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Comparison of the photosynthetic characteristics of four *Lycoris* species with leaf appearing in autumn under field conditions

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Abstract

The diurnal trends of gas exchange and chlorophyll fluorescence parameters in four *Lycoris* species (*L. houdyshelii*, *L. aurea*, *L. radiata* var. *pumila* and *L. albiflora*) were determined and compared with a portable photosynthesis analysis system. Our study revealed that *L. houdyshelii* had the lowest light compensation point (LCP), while the other three species had higher LCP (12.37–14.99 μmol m^{-2} s^{-1}); *L. aurea* had the highest light saturation point (LSP) (1,189 μmol m^{-2} s^{-1}), and *L. houdyshelii* and *L. albiflora* had lower LSP with the values being 322 and 345 μmol m^{-2} s^{-1}, respectively, and *L. radiata* var. *pumila* showed the intermediate LSP. Both the species *L. houdyshelii* and *L. albiflora* exhibited a typical and obvious decline in net photosynthetic rate (P_N) during midday, which was not observed in *L. aurea*. This indicated a possible photoinhibition in *L. houdyshelii* and *L. albiflora* as the ratio of variable to maximum fluorescence (F_v/F_m) values were higher in these two species. The minimal fluorescence (F_0) values were lower in *L. aurea* and *L. radiata* var. *pumila*. The diurnal changes of transpiration rate (*E*) in all four species presented only one peak, appearing between 11:00 h or 13:00 h. By using simple correlation analyses, it was observed that the environmental factors affecting P_N were different among four species and the main factors were photosynthetic photon flux density (PPFD) and relative humidity especially for *L. aurea* and *L. radiata*. The results of studying indicated that the four species could be divided into two groups. The species *L. radiata* var. *pumila* and *L. aurea* were more adapted to a relatively high irradiance, and *L. houdyshelii* and *L. albiflora* could be grown in moderate-shade environment in order to scale up their growth and productivity.

Additional key words: chlorophyll fluorescence; diurnal change; *Lycoris* species; photosynthesis.

Introduction

Lycoris Herb. (Amaryllidaceae) is comprised of about 20 species native to the subtropical regions of eastern Asia, of which 15 (10 endemic) are distributed in China. Most of the species are commonly cultivated in China, Japan, and the United States as bulbous plants (Hsu *et al.* 1994, Shi *et al.* 2006). The *Lycoris* species are all very popular bulb flowers worldwide with considerable acceptance as ornamental plant (Zhou *et al.* 2007). Most of the *Lycoris* species have been successfully cultivated. They are summer- and autumn-blooming plants of great beauty and common in the gardens of China, Japan, and the United States. In comparison with other well-known bulb flowers, such as narcissi and lilies, *Lycoris* has its own characteristics and merits. *Lycoris* comes into flower at a time when few other bulbous plants are active. The flowers are characterized by their pastel and plentiful colors as well as by beautiful and varied shapes (Hsu *et al.* 1994).

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Abbreviations: AQY – apparent quantum yield; C_i – intercellular CO_2 concentration; Chl – chlorophyll; *E* – transpiration rate; F_0 – minimal fluorescence of dark adapted state; F_v/F_m – ratio of variable to maximum fluorescence; g_s – stomatal conductance for CO_2; LCP – light compensation point; LSP – light saturation point; P_{max} – photon-saturated photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; T_{air} – air temperature.

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Recently, the demand for cut flowers of *Lycoris* has increased with diversification of flower consumption, so breeding of varieties with new flower forms and/or colors has become desirable for *Lycoris* (Katsukawa *et al.* 2000). Moreover, *Lycoris* species are all of medical value. For example, the compound galantamine, isolated from several plants including *Lycoris radiata* Herb., which was used in traditional Chinese medicine (TCM), is licensed in the United Kingdom for the treatment of mild to moderate neurodegenerative diseases such as Alzheimer's disease (AD) (Howes and Houghton 2003); the compound lycorine from *L. radiata* extract was an anti-SARS-CoV component and a candidate for the development of new anti-SARS-CoV drugs in the treatment of SARS (Li *et al.* 2005).

