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

K. LIU*, C.F. TANG*, S.B. ZHOU*, Y.P. WANG**, D. ZHANG*, G.W. WU*, and L.L. CHANG*

The Key Lab of Biological Resources Conservation and Utilization, College of Life Sciences, Anhui Normal University, Wuhu, 241000, P.R.China*
Anhui Agricultural University, Hefei, 230036, P.R.China**

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 (Pn) 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 (Fv/Fm) values were higher in these two species. The minimal fluorescence (F₀) 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 Pn 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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*Corresponding author; tel: +86 (0)551 5910810; e-mail: zhoushoubiao@vip.163.com

Abbreviations: AQY – apparent quantum yield; Ci – intercellular CO₂ concentration; Chl – chlorophyll; E – transpiration rate; F₀ – minimal fluorescence of dark adapted state; Fv/Fm – ratio of variable to maximum fluorescence; gₘ – stomatal conductance for CO₂; LCP – light compensation point; LSP – light saturation point; Pmax – photon-saturated photosynthetic rate; Pn – net photosynthetic rate; PPFD – photosynthetic photon flux density; Ta – 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. 2005, Zhou et al. 2006), 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 (Alerie 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 PN and relative parameters of four Lycoris species with leaf appearing in autumn, in addition to correlations between PN 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 (118°22'E, 31°20'N). The bulbs of four Lycoris species (L. houyshshelii, 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. PN, stomatal conductance (gs), intercellular CO₂ concentration (Ci) 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 PN:** The response of PN 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 CO₂ 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 PN 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 \(P_N\) (\(P_{\text{max}}\)) 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 \(P_N = P_{\text{max}} (1-C_0 e^{-aPPFD/P_{\text{max}}})\) (\(a\), efficiency of quantum yield in weak light; \(C_0\), constant); LCP was estimated using the model \(LCP = P_{\text{max}} \ln(C_0/a)\), and LSP was calculated by \(LSP = P_{\text{max}} \ln(100C_0/a)\) (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. 1A, 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. 1B). The values of \(C_a\) at sunrise were remarkably higher than those at sunset (Fig. 1C). 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. 1D).

**\(P_N\)-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 \(P_{\text{max}}\), 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).

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**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, \(n=4\).
Photosynthetic Characteristics of Four *Lycoris* Species

**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. 3A), 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$^b$                | 13.12 ± 0.84$^b$          | 0.0798 ± 0.0012$^a$ |
| *L. albiflora*     | 13.09 ± 0.93$^a$                 | 322 ± 21$^a$                | 12.37 ± 1.27$^a$          | 0.0778 ± 0.0009$^a$ |

No significant difference in transpiration rate ($E$) was observed among all the four species (Fig. 3B), 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. 3B).

The stomatal conductance ($g_s$) was lower at about 7:00 h than at about 9:00 h in all the four species (Fig. 3D), 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. 3C).
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*<sub>N</sub>) in leaves of four *Lycoris* species and ecological factors. * – significant at the 0.05 level. *n* = 4. PPFD – photosynthetic photon flux density; *T*<sub>a</sub> – air temperature; *C*<sub>a</sub> – air CO<sub>2</sub> concentration; RH – relative humidity.

| Species                    | Correlation coefficient between *P*<sub>N</sub> and the parameter |
|----------------------------|---------------------------------------------------------------|
|                            | PPFD  | *T*<sub>a</sub>  | *C*<sub>a</sub>  | 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<sub>v</sub>/F<sub>m</sub> 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. 4B). The values of F<sub>0</sub> in the former two species were higher than those in the latter two species throughout the day. There were no significant differences in F<sub>0</sub> between the former two species, and the latter two species were the same (Fig. 4A).

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*<sub>max</sub>, 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*<sub>max</sub> 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<sup>−2</sup> s<sup>−1</sup> and 50–100 μmol m<sup>−2</sup> s<sup>−1</sup>, respectively; as to the shade plants, generally, LCP was below 20 μmol m<sup>−2</sup> s<sup>−1</sup> 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<sup>−2</sup> s<sup>−1</sup> and 20 μmol m<sup>−2</sup> s<sup>−1</sup>, 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<sup>−2</sup> s<sup>−1</sup>, 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. albilflora 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. albilflora 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. 4B, 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. albilflora 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$_{o}$ (Wu et al. 1997). As shown in Fig. 4E, increases in F$_{o}$ suggested some damage of the apparatus of PSII or rearrangement of LHC complexes in L. houdyshelii and L. albilflora 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. albilflora 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.

