PHOTOSYNTHETICA 42 (4): 529-534, 2004

Gas exchanges of an endangered species *Syringa pinnatifolia* and a widespread congener *S. oblata*

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Abstract

Net photosynthetic rate (P_N), transpiration rate (E), water use efficiency (WUE), stomatal conductance (g_s), and stomatal limitation (L_s) were investigated in two *Syringa* species. The saturation irradiance (SI) was 400 µmol m^{-2} s^{-1} for *S. pinnatifolia* and 1 700 µmol m^{-2} s^{-1} for *S. oblata*. Compared with *S. oblata*, *S. pinnatifolia* had extremely low g_s. Unlike *S. oblata*, the maximal photosynthetic rate (P_{max}) in *S. pinnatifolia* occurred around 08:00 and then fell down, indicating this species was sensitive to higher temperature and high photosynthetic photon flux density. However, such phenomenon was interrupted by the leaf development rhythms before summer. A relatively lower P_N together with a lower leaf area and shoot growth showed the capacity for carbon assimilation was poorer in *S. pinnatifolia*.

Additional key words: high irradiance; photosynthesis; stomatal conductance; transpiration rate; water use efficiency.

Introduction

China is a distribution centre for *Syringa* genus. For example*,* 22 out of 27 *Syringa* species in the world are distributed here, with 18 species appearing only in China (Zang and Cui 2000). Geographically, most indigenous species are widely distributed in the southwest, northwest, north, and northeast of China (Wu 1991). *S. oblata* is generally found in North China, occurring at 300–2 000 m in altitude. As the merely endangered species of this genus, the limited individuals (Fu 1989) of *S. pinnatifolia* lie in the mountain areas (2 000–2 300 m a.s.l.) in Qinghai, Shanxi, Gansu, and Sichuan provinces where summer is cool and full of sunlight (Chang and Qiu 1992). Bearing pinnate leaves, it is an important species for tracing the origin and evolution of the *Syringa* genus, because of its intermediate position in systematic evolution (Kim and Robert 1998). Unfortunately, in the past few decades this species has experienced extensive destruction from humans. The plants have been dug excessively for a medical purpose in their distribution areas (Song *et al*. 1989).

Ex situ conservation is considered an effective method suitable for this endangered species. Nevertheless, we could only successfully realize batch propagation when the eco-physiological adaptations to potential stresses have become understood after a long-term domestication. Most studies on *Syringa* genus, however, have focused on matters such as nomenclature (Pringle 1983, Wallander and Albert 2000), molecular systematic evolution (Kim and Robert 1998), inter-specific relationships (Marsolais *et al.* 1993, Li *et al.* 2002), as well as tissue culture (Marks and Simpson 2000). There has been relatively little eco-physiological research conducted on *Syringa*, except for a limited physiological investigation of *S. vulgaris* (Caprio 1993). The physiological adaptations of *S. pinnatifolia* have never been conducted although *ex situ* conservation has been executed for many years in a number of botanical gardens in the world.

Because of the differential habitats, especially temperature difference between the origin and the introduced site, we have noted that *S. pinnatifolia* performed differently in half-shaded and full sunlight habitats from early spring to hot summer. We therefore need to know the eco-physiological differences between endangered and widespread species growing in our garden, so as to take the suitable measures in *ex situ* conservation. Further, observation on vegetative growth showed that *S. pinnati-*

Received 25 March 2004, *accepted* 20 August 2004.

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Abbreviations: E – transpiration rate; g_s – stomatal conductance; L_s – stomatal limitation; P_{max} – maximal photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; SI – saturating irradiance; WUE – water use efficiency.

Acknowledgements: We thank Ms. J. Yao for assistance in making field measurements. This work was jointly supported by Beijing Natural Science Fund (6002013), the Office of Agricultural Project, the Chinese Academy of Sciences (NK, Tenth Five-year Plan – C-13) and the Ministry of Science and Technology, the People's Republic of China (03EFN216600359).

folia could complete leaf growth before the onset of hot summer to avoid heat under high irradiance, while the widespread congeneric species *S. oblata* did not exhibit such special presents. Hence *S. pinnatifolia* must develop different physiological acclimation, and such acclimation has been engraved in the body of the species even though it was transplanted from its original habitats.