So far, studies of *Lycoris* have focused mainly on karyotypes (Bose 1963, Kurita 1987, Kurita 1988, Hsu *et al.* 1994, Zhou *et al.* 2007), morphology (Deng and Zhou 2005, Zhou *et al.* 2006), artificial propagation (Li *et al.* 2005), medicine (Howes and Houghton 2003, Li *et al.* 2005, Wu *et al.* 2005, Du *et al.* 2007), allozyme (Chung 1999) and molecular aspect (Ogawa *et al.* 2005, Shi *et al.* 2006, Hori *et al.* 2006, Zuo *et al.* 2008, He *et al.* 2010). Measurements of photosynthetic and morphological responses to light may reveal the tolerance of species to light intensity and have been useful in agriculture, ecology, forestry and horticulture (Aleric and Kirkman 2005, Wang *et al.* 2006). Efficient photosynthetic activity is necessary for the high production of plant biomass. Chlorophyll fluorescence is a quantitative and qualitative indicator of light-dependent photosynthetic processes, provides a nondestructive, rapid means of assessing both photochemical quantum yield and photoinhibition and has been widely employed as an indicator of plant response to stresses (Mauromicale *et al.* 2006, Mauro *et al.* 2011). Little is known about the leaf photosynthesis characteristics of *Lycoris* species (Guo *et al.* 2007, Zhou *et al.* 2010). The growth and photosynthetic responses of three *Lycoris* species with leaf appearing in spring to levels of irradiance were studied, and no attention was paid to the diurnal changes in gas exchange and chlorophyll fluorescence parameters of these species (Meng *et al.* 2008). In this study, we investigated the diurnal changes of P_N and relative parameters of four *Lycoris* species with leaf appearing in autumn, in addition to correlations between P_N and environmental factors by correlation analysis. This was done to help determine which factors limit gas exchange under field conditions for the four species. It was the final objective to provide basic information for their cultivation and promote their productivity.

Materials and methods

Plants and growing conditions: The experiment was conducted in autumn, 2007 in campus of Anhui Normal University (118º22'E, 31º20'N). The bulbs of four *Lycoris* species (*L. houdyshelii*, *L. aurea*, *L. radiata* var. *pumila* and *L. albiflora*) were introduced from mountains nearby in Anhui Province. The bulbs of four *Lycoris* species were planted on August 5, 2007 under identical conditions at the research station of Anhui Normal University. All four *Lycoris* species are bulbous perennial herbs with linear basal leaf, and all bulbs are elongated-ovoid, 3.0–4.5 cm in diameter. The experimental site had a similar temperate climate with the original location and an annual mean temperature 15°C, bright sunshine of 2,000 h; and 1,200 mm rainfall (Meteorological Station of the Wuhu, China). The main characteristics of the climate are windy, mild and rainy spring; hot, rainy summer with some storms; cool, dry, short autumn with later frosts; and long, cold winter with a litter snow. During the experiments, the bulbs were cultivated using standard methods and watered depending on the weather and soil moisture status.

Photosynthesis measurements: The leaves of all four species began to sprout out in early September. At the vigorous vegetation growth stage, the photosynthetic characteristics of the four *Lycoris* species were measured on clear days (November 21–23, 2007) throughout daytime from 7:00 h to 17:00 h at 2-h intervals. P_N, stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and E were measured using a hand-held photosynthesis system with flow rate 0.3 L min^{-1} and an open system (*CI-340*, *CID*, Camas, WA, USA). For measurements four bulbs of each species were selected with one leaf per bulb and the central portion of the attached leaf was used for measurement. The final value was the mean of four replicates.