References

Aleric, K.M., Kirkman, L.K.: Growth and photosynthetic responses of the federally endangered shrub, Lindera melissifolia (Lauraceae), to varied light environments. – Amer. J. Bot. 92: 682-689, 2005.

Bassman, J.H., Zwier, J.C.: Gas exchange characteristics of Populus trichocarpa, Populus deltoides and Populus trichocarpa × P. deltoides clones. – Tree Physiol. 8: 145-159, 1991.

Björkman, O., Demmig, B.: Photon yield of O$_2$ evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. – Planta 170: 489-504, 1987.

Bose, S.: A new chromosome number and karyotype in L. radiata. – Nature 197: 1229-1230, 1963.

Chung, M.G.: Notes on allozyme variation in Lycoris aurea. – Nature 251: 355-362, 2005. [In Chin.]

Du, F.Y., Xiao, X.H., Li, G.K.: [Microwave-assisted extractin of alkaloids in Lycoris radiata using ionic liquids solution.] – Chinese J. Anal. Chem. 11: 1570-1574, 2007. [In Chin.]

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Ann. Rev. Plant. Physiol. 33: 317-345, 1982.

Guo, Z.W., Guo, G.C., Xiong, Y.F., Xiong, H.R., Yue, S.X., Huang, Z.G.: [The photosynthesis physiology, cytology and cultural characteristics of Lycoris aurea Herb. and Lycoris radiata Herb.] – Acta Agric. Boreal-occident. Sin. 16: 136-141, 2007. [In Chin.]

He, Q.L., Cui, S.J., Gu, J.L., Zhang, H., Wang, M.X., Zhou, Y., Zhang, L., Huang, M.R.: Analysis of floral transcription factors from Lycoris longituba. – Genomics 96: 119-127, 2010.

Hori, T., Hanashi, A., Sanasuma, T., Kurita, S.: Genetic variation in the chloroplast genome and phylogenetic clustering of Lycoris species. – Genes Genet. Syst. 81: 243-253, 2006.

Howes, M.J., Houghton, P.: Plants used in Chinese and Indian traditional medicine for improvement of memory and cognitive function. – Pharmacol. Biochem. Be. 75: 513-527, 2003.

Hsu, B.S., Kurita, S., Yu, Z.Z., Lin, J.Z.: Synopsis of the genus Lycoris (Amaryllidaceae). – SIDA 16: 301-331, 1994.

Huang, H.Y., Dou, X.Y., Sun, B.Y., Deng, B., Wu, G.J., Peng, C.L.: [Comparison of photosynthetic characteristics in two
ecotypes of *Jatropha curcas* in summer.] – Acta Ecol. Sin. 29: 2861-2867, 2009. [In Chin.]

Jiang, G.M., Chang, J., Gao, Y.B.: [The main affected environment factors of photosynthesis.] – In: Jiang, G.M.: Plant Ecophysiology. Pp. 65-67. Higher Educ. Press, Beijing 2004. [In Chin.]

Katsukawa, K., Mori, G., Imanishi, H.: [Effect of applying naphthaleneacetic acid (NAA) onto stigma on fruit set and seed formation in interspecific hybrids between *Lycoris* species.] – J. Japan. Soc. Hort. Sci. 69: 224-226, 2000. [In Japanese with English summary.]

Kurita, S.: Variation and evolution in the karyotype of *Lycoris IV*. Intraspecific variation in the karyotype of *L. radiata* Herb. and the origin of this triploid species. – Cytologia 52: 137-149, 1987.

Kurita, S.: Variation and evolution in the karyotype of *Lycoris*, Amaryllidaceae VII. Modes of karyotype alteration within species and probable trend of karyotype evolution in the genus. – Cytologia 53: 323-335, 1988.

Lee, D.W., Bone, R.A., Tarsis, S.L., Storch, D.: Correlates of leaf optical properties in tropical forest sun and extreme two shade plants. – Amer. J. Bot. 77: 370-380, 1990.

Li, S.Y., Chen, C., Zhang, H.Q., Guo, H.Y., Wang, H., Wang, L., Zhang, X., Hua, S.N., Yu, J., Xiao, P.G., Li, R.S., Tan, X.H.: Identification of natural compounds with antiviral activities against SARS-associated coronavirus. – Antivir. Res. 67: 18-23, 2005.

Li, X.W., Chen, S.L.: Diurnal changes in gas exchange and chlorophyll fluorescence parameters of *Fritillaria cirrhosa* and *F. delavayi* under field conditions. – Photosynthetica 47: 191-195, 2009.

Li, X.W., Dai, Y., Chen, S.L.: Growth and physiological characteristics of *Fritillaria cirrhosa* in response to high irradiance and shade in age-related growth phases. – Environ. Exp. Bot. 67: 77-83, 2009.