Therefore, the aim of this investigation was to perceive the differences in physiological adaptive strategy between the endangered and widespread congener, and to test if a new adaptive strategy had been well-established after a long-term domestication. Finally, proper cultivation methods for this precious species were suggested based on our research.

Materials and methods

Plants: The species were studied simultaneously in order to explore their different ecological and physiological characteristics. Seeds of both species were collected from field in the year of 1986 and then planted in the Botanical Garden, Institute of Botany of the Chinese Academy of Sciences (IB-CAS). *S. pinnatifolia* came from the mountainous areas of Gansu Province and *S. oblata* from the hill areas of Beijing City, the altitudes being 2 300 and 500 m, respectively (Table 1). For experiments, we only chose the vigorous plants growing in the same soil and well-watered conditions, with the tested branches tagged for making continuous observations and determinations in the year of 2003. The growth observation spanned all the growing seasons.

Table 1. Basic information of biological and ecological traits of the two species studied. *S. pinnatifolia* is an endangered species, while *S. oblata* is a widespread congener. Both species were introduced 17 years ago into the Botanical Garden of the IB-CAS. Sprouting on March 28.

	S. pinnatifolia	*S. oblata*
Distribution	West China	North China
Altitude [m]	2 000–2 800	300–2 000
Age [y]	17	17
Height (m)	1.6	1.8
Length of shoot [cm]	Less than 20	More than 20
Base diameter of shoot [mm]	3	6
Span of leaf growth [d]	37	100
Leaf area [cm^2]	2.4	98

Study area: The experiment was carried out in Beijing Botanical Garden, IB-CAS (39°48'N, 116°28'E, 76 m a.s.l.), where an annual mean temperature is 11.6 °C, the extreme maximum 41.3 °C, annual precipitation 634.2 mm, and the relative humidity 43–79 % (Tong 1997). The soil type in the garden belongs to alkaline soils with a pH of 8.0. The annual sunshine time is 2 780 h and effective accumulated temperature (≥10 °C) is 2 524 °C.

Gas exchange measurements were performed on June 5, 7, and 8, 2003 on all clear days. The highest photosynthetic photon flux density (PPFD) was 2 010 µmol m^{-2} s^{-1}, the concentration of CO_2 was 367 µmol mol^{-1}, and the air temperature was 37 °C. Photosynthesis was measured with a portable gas exchange system (*LCA*-4, *ADC*, Hoddesdon, UK). The leaf area was measured by an area meter (*AM100*, *ADC*). The fully expanded, healthy and mature leaves were used for measurements. Three replications were done. Data of net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were automatically recorded by the machine. Water use efficiency (WUE) was calculated as P_N/E. Diurnal measurements of gas exchange for the two species were made on three typical functional leaves at approximately 2-h intervals from 06:00 to 20:00 on clear days on June 25, 26, and 28, 2003. The leaf surface was held perpendicularly to the sunrays. An average of three measurements was taken as a measured value. L_s was calculated as $1 - C_i/C_a$, where C_i is intercellular CO_2 concentration and C_a is an ambient one (Berry and Downton 1982).

Data analysis: The data sets of photosynthesis were entered into an *EXCELL* spread sheet in *Windows 2000* and analysis of variance for measurements was made by a paired-sample *t*-test in *SPSS 10.0*. The graphs were processed by *Sigma-Plot 6.0*. Significant differences among different plants were reported at $p<0.05$, if not indicated otherwise.

Results

Photosynthesis: P_N of the two species responded differently to various PPFD (Fig. 1*A*). Saturation irradiance (SI) for *S. pinnatifolia* was about 400 µmol m^{-2} s^{-1}, and P_N went down when PPFD increased above SI. In *S. oblata*, P_N increased continuously with PPFD. At 1 700 µmol m^{-2} s^{-1}, P_N of *S. oblata* was 40 % higher than that of *S. pinnatifolia*. P_N values of *S. oblata* were significantly higher than those of *S. pinnatifolia* ($p<0.05$) when PPFD was above 800 µmol m^{-2} s^{-1}, while P_N for both species was similar under 400 µmol m^{-2} s^{-1}.