Irradiance response of P_N: The response of P_N to step changes in PPFD was examined by a red + blue LED light source (*CI-301LA*, *CID*, Camas, WA, USA). The light-response curve measurements were carried out on the morning from 8:30 h to 11:30 h. The CO_2 concentration and air temperature in the leaf chamber were maintained at about 360 μmol mol^{-1} and 25 ± 2°C, respectively. The air humidity in the measuring chamber was about 65 ± 5%. The irradiance was designed as follows: 1,500; 1,200; 1,000; 700, 500, 400, 300, 200, 100, 50, and 0 μmol m^{-2} s^{-1} PPFD. Leaves were allowed to acclimate to each PPFD for a 5-min acclimation period. The steady-state gas-exchange properties were observed and logged, and subsequently the PPFD in the cuvette was changed for next observation at different irradiance level. Light-response curves were plotted using the mean values of P_N measured at each PPFD. Duplicate measurements were taken from the same leaf of four bulbs of each *Lycoris* species previously used for photosynthesis measurements. Four replicates were made. Apparent quantum yield (AQY) was calculated from the initial slopes by linear regression using PPFD values below 200 µmol m^{-2} s^{-1}. Light compensation point (LCP), light saturation point (LSP), and PPFD-saturated P_N (P_{max}) were estimated by the method of Bassman and Zwier (1991) and Zhou *et al*. (2010).

Chlorophyll (Chl) fluorescence: Parameters were monitored using a *CI-510CF* Chl Fluorescence Module (*CID*, Camas, WA, USA). Leaf clips were used to ensure the dark adaptation in field. Chl fluorescence was monitored on 10 different leaves. After at least 20 min of dark adaptation, the minimal level of Chl *a* fluorescence (F_0) was measured under modulated light intensity of 0.25 µmol m^{-2} s^{-1} and the maximal level of Chl *a* fluorescence (F_m) was induced by a 1-s saturating flash with the intensity of the saturating pulse being 3,000 µmol m^{-2} s^{-1} provided by the *CI-510CF* (Zhou *et al*. 2010). Variable Chl *a* fluorescence (F_v) equals F_m minus F_0. From the various fluorescence levels, the maximum quantum yield of PSII electron transport (F_v/F_m) was calculated (Schreiber *et al*. 1986).

Data analysis: P_N was calculated using the regression model ($P_N = P_{max}$ $(1-C_0$ $e^{-a\mathrm{PPFD}/P\mathrm{max}})$ (a, efficiency of quantum yield in weak light; C_0, constant); LCP was estimated using the model (LCP = P_{max} $\ln(C_0)/a$), and LSP was calculated by (LSP = P_{max} $\ln(100C_0)/a$) (Li *et al*. 2009). Standard error (SE) was calculated and differences in measured variables between treatments were analyzed by *ANOVA*, and the means were compared with *Student-Newman-Keuls*' multiple comparison tests. All tests for significance were done at $p<0.05$, unless otherwise indicated. All the analyses were performed using the "Statistical Package for Social Sciences" program (*SPSS 13.0, SPSS Inc.*, USA).

Results

Environmental conditions: As showed in Fig. 1*A*, PPFD increased rapidly and reached its maximum value at about 13:00 h after sunrise, and then declined. The air temperature increased with increase in PPFD just since morning. Thereafter the PPFD declined in the afternoon (Fig. 1*B*). The values of C_a at sunrise were remarkably higher than those at sunset (Fig. 1*C*). The diurnal change of RH was opposite to the diurnal changes of PPFD and T_a, with its minimum at about 13:00 h (Fig. 1*D*).

***P*$_N$-PPFD response of different species**: As the light-response curves of the four *Lycoris* species showed (Fig. 2), when the PPFD was below 150 µmol m^{-2} s^{-1}, all the curves responded linearly and rapidly. It suggested that all the four *Lycoris* species had relatively higher light-use efficiency under low irradiance, corresponding with the high values of apparent quantum yield (AQY) of these species being from 0.0676 to 0.0798. With the exception of *L. aurea*, the net assimilation in all species were almost constant with decreased light intensity until the PPFD was 300 µmol m^{-2} s^{-1}. The curve of *L. aurea* was gradually at a plateau, when the PPFD exceeded about 1,000 µmol m^{-2} s^{-1}. The P_{max}, LSP, and LCP of *L. aurea* were all remarkably higher than those of the other three species, with the values being 17.10, 1,189 and 14.9 µmol m^{-2} s^{-1}, respectively (Table 1).

