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Temperature-dependent gas exchange and stomatal/non-stomatal limitation to CO_2 assimilation of *Quercus liaotungensis* under midday high irradiance

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Abstract

The effects of varying leaf temperature (T_l) on some ecophysiological characteristics of photosynthesis for *Quercus liaotungensis* Koiz. under ambient radiation stress around midday on clear summer days were investigated using an IRGA equipped with a temperature-controlled cuvette. Net photosynthetic rate (P_N) decreased as T_l increased from 30 to 35 °C as a result of stomatal closure, whereas non-stomatal limitation led to decreased P_N in the T_l range of 35-45 °C. Decreased transpiration rate (E) and stomatal conductance (g_s) at leaf temperatures above 30 °C were interpreted as a combined 'feedward' effect as a result of enhanced leaf-air vapour pressure deficit (VPD) and stomatal closure. Changes in E from T_l 30 to 20 °C depended on VPD when g_s was maintained constant. Water use efficiency (WUE) varied inversely with T_l by following a hyperbola. A decrease in intercellular CO_2 concentration (C_i) occurred as a result of stomatal closure and a relatively high carboxylation capacity, whereas inactivation of mesophyll carboxylation in combination with photorespiration might be associated with the observed increase in C_i in the T_l range of 40 to 45 °C.

Additional key words: carboxylation rate; diurnal course of gas exchange; internal CO_2 concentration; photosynthesis; stomatal conductance; transpiration rate; water use efficiency.

Introduction

There is a significant midday depression of photosynthesis for most plants when the leaves are subjected to radiation stress. However, the mechanism of photosynthetic depression has not been completely elucidated, although much is known about the progress (*e.g.*, Powles and Björkman 1982, Terashima 1992, Björkman and Demmig-Adams 1994, Mott 1995, Demmig-Adams *et al.* 1996, Buckley *et al.* 1997). Most interpretations of midday depression of photosynthesis are based on radiation stress or related to irradiance.

However, there is an unavoidable concomitant heat stress when a leaf is exposed to high irradiance. Few studies have considered this concomitant heat stress, although temperature is one of the most important factors limiting photosynthesis. Photosynthetic yield and CO_2 uptake decrease or even cease as temperatures go beyond an optimal range. High temperature can change the thylakoid membrane, altering both its biochemical properties and functional organism (Berry and Björkman 1980, Pastenes and Horton 1996). A harder heat treatment leads to inactivation of the O_2-evolving complex with evidence of a K-peak at 200 µs in the fluorescence rise (Srivastava *et al.* 1997). Nash *et al.* (1985) found that heat stress damaged the photosystem 2 (PS2) complex by releasing functional manganese ions. Low temperature brings about phase transition in the bio-membranes, leading to metabolic disorders (Lyons 1973), inhibiting water-splitting side of PS2 (Havaux and Lannoye 1984) and suppressing re-oxidation of Q_A^- (Havaux 1987). PS2 is the most sensitive component of the photosynthetic system (Berry and Björkman 1980, Mamedov *et al.* 1993). Havaux (1996) reported that a 15-min treatment at 38 °C for 23 °C-grown potato leaves resulted in an obvious and preferential inactivation of PS2. However, at least to some extent, both cold acclimation (Krivosheeva *et al.* 1996) and short exposure to high temperatures under low irradiance (Schreiber and Berry 1977, Havaux and Strasser 1990, 1992, Havaux 1996) can result in significant increase in resistance to photoinhibition.

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Temperature stress may have impacts on CO_2/H_2O exchange by altering the leaf-air vapour pressure deficit (VPD). The traditional 'feedback' hypothesis states that stomatal response to VPD is mediated by transpiration effect on leaf water status or the gradient in water potential between guard cells and other epidermal cells. However, the 'feedback' mechanism is