments were calculated as the ratios of the measured values to the value measured before chilling treatment, respectively. *$p<0.05$; **$p<0.01$; ***$p<0.001$. P_{max} – light-saturated photosynthetic rate [μmol m^{-2} s^{-1}]; C_i – intercellular CO_2 concentration [μmol mol^{-1}]; g_s – stomatal conductance [mol m^{-2} s^{-1}]; F_v/F_m – maximum photochemical efficiency of PSII; Φ_{PSII} – actual photochemical efficiency of PSII; NPQ – nonphotochemical quenching; proteins – soluble protein content [g m^{-2}]; MDA – malondialdehyde content [g m^{-2}].

| Variable | F-values | | | | |
| | Before night chilling | After night chilling | | After recovery | |
	Absolute value	Absolute value	Relative value	Absolute value	Relative value
P_{max}	1.289	1.845	3.108**	3.244**	4.755***
C_i	1.125	1.431	2.196*	1.488	0.553
g_s	0.278	0.328	0.675	0.482	0.811
F_v/F_m	1.085	2.187*	1.064	1.726	0.485
Φ_{PSII}	2.743**	2.088*	1.849	2.510*	2.157*
NPQ	1.631	7.738***	1.563	2.750**	0.425
Proteins	1.267	1.528	2.205*	1.097	1.844
MDA	4.561***	3.180**	12.688***	2.105*	12.779***

Φ_{PSII}, NPQ, and MDA were significantly different after five-day recovery from the chilling treatment, while only Φ_{PSII} and MDA were significantly different among populations before night chilling treatment (Table 2). These results indicated potential intraspecific differences in chilling tolerance among populations. Among populations, relative values of P_{max}, C_i, MDA, and soluble protein content were significantly different after chilling treatment and relative values of P_{max}, Φ_{PSII}, and MDA were significantly different after recovery treatment, confirming the intraspecific differences in chilling tolerance.

Chilling treatment decreased P_{max} the most in populations A and J (followed by B), and the least for populations F, H, and L (followed by E). After five-day recovery, population H showed the highest relative value of P_{max} (followed by L, I, and E) among the studied populations, while populations J and K showed the lowest relative P_{max} (Fig. 2A). Chilling treatment increased MDA content the most in population B (followed by A and C), and the least in populations L and I (followed by H and F). After five-day recovery, populations J and B (followed by A and C) showed the highest relative MDA content, while populations L, I, H, F, and E showed the lowest relative MDA content (Fig. 2B). After five-night chilling treatment, population H (followed by I) showed the highest relative soluble

protein content, while population J the lowest one. After five-day recovery, population L (followed by F–I) showed the highest relative protein content (Fig. 2C). After night chilling treatment, populations H, I, and L showed the highest relative Φ_{PSII}, while population J the lowest one. After recovery, population H (followed by L) showed the highest relative Φ_{PSII}, while population J the lowest (Fig. 2D). Taking into all differences among populations in above variables, populations J and B were, and populations H, L, I, and F were not vulnerable to night chilling.

Correlations between variables: After night chilling treatment and five-day recovery, relative value of P_{max} increased significantly with increasing relative values of Φ_{PSII}, NPQ, and soluble protein content but decreased with increasing relative MDA content (Fig. 3C–F), while the correlation between relative P_{max} and C_i was not significant (Fig. 3A). The correlation between P_{max} and F_v/F_m was significant after night chilling treatment but not significant after recovery (Fig. 3B). All correlations were significantly different ($p<0.001$) between night chilling and recovery treatments except that between relative P_{max} and relative soluble protein content ($p=0.640$).

Discussion

Reduced P_{max} after chilling treatment: Five-night chilling treatment decreased P_{max} greatly for all studied *J. curcas* populations (Figs. 1C, 2A), which was consistent with the results of other studies (Flexas *et al.* 1999, Allen *et al.* 2000, Feng and Cao 2005). Stomatal limitation could not explain the decreased P_{max} because g_s and C_i was not significantly reduced by night chilling treatment for all populations except E (Fig. 1A,B) and relative value of P_{max} was not correlated with relative C_i