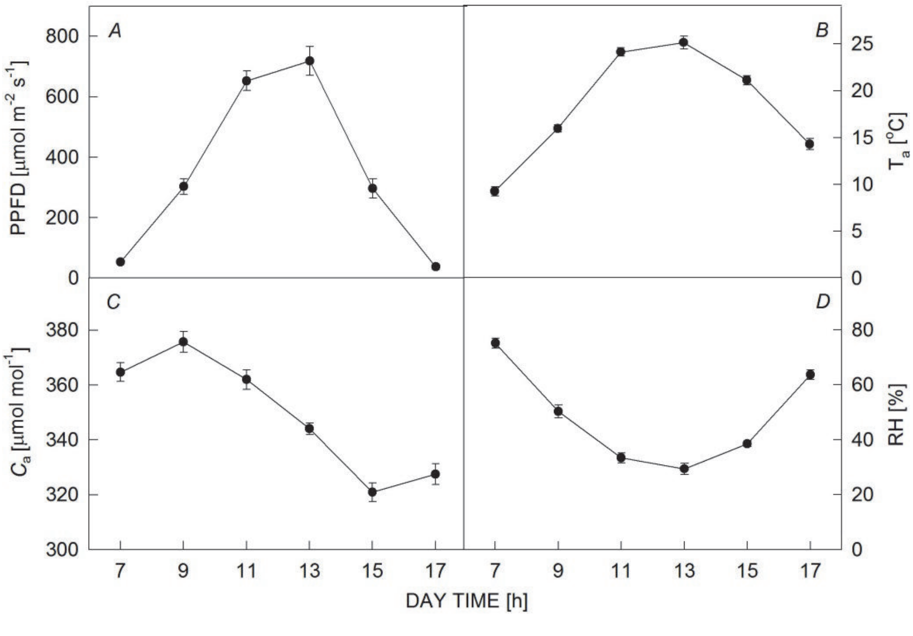

Fig. 1. Diurnal changes in photosynthetic photon flux density (PPFD) (*A*), air temperature (T_a) (*B*), air CO_2 concentration (C_a) (*C*), and relative humidity (RH) (*D*). Means ± SE, $n = 4$.

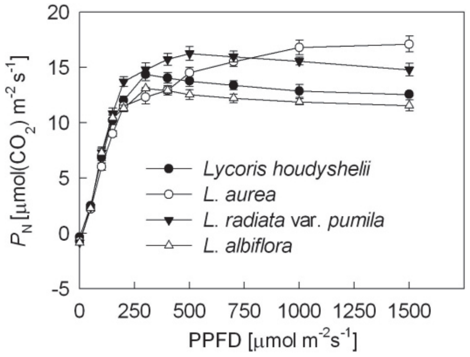

Fig. 2. Response of net photosynthetic rate (P_N) in four *Lycoris* species to photosynthetic photon flux density (PPFD). Means ± SE, *n* = 4.

P_N, g_s, C_i, and E of leaves: Diurnal changes of P_N showed similar patterns in *L. houdyshelii* and *L. albiflora* (Fig. 3*A*), where P_N increased steeply in the morning. After reaching a minimum at about 13:00 h, with a slow recovery in the later afternoon, finally P_N in all four species showed a sharp decline. The trend is typical of altiplano plants. However the species *L. radiata* var. *pumila* exhibited a slight decline in P_N to 11.19 μmol m^{-2} s^{-1} at 13:00 h during midday, and also had two peaks at 11:00 h and 15:00 h eventhough the second peak was not conspicuous. In contrast to the other three species, *L. aurea* had only one peak of P_N, reaching the maximum 14.66 μmol m^{-2} s^{-1} at about 11:00 h, and kept relatively high P_N during midday till 13:00 h, indicating *L. aurea* was more adapted to irradiance and high-temperature stress.