Stomatal conductance was positively correlated with PPFD for *S. oblata*. Its g_s was consistent with the increasing P_N. In *S. pinnatifolia*, however, g_s was extremely low and the fluctuation with PPFD was smaller (Fig. 1*D*). This result was further proved by the PPFD–L_s (Fig. 1*E*) and P_N–g_s curves (Fig. 2). Stomatal limitation in *S. pinnatifolia* was much stronger than in *S. oblata*.

Transpiration and WUE: *E* for both species increased along with PPFD elevation (Fig. 1*B*). However, *E* of *S. oblata* was about 2-fold higher than that of *S. pinnatifolia* throughout the PPFD treatments. WUE of *S. pinnatifolia* was higher than that of *S. oblata* when PPFD was less than 1 500 µmol m^{-2} s^{-1} (Fig. 1*C*). In particular, the increase in WUE for *S. pinnatifolia* emerged when PPFD was less than 600 µmol m^{-2} s^{-1}, however, WUE decreased when PPFD continued to increase, although a little fluctuation existed thereafter.

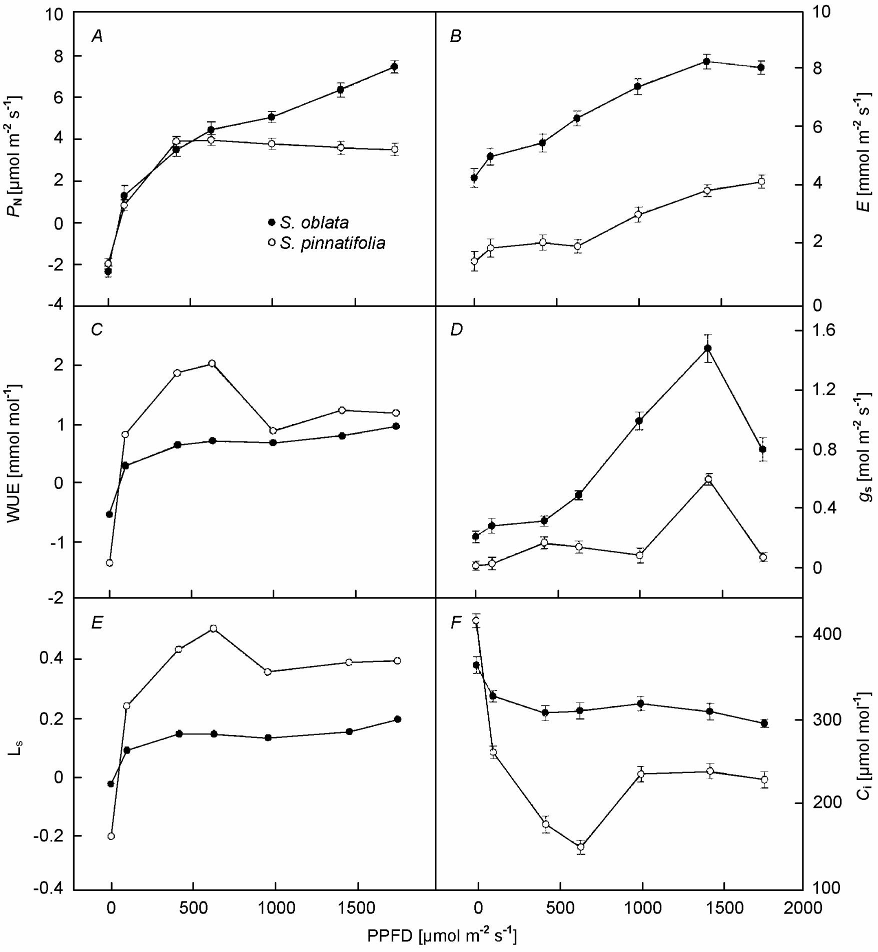

Fig. 1. Net photosynthetic rate, P_N (*A*), transpiration rate, *E* (*B*), water use efficiency, WUE (*C*), stomatal conductance, g_s (*D*), stomatal limitation, L_s (*E*), and intercellular CO$_2$ concentration, C_i (*F*) of *Syringa pinnatifolia* and *S. oblata*. Means±SE (*n* = 8).

Diurnal courses of photosynthetic parameters: The highest PPFD, approximately 2 010 µmol m^{-2} s^{-1}, normally occurred during the period of 12:00 to 16:00 of the experimental days. PPFD of 1 700 µmol m^{-2} s^{-1} emerged at 10:00 and the time with PPFD larger than that value continued for 8 h, with the air temperature above 35 °C in the afternoon (Fig. 3*A*). Leaf temperatures of both species were similar, but T_{leaf} of *S. pinnatifolia* was obviously higher owing to a weak stomatal regulation and a small evaporation at midday (Fig. 3*B,D,E*). P_N of *S. oblata* was significantly higher than that of *S. pinnatifolia* in diurnal courses. P_{sat} emerged nearly at 08:00 for *S. pinnatifolia* (PPFD was around 800 µmol m^{-2} s^{-1} at that time, but air temperature was lower than at midday), then P_N decreased till 16:00. P_{sat} in *S. oblata* peaked around 10:00 when PPFD reached 1 700 µmol m^{-2} s^{-1} and decreased later on. P_N of *S. oblata* was much higher than that of *S. pinnatifolia* all day long even though the magnitude of decrease was nearly the same (Fig. 3*C*). g_s of *S. pinnatifolia* was significantly lower than that of *S. oblata* throughout the day (Fig. 3*E*). Both species showed the depression of P_N and increase of C_i after 17:00, which was the result of decrease in PPFD (Xu 2002) and the non-stomatal limitation (Zhang *et al.* 2003).

Discussion

The requirements for photon energy were different for the endangered and widespread congener *Syringa* species after 17 years of *ex situ* cultivation (Figs. 1*A* and 3*C*). *S. pinnatifolia* (endangered) adopted a strategy of weak-light growth because of its sensitivity to higher environmental temperature. The substantial increase of P_N of *S. pinnatifolia* with PPFD (0–400 µmol m^{-2} s^{-1} in this experiment) could support this conclusion. The same trend was found in daily courses (Fig. 3*C*). P_N of *S. pinnatifolia* peaked approximately at 08:00, thereafter P_N was reduced. For the widespread congener *S. oblata* SI was as high as 1 700 µmol m^{-2} s^{-1} (Fig. 1*A*). The decreased P_N of *S. oblata* appeared at noon, which is in agreement with many other reports (Osmond *et al.* 1980, Jiang and Zhu 2001, Niu *et al.* 2003). The differences in the growing period of the two species could give further evidence. The growing season of *S. oblata* spanned 100 d from the end of March to the beginning of July despite of high PPFD and temperature in mid-summer. For *S. pinnatifolia*, however, a much shorter growing season of 37 d was noted. It sprouted at the same time as *S. oblate*, but stopped growing in early May. In the Beijing area, where our experiment was conducted, PPFD in the atmosphere changed with day and season (Yu and Khalil 1996), the zenith angle being large and irradiance low before May. The temperature in April was more favourable for the growth of *S. pinnatifolia* than in May, June, and July. Inevitable damage of photosynthetic apparatus was attributed to the excessive irradiation (Long *et al.* 1994, Demmig-Adams *et al.* 1994) especially when hot summer was coming. For *S. pinnatifolia* that originates in cool area, the combination of high temperature and high irradiance might be harmful. It could be the case of our observation: the leaves of *S. pinnatifolia* exposed to sunlight always speckled and the growth was weak, whereas those shaded by big trees developed very well. The results indicated that high temperature changed photosynthesis and then growth of *S. pinnatifolia*, after it was transplanted from a high altitude (2 300 m) to low altitude (75 m). Plants of *S. oblata,* however, were vigorous both in sunlight and shade. Some clear differences in leaf morphology between the two species give more explanation. The leaves of *S. oblata* are thick and dark green, while those of *S. pinnatifolia* are thin and light green (Rehder 1940). Increase in leaf thickness might alter the penetration of visible radiation into leaf tissues (Prabhat *et al.* 1997, Krauss *et al.* 1997), avoiding severe damages.