(Fig. 3A). The decreased P_{max} may be associated with the decreased soluble protein content (Figs. 1H, 2C), approximately half of which were Rubisco (Miller and Huffaker 1982, Pell *et al.* 1994). Positive correlation between relative P_{max} and relative soluble protein content was indeed found for *J. curcas* (Fig. 3F). At similar relative C_i, relative P_{max} was significantly lower after night chilling than that measured after recovery (Fig. 3A), indicating that night chilling reduced biochemical

capacity for photosynthesis, which is correlated with Rubisco (Feng *et al.* 2007a). Similarly, our previous study showed that night chilling reduces carboxylation efficiency (Feng and Cao 2005), indicating increased degradation of Rubisco and/or decreased Rubisco-related gene expression (Martino-Cart and Ort 1992). The increased content of MDA (Figs. 1*G*, 2*B*), the product of membrane lipid peroxidation, revealed that ROS accumulated in leaves after night chilling treatment, which may be associated with decreased ability to scavenge ROS (Foyer *et al.* 1994). Both ROS and MDA can suppress the activities of photosynthetic enzymes such as Rubisco (Lin *et al.* 2000).
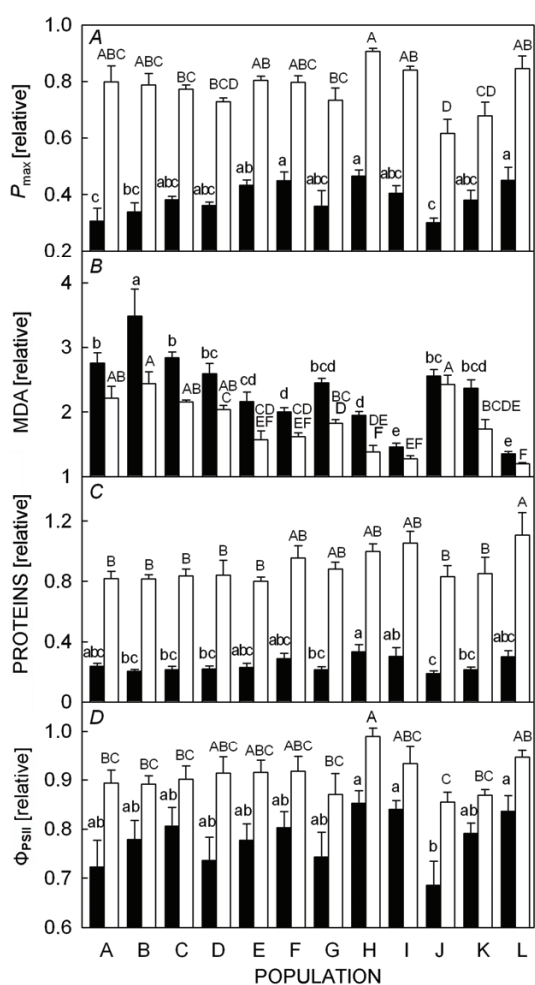

Fig. 2. *A*: Relative values of: *A*: light-saturated photosynthetic rate (P_{max}), *B*: malondialdehyde content (MDA), *C*: soluble protein content, and *D*: actual photochemical efficiency of PSII (Φ_{PSII}) in different populations of *Jatropha curcas* after night chilling (*black bars*) and recovery (*open bars*) treatments. Relative values of each variable after chilling and recovery treatments were calculated as the ratios of the measured values to the value measured before chilling treatment, respectively. Mean ± SE ($n = 5$). Different small and capital letters indicate significant differences among populations after night chilling and recovery treatments, respectively ($p < 0.05$).

Excessive energy after chilling treatment: The accumulations of ROS and MDA indicated that excessive energy occurred in the photosynthetic machinery of *J. curcas* after night chilling treatment. This was clearly shown by the reduced F_v/F_m and Φ_{PSII} (Figs. 1*D,E*; 2*D*), which indicated the occurrence of photoinhibition (Nir *et al.* 1997, Feng and Cao 2005). Accumulation of the excessive energy may be associated with the unproportionate decreases in P_{max} and Φ_{PSII}, and the slight increase in NPQ. Φ_{PSII} is positively correlated with the amount of electrons transported through PSII (Genty *et al.* 1989, Hormann *et al.* 1994), and in general most of the electrons are used by photosynthetic CO_2 assimilation. The decrease in P_{max} caused by night chilling treatment was much greater than that in Φ_{PSII} (Fig. 2*A,D*), leaving more electrons available for other processes such as production of ROS. Besides photosynthetic CO_2 assimilation, NPQ, an indicator of the ability of thermal dissipation of excessive energy, can also protect the photosynthetic machinery from photodamage (Gilmore *et al.* 1995, Feng *et al.* 2002, 2007b, Dai *et al.* 2007). Increased NPQ are found after night chilling in many plant species (Fig. 1*F*; Flexas *et al.* 1999, Feng and Cao 2005, Dai *et al.* 2007). However, the increase in NPQ was not significant in most of the studied populations of *J. curcas*. Our results suggested that excessive energy or electrons may accumulate in chloroplast after night chilling, contributing to production of ROS (Niyogi 1999).

Vulnerable to chilling: The present study showed that photosynthesis of *J. curcas* was vulnerable to night chilling. After five-day recovery, F_v/F_m and Φ_{PSII} still did not increase to the levels as those before night chilling treatment in some populations, indicating that five-night chilling treatment caused long-term photoinhibition or even photodamage. The results were consistent with the higher MDA content and lower P_{max} after recovery compared with values before night chilling treatment. This study indicated that night chilling could impair photosynthesis of *J. curcas* by different physiological processes such as photoinhibition, decrease of soluble protein content, and accumulations of ROS and MDA (Fig. 3). Previous studies also showed that low temperature affects photosynthesis by influencing stomatal conductance (Flexas *et al.* 1999, Allen *et al.* 2000, Feng and Cao 2005), photosynthetic enzymes (Liang *et al.* 2004), metabolism (Anniccharico *et al.* 2001, Hara *et al.* 2003), and gene expression (Martino-Cart and Ort 1992).

Intraspecific differences in chilling tolerance: Based on the differences among the studied populations of *J. curcas* in responses to night chilling and recovery treatments, populations H, L, I, and F had relatively high chilling-tolerant abilities, whereas populations J and B were vulnerable to night chilling (Figs. 1, 2). Interestingly, populations H, L, I, and F originated from high elevations, whereas populations J and B originated from
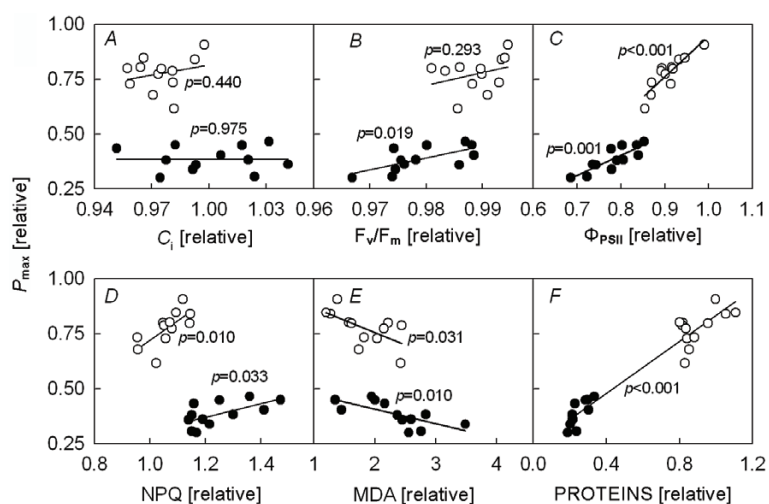
Fig. 3. Relative light-saturated photosynthetic rate (P_{max}) as a function of relative values of *A*: intercellular CO_2 concentration (C_i), *B*: maximum photochemical efficiency of PSII (F_v/F_m), *C*: actual photochemical efficiency of PSII (Φ_{PSII}), *D*: nonphotochemical quenching (NPQ), *E*: malondialdehyde content (MDA), and *F*: soluble protein content in different populations of *Jatropha curcas* after night chilling treatment (*black circles*) and recovery (*open circles*). Relative values of each variable after chilling and recovery treatments were calculated as the ratios of the measured values to the value measured before chilling treatment, respectively. Mean (*n* = 5). Correlations were not significantly different between night chilling and recovery treatments in panel *F* (*see* the text), and only one line fitted for pooled data was given.

the low ones (Table 1). The results indicated that populations originating from high elevations were more tolerant to night chilling than populations originating from the low ones, which is consistent with the results of other studies (Taschler and Neuner 2004, Kalberer *et al*. 2007). For example, Taschler and Neuner (2004) found that frost tolerance increases with increasing elevation. The genetically based difference among populations in chilling tolerance may be the result of long-term adaptation to growth environmental temperature. Populations distributing at high elevations may be more tolerant to chilling than populations distributing at the low ones due to responses to the selection pressure of low temperature. Local adaptation is often found for plant species with wide distribution areas (Li and Feng 2009, Zhang *et al*. 2009). Our study indicates that it is possible to find or breed chilling-tolerant genotypes of *J. curcas* for cultivation in cold areas.

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