Table 1. Comparison of photosynthetic characteristics of four *Lycoris* species from P_N-PPFD response. (P_{max} – photon-saturated photosynthetic rate; LSP – light saturation point; LCP – light compensation point; AQY – apparent quantum yield). *Different letters* in superscript following the values in each column indicate significant differences ($p<0.05$) among 4 species. Means ± SE, *n* = 4.

Species	P_{max} [μmol m^{-2} s^{-1}]	LSP [μmol m^{-2} s^{-1}]	LCP [μmol m^{-2} s^{-1}]	AQY [mol mol^{-1}]
L. houdyshelii	14.36 ± 0.63^a	345 ± 18^a	8.11 ± 1.01^a	0.0721 ± 0.0034^{ab}
L. aurea	17.10 ± 1.06^b	1,189 ± 36^b	17.62 ± 1.06^b	0.0694 ± 0.0045^b
L. radiata var. *pumila*	16.26 ± 0.75^b	574 ± 23^c	13.12 ± 0.84^c	0.0798 ± 0.0012^a
L. albiflora	13.09 ± 0.93^a	322 ± 21^a	12.37 ± 1.27^c	0.0778 ± 0.0009^a

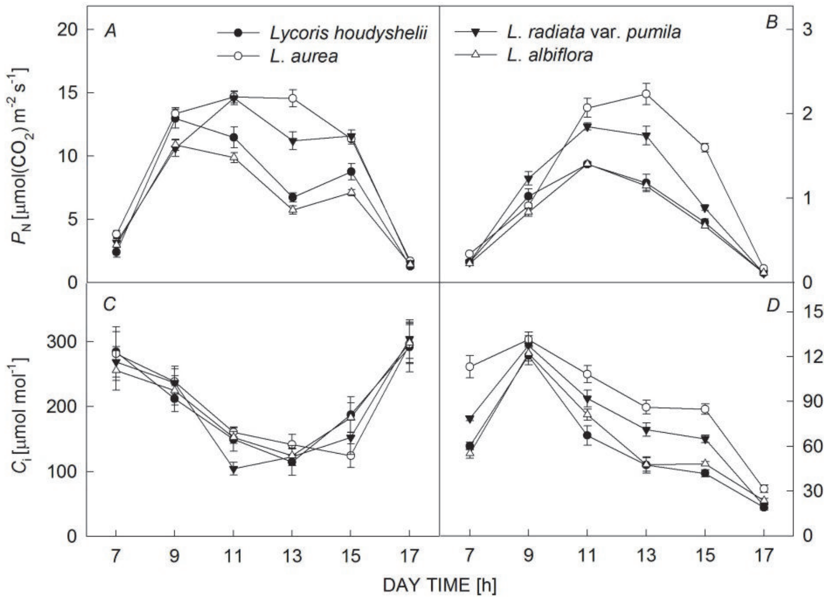

Fig. 3. The diurnal courses of net photosynthetic rate (P_N) (*A*), transpiration rate (E) (*B*), intercellular CO$_2$ concentration (C_i) (*C*) and stomatal conductance (g_s) (*D*) in leaves of four *Lycoris* species. Means ± SE, *n* = 4.

No significant difference in transpiration rate (E) was observed among all the four species (Fig. 3*B*), except that the values of E in *L. radiata* var. *pumila* and *L. aurea* were markedly higher than those in *L. houdyshelii* and *L. albiflora* during midday and the peak value of *L. aurea* appeared at about 13:00 h with the other three ones appearing at about 11:00 h (Fig. 3*B*).

The stomatal conductance (g_s) was lower at about 7:00 h than at about 9:00 h in all the four species (Fig. 3*D*), then decreased gradually towards the late afternoon. For the four species, C_i concentrations decreased in the first time towards midday, and then increased in the afternoon (Fig. 3*C*).

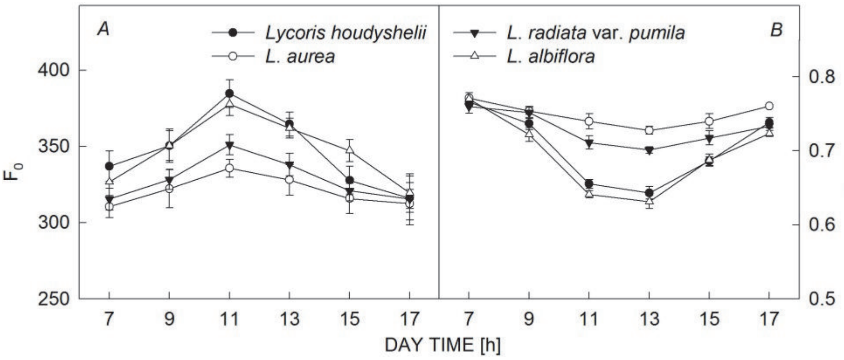

Fig. 4. Diurnal changes of chlorophyll fluorescence parameters in four *Lycoris* species. Means ± SE, $n = 10$.

Table 2. Correlation coefficient between net photosynthetic rate (P_N) in leaves of four *Lycoris* species and ecological factors. * – significant at the 0.05 level. $n = 4$. PPFD – photosynthetic photon flux density; T_a – air temperature; C_a – air CO_2 concentration; RH – relative humidity.

Species	Correlation coefficient between P_N and the parameter			
	PPFD	T_a	C_a	RH
L. houdyshelii	0.600	0.555	0.459	–0.637
L. aurea	0.871^*	0.805	0.273	$–0.881^*$
L. radiata var. *pumila*	0.861^*	0.808	0.102	$–0.887^*$
L. albiflora	0.580	0.511	0.535	–0.572

Chl fluorescence: The F_v/F_m in the both leaves of *L. radiata* var. *pumila* and *L. aurea* remained high (~0.74) throughout the day, and a decrease was observed during noon in the leaves of *L. houdyshelii* and *L. albiflora*, followed by a recovery in the late afternoon (Fig. 4*B*). The values of F_0 in the former two species were higher than those in the latter two species throughout the day. There were no significant differences in F_0 between the former two species, and the latter two species were the same (Fig. 4*A*).

Correlations between P_N and environmental factors in the leaves of *L. aurea* showed that PPFD and relative humidity had significant effects on P_N, of which relative humidity was negatively and significantly related with photosynthetic yield (Table 2). And *L. radiata* var. *pumila* was the same. No environmental factor had significant effects on P_N of *L. houdyshelii* and *L. albiflora*.

Discussion

The diurnal changes of gas-exchange and chlorophyll fluorescence parameters in four *Lycoris* species were studied in this paper. The findings presented here will improve our understanding of photosynthetic characteristics of the four species and assist in the optimization of irradiances needed to improve their productivity.

It is suggested that the photosynthetic capacity of a plant was determined to large extent by its natural habitat and itself, and some photosynthesis parameters, such as P_{max}, LCP, LSP and AQY were important factors for assisting in the optimization of growth irradiance and improving its productivity (Zhu and Ma 2009, Huang *et al.* 2009). As important indexes for determining the shade-tolerant ability in a plant, LCP and LSP could exhibit directly its photosynthetic capacity under poor irradiance environments. The lower the LCP of a plant, the higher its photosynthetic capacity; the lower the LSP of a plant, the less the time took for it to reach P_{max} with the PPFD increasing (Liu *et al.* 2007). For many sun plants, the range of LSP and LCP are about 1,500–2,000 µmol m^{-2} s^{-1} and 50–100 µmol m^{-2} s^{-1}, respectively; as to the shade plants, generally, LCP was below 20 µmol m^{-2} s^{-1} and LSP is lower than that of the sun plant (Jiang *et al.* 2004). The shade-tolerant plants have relatively large AQY and possess strong ability of capturing photons for photosynthesis in natural low light environments, with the AQY being from 0.02 to 0.05 (Osborne and Raven 1986, Lee *et al.* 1990, Liu *et al.* 2007). The values of LSP and LCP of the four species were all below 1,200 µmol m^{-2} s^{-1} and 20 µmol m^{-2} s^{-1}, respectively, and the values of AQY were all about 0.7, indicating that all the four species should share some photosynthetic characteristics of shade plants, such as low LSP, LCP, and high AQY. Comparing with *L. radiata* var. *pumila* and *L. aurea*, the values of light saturation points of both *L. houdyshelii* and *L. albiflora* were lower, suggesting that the latter two species could not efficiently utilize relatively strong light and could be considered as typical shade-loving plants. However, *L. aurea* had relatively higher LSP 1,189 µmol m^{-2} s^{-1}, indicating that it could acclimate to strong irradiance to some extent, corresponding with the high photosynthesis rate, suggesting it as a shade-tolerant plant preferring moderate-light environment.

L. houdyshelii and *L. albiflora* both showed typical two-peak patterns of diurnal photosynthesis changes and exhibited a distinct midday depression in P_N, and *L. radiata* var. *pumila* also experienced a slight depression. However *L. aurea* exhibited a single-peak curve. Stomatal limitation and nonstomatal limitation are both important factors resulting in decline of P_N in plant (Xu 1997). When C_i and g_s decreased simultaneously, the decline in P_N was mainly caused by stomatal limitation (Farquhar and Sharkey 1982). As shown in Fig. 3, the change of C_i and g_s was nearly similar in *L. houdyshelii* and *L. albiflora* at midday from 11:00 h to 13:00 h, and both showed declining trend. Therefore the decrease in P_N of the two species at midday was mainly under stomatal control and g_s appeared to be limiting factor in these two species.

Chl fluorescence measurements were performed on dark-adapted attached leaves of four *Lycoris* species. The F_v/F_m ratio indicates the intrinsic efficiency of PSII photochemistry (Wu *et al.* 1997). A reduction in F_v/F_m is often taken to indicate photoinhibition (Powles 1984). As shown in Fig. 4*B*, there were no significant differences in F_v/F_m measured at 7:00 h among four species, and all values were greater than 0.76. The value was slightly lower than the average of the values found in leaves of a wide range of C_3 species (0.83; Björkman and Demmig 1987). This indicated that the four species were either not stressed or were mostly unaffected by light stress in the morning (Li and Chen 2009). The values of F_v/F_m measured in the midday (12:00–14:00 h) showed transient slight decreases (1.7 % and 1.4 %, respectively) in *L. radiata* var. *pumila* and *L. aurea*, which is a general feature of photosynthesis in natural environment (Veres *et al.* 2002, Li and Chen 2009). In comparison decline was greater in *L. houdyshelii* and *L. albiflora* than in *L. radiata* var. *pumila* and *L. aurea*,. In the strong irradiance of midday, the values of F_v/F_m of the former two species were all higher than the latter two species, which proved that *L. radiata* var. *pumila* and *L. aurea* were more tolerant to high T_{air} and irradiance, corresponding to the results of the light-response curves. The damage of the apparatus of PSII often results in increase in F_0 (Wu *et al.* 1997). As shown in Fig. 4*A*, increases in F_0 suggested some damage of the apparatus of PSII or rearrangement of LHC complexes in *L. houdyshelii* and *L. albiflora* during midday.

Our study revealed for the first time that *L. radiata* var. *pumila* and *L. aurea* could be efficiently acclimated under field conditions, although the P_N of *L. radiata* var. *pumila* exhibited a slight decrease. The photosynthetic characteristics of four *Lycoris* species showed great differences. The correlation between the photosynthetic rate and environmental factors in the leaves of *L. radiata* var. *pumila* and *L. aurea* revealed that the two factors of primary importance were PPFD and relative humidity. Therefore these two environmental factors should be carefully considered for cultivation of *Lycoris* sp. *L. radiata* var. *pumila* and *L. aurea* were more adapted to a relatively high irradiance. *L. houdyshelii* and *L. albiflora* could be grown in moderate-shade environment in order to scale up its growth and productivity. We can choose the suitable species to cultivate and conditions of growth according to our aims in the future research and utilization.

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