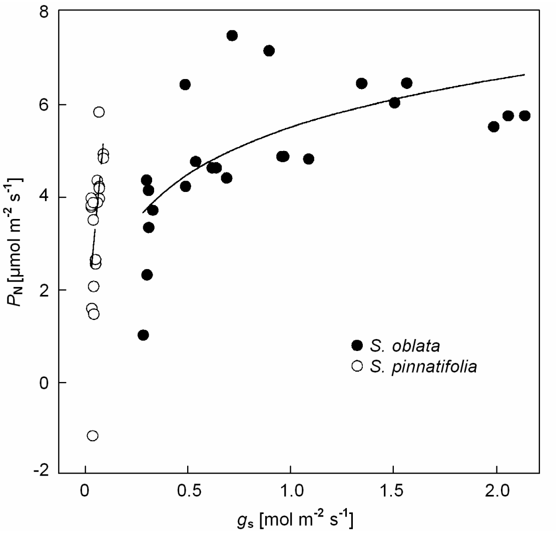

Fig. 2. Relationship between leaf net photosynthetic rate (P_N) and stomatal conductance (g_s) for *S. pinnatifolia* and *S. oblata*.

P_N in diurnal courses of *S. oblata* was notably higher than that of *S. pinnatifolia* indicating a distinctive difference in carbon assimilation capacity of the two species. Most of photons captured by photosynthetic apparatus were used for carbon assimilation in *S. oblata,* while in *S. pinnatifolia* more photons were dissipated with less carbon assimilation. *S. oblata* has much larger leaf area and shoot biomass, much taller and bigger canopy, and bears more fruits and seeds (Zang and Cui 2000). This widespread species has an extraordinary photosynthesis efficiency (Xu 1999), allocating enough assimilates into flowering, development of fruits, and growth of branches and roots especially throughout growing seasons. In the endangered *S. pinnatifolia*, however, lower P_N and growth under high temperature and irradiance were noted, implying the logical mechanism for the endangerment of this species.

Increase in g_s accompanying irradiance reflected a greater potential for carbon gain at a given conductance and associated transpiration costs (Thomas 1988). It might explain the high P_N of widespread species. We stated that the low P_N and the low biomass of *S. pinnatifolia* may be caused by low g_s under higher PPFD (Fig. 1*D*). Stomatal limitation led to low regulation of photosynthesis and growth (Kubiske and Abrams 1993). Stomatal limitation of *S. pinnatifolia* was significantly higher than that of *S. oblata* at a given PPFD (Fig. 1*E*), suggesting the lower P_N might be caused by a higher stomatal limitation. A similar conclusion can be drawn from the relationship between P_N and g_s (Fig. 2). The correlation between g_s and P_N could be represented by the P_N–g_s curve (Wong *et al.* 1979, Tadashi and Theodore 1999). Generally, a variable response of P_N to g_s could represent a close relationship between g_s and P_N (Ken and James 2003). If not, photosynthesis was regulated by non-stomatal factors (Farquhar and Sharkey 1982, Xu 1995), such as increased mesophyll conductance (Hugh 2002). It means that there existed a much weaker stomatal regulation for *S. pinnatifolia* compared with *S. oblata* and non-stomatal factors, for example, the biochemical control affected by assimilation (Wise *et al.* 1991) might exist as well for this endangered species.

The stomatal control over water loss by transpiration functions well (Soares and Almeida 2001). In *S. pinnatifolia*, a low g_s along daytime did benefit to obviously reduce *E* (Fig. 1*B*) and promote instantaneous WUE (Fig. 1*C*). The leaf temperature of *S. pinnatifolia* was higher than that of *S. oblata* (Fig. 3*B*), which was the result of low g_s and *E*. Higher leaf temperature might damage photosynthetic apparatus, aggravate the depression in P_N in midday (Jiang and Zhu 2001), and even affect the biochemical process. This is why the same *S. pinnatifolia* species bore different results when planted in different habitats: those under sunlight grew poorly while normally when shaded.