Li, Y.P., Zhang, Q.F., Tang, G.G.: [Quick propagation of bulb-scale of *Lycoris radiata*.] – J. Nanjing Forest. Univ. 29: 103-105, 2005. [In Chin.]

Liu Y.Q., Sun X.Y., Wang Y., Liu Y.: [Effects of shades on the photosynthetic characteristics and chlorophyll fluorescence parameters of *Urtica dioica*.] – Acta Ecol. Sin. 27: 3457-3464, 2007. [In Chin.]

Mauro, R.P., Occhipinti, A., Longo, A.M.G., Mauronicale, G.: Effects of shading on chlorophyll content, chlorophyll fluorescence and photosynthesis of subterranean clover. – J. Agron. Crop Sci. 197: 57-66, 2011.

Mauronicale, G., Ierna, A., Marchese, M.: Chlorophyll fluorescence and chlorophyll content in field-grown potato as affected by nitrogen supply, genotype, and plant age. – Photosynthetica 44: 76-82, 2006.

Meng, P.P., Ge, Y., Cao, Q.J., et al.: Growth and photosynthetic responses of three *Lycoris* species to levels of irradiance. – HortScience 43: 134-137, 2008.

Ogawa, T., Tarumoto, I., Ma, B., Ueno, M., Kurita, S.: Genome differentiation in *Lycoris* species (Amaryllidaceae) identified by genomic *in situ* hybridization. – Breeding Sci. 55: 265-269, 2005.

Osborne, B.A., Raven, J.A.: Light absorption by plants and its implications for photosynthesis. – Biol. Rev. 61: 1-61, 1986.

Powles, S.B.: Photoinhibition of photosynthesis induced by visible irradiance. – Annu. Rev. Plant Physiol. 35: 15-44, 1984.

Schreiber, U., Schliwa, U., Bilger, W.: Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. – Photosynth. Res. 10: 51-62, 1986.

Shi S.D., Qiu Y.X., Li, E.X., Wu, L., Fu C.X.: Phylogenetic relationships and possible hybrid origin of *Lycoris* species (Amaryllidaceae) revealed by ITS sequences. – Biochem. Genet. 44: 198-206, 2006.

Veres, S., Mile, O., Láposi, R., Lakatos, G. y., Mészáros, I.: Interspecific variations of photochemical properties in a xerotherm grassland community. – Acta Biol. Szegediensis 46: 237-238, 2002.

Wang, G.G., Bauerle, W.L., Mudder, B.T.: Effects of light acclimation on the photosynthesis, growth, and biomass allocation in American chestnut (*Castanea dentata*) seedlings. – Forest Ecol. Manag. 226: 173-180, 2006.

Wu, F.L., Li, A.Z., Mao, H.F.: Determination of galanthamine in bulb of *Lycoris radiata* by RP-HPLC. – China J. Chin. Materia Med. 30: 523-525, 2005. [In Chin.]

Wu, H., Zhang, S.Y., Xu, D.Q., Guo, L.W., Shen, Y.G.: Diurnal and seasonal variations of non-photochemical quenching of chlorophyll fluorescence in sweet *Fiburnum* leaves.] – Acta Phytophysiol. Sin. 23: 145-150, 1997. [In Chin.]

Xu, D.Q.: Some problems in stomatal limitation analysis of photosynthesis. – Plant Physiol. Commun. 33: 241-244, 1997. [In Chin.]

Zhou, S.B., Liu, K., Zhang, D., Li, Q.F., Zhu, G.P.: Photosynthetic performance of *Lycoris radiata* var. *radiata* to shade treatments. – Photosynthetica 48: 241-248, 2010.

Zhou, S.B., Luo, Q., Li, J.H., Wang, Y.: Comparative anatomy of leaves in 12 species of *Lycoris* (Amaryllidaceae). – Acta Bot. Yunnan. 28: 473-480, 2006. [In Chin.]

Zhou, S.B., Yue, B.Q., Luo, Q., Hu, J.R., Bi, D.: Karyotypes of six populations of *Lycoris radiata* and discovery of the tetraploid. – Acta Phytotaxon. Sin. 45: 513-522, 2007.

Zhu, H., Ma, R.J.: Photosynthetic characteristics comparison between an invasive plant, *Lantana camara* L., and associated species. – Acta Ecol. Sin. 29: 2701-2709, 2009. [In Chin.]

Zuo, H., Yang, Z.L., Yang, X., Tan, Z.F., Yu, H.H.: Analysis of genetic diversity in *Lycoris radiata* using ISSR marker. – Forest Res. 21: 768-772, 2008. [In Chin.]