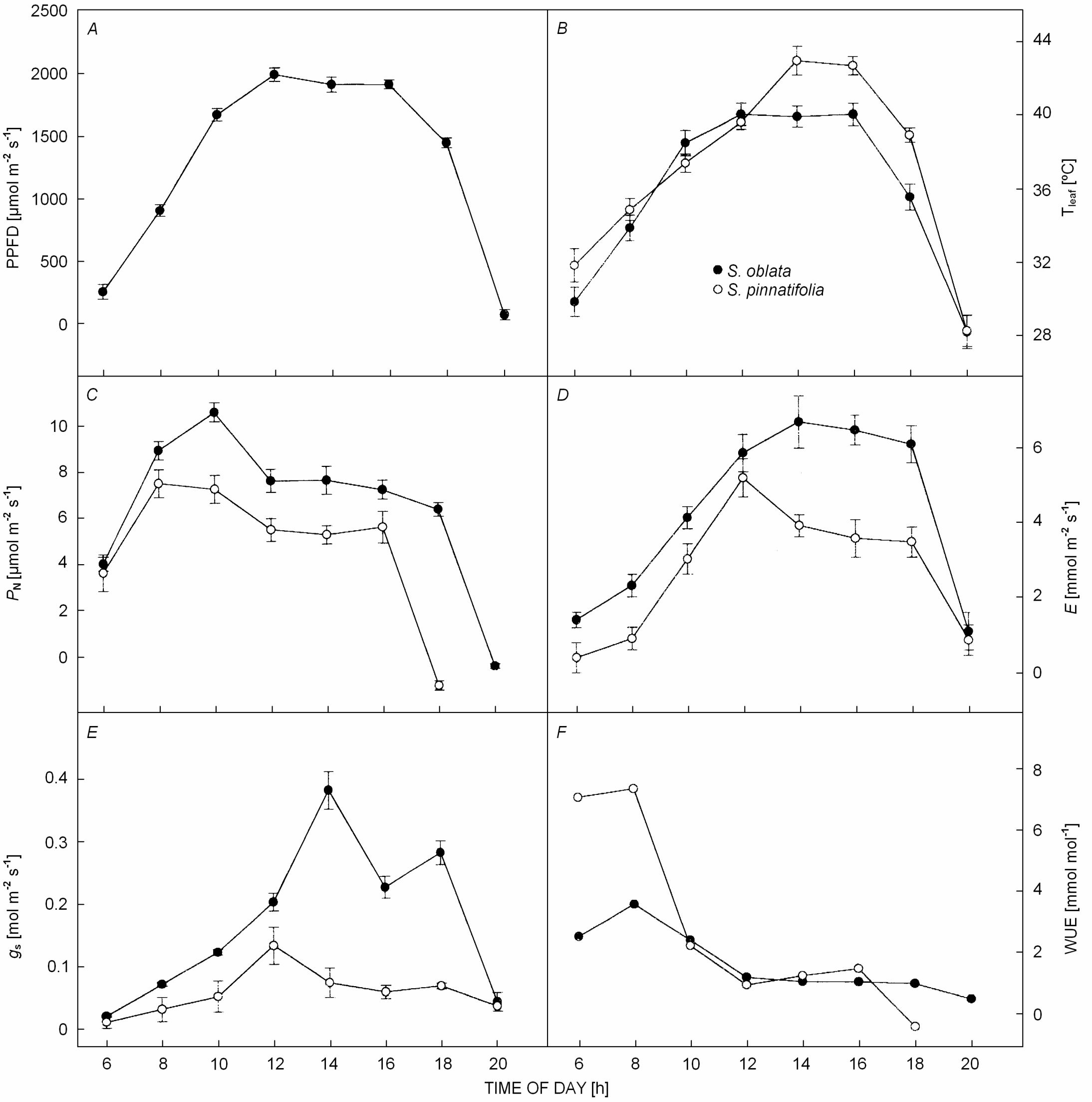

Fig. 3. Diurnal pattern in photosynthetic photon flux density, PPFD (*A*), leaf temperature, T_{leaf} (*B*), net photosynthetic rate, P_N (*C*), transpiration rate, *E* (*D*), stomatal conductance, g_s (*E*), and intercellular CO_2 concentration, C_i (*F*) of *Syringa pinnatifolia* and *S. oblata*. Means±SE ($n = 8$).

After *S. pinnatifolia* was transplanted from a habitat of high altitude and low temperature in summer to a new place of hot summer, it had to develop a new mechanism to resist high temperature. But this adaptation was limited, since a strong evaporation should be the embodiment of real adaptation to heat. It would be helpful to decrease the water content of cells, increase the concentration of salts and sugars, and slow the metabolism (Shang 2002). In fact, such a strong evaporation corresponding to high ambient temperature did not exist for *S. pinnatifolia*. Actually, this species had finally developed an evadable strategy in reducing photosynthesis and growth, resulting in limitation of its distribution extension. Practical significance of our finding, therefore, is that the shaded place with low summer temperature, high humidity, and moderate sunlight should be chosen for the *ex-situ* conservation of this endangered species.

References

Berry, J.A., Downton, W.J.S.: Environmental regulation of photosynthesis. – In: Govindjee (ed.): Photosynthesis. Vol. II. Pp. 263-343. Academic Press, New York – London – Paris – San Diego – San Francisco – São Paulo – Sydney – Tokyo – Toronto 1982.

Caprio, J.M.: Flowering dates, potential evapotranspiration and water use efficiency of *Syringa vulgaris* L. at different elevations in the western United States of America. – Agr. Forest Meteorol. **63**: 55-71, 1993.

Chang, M.C., Qiu, L.Q.: [Flora Reipublicae Popularis Sinicae. Tomus 61.] – Pp. 79-81. Science Press, Beijing 1992. [In Chin.]

Demmig-Adams, B., Adams, W.W., III: Capacity for energy dissipation in the pigment bed in leaves with different xantophyll cycle pools. – Aust. J. Plant Physiol. **21**: 575-588, 1994.

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

Fu, L.G.: [Rare and Endangered Plants in China.] – Pp. 242-243. Shanghai Education Press, Shanghai 1989. [In Chin.]

Hugh, J.E.: Stomatal and non-stomatal restrictions to carbon assimilation in soybean (*Glycine max*) lines differing in water use efficiency. – Environ. exp. Bot. **48**: 237-246, 2002.

Jiang, G.M., Zhu, G.J.: Effects of natural high temperature and irradiation on photosynthesis and related parameters in three arid sandy shrub species. – Acta phytoecol. sin. **25**: 525-531, 2001.

Jiang, G.M., Zhu, G. J.: Different patterns of gas exchange and photochemical efficiency in three desert shrub species under two natural temperatures and irradiances in Mu Us Sandy Area of China. – Photosynthetica **39**: 257-262, 2001.

Ken, W.K., James, A.A.: Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. – Aquat. Bot. **77**: 311-324, 2003.

Kim, J.K., Robert, K.J.: A chloroplast DNA phylogeny of lilacs (*Syringa*, Oleaceae): plastome groups show a strong correlation with crossing groups. – Amer. J. Bot. **85**: 1338-1351, 1998.

Krauss, P., Markstadter, C., Riederer, M.: Attenuation of UV radiation by plant cuticle from woody species. – Plant Cell Environ. **20**: 1079-1085, 1997.

Kubiske, M.E., Abrams, M.D.: Stomatal and nonstomatal limitations of photosynthesis in 19 temperate tree species on contrasting sites during wet and dry years. – Plant Cell Environ. **16**: 1123-1129, 1993.

Li, J.H., Alexander, J.H., Zhang, D.L.: Paraphyletic *Syringa* (Oleaceae): Evidence from sequences of Nuclear Ribosomal DNA ITS and ETS regions. – Syst. Bot. **27**: 592-597, 2002.

Long, S., Humphries, S., Falkowsky, P.G.: Photoinhibition of photosynthesis in nature. – Annu. Rev. Plant Physiol. Plant mol. Biol. **45**: 633-662, 1994.

Marks, T.R., Simpson, S.E.: Rhizogenesis in *Forsythia*×*intermedia* and *Syringa vulgaris*; application of a simple internode experimental system. – Plant Cell Rep. **19**: 1171-1176, 2000.

Marsolais, J.V., Pringle, J.S., White, B.N.: Assessment of random amplified polymorphic DNA (RAPD) as genetic markers for determining the origin of interspecific lilac hybrids. – Taxon **42**: 531-537, 1993.

Niu, S.L., Jiang, G.M., Li, Y.G., Gao, L.M., Liu, M.Z., Peng, Y., Ding, L.: Comparison of photosynthetic traits between two typical shrubs: legume and non-legume in Hunshandak Sandland. – Photosynthetica **41**: 111-116, 2003.

Osmond, C.B., Winter, K., Powles, S.B.: Adaptive significance of carbon dioxide cycling during photosynthesis in water-stressed plants. – In: Turner, N.C., Kramer, P.J. (ed.): Adaptation of Plants to Water and High Temperature Stress. Pp. 139-154. Wiley, New York – Chichester – Brisbane – Toronto 1980.

Prabhat, K.S., Preetha, A., Sangeeta, S., Rajendra, S.: Photochemical and biochemical changes in wheat seedlings exposed to supplementary ultraviolet-B radiation. – Plant Sci. **32**: 21-30, 1997.

Pringle, J.S.: A summary of currently accepted nomenclature at the specific and varietal levels in *Syringa*. – Lilac Newslett. **9**: 1-6, 1983.

Rehder, A.: Manual of Cultivated Trees and Shrubs. – Pp. 781-782. Macmillan, New York 1940.

Shang, Y.C.: [General Ecology.] – P. 39. Peking University Press, Beijing 2002. [In Chin.]

Soares, J.V., Almeida, A.C.: Modeling the water balance and soil water fluxes in a fast growing *Eucalyptus* plantation in Brazil. – J. Hydrol. **253**: 130-147, 2001.

Song, C.S., Xu, R.Z., Zhang, Q.H.: [Rare and Endangered Plants in China.] – Pp. 78. China Forest Press, Beijing 1989. [In Chin.]

Tadashi, H., Theodore, C.H.: Some characteristics of reduced leaf photosynthesis at midday in maize growing in the field. – Field Crops Res. **62**: 53-62, 1999.

Thomas, J.G.: Adaptation to sun and shade: A whole-plant perspective. – Aust. J. Plant Physiol. **15**: 63-92, 1988.

Tong, F.Q.: The Blossoming Botanical Gardens of the Chinese Academy of Sciences. Beijing Botanical Garden. – Science Press, Beijing 1997.

Wallander, E., Albert, V.A.: Phylogeny and classification of Oleaceae based on RPS 16 and TRNL-F sequence data. – Amer. J. Bot. **87**: 1827-1841, 2000.

Wise, R.R., Sparrow, D.H., Ortiz-Lopez, A., Ort, D.R.: Biochemical regulation during the mid-day decline of photosynthesis in field-grown sunflower. – Plant Sci. **74**: 45-52, 1991.

Wong, S.C., Cowan, I.R., Farquhar, G.D.: Stomatal conductance correlates with photosynthetic capacity. – Nature **282**: 424-426, 1979.

Wu, Z.Y.: The distribution style of seed-plant genus in China. – Acta bot. yunnan. Suppl.: 1-139, 1991.

Xu, D.Q.: [Photosynthetic rate, photosynthetic efficiency and the output of crops.] – Plant Physiol. Commun. **34**: 8-10, 1999. [In Chin.]

Xu, D.Q.: [Non-uniform stomatal closure and non-stomatal limitation of photosynthesis.] – Plant Physiol. Commun. **31**: 246-252, 1995. [In Chin.]

Xu, D.Q.: [Efficiency of Photosynthesis.] – Pp. 88, 137, 173. Shanghai Science Technical Press, Shanghai 2002. [In Chin.]

Yu, L., Khalil, M.A.K.: The distribution of solar radiation in the earth's atmosphere: the effects of ozone, aerosols and clouds. – Chemosphere **32**: 739-758, 1996.

Zang, S.Y., Cui, H.X.: [Lilac.] – Pp. 12-15. Shanghai Science Technical Press, Shanghai 2000. [In Chin.]

Zhang, S., Ma, K., Chen, L.: Response of photosynthetic plasticity of *Paeonia suffruticosa* to changed light environments. – Environ. exp. Bot. **49**: 121-133, 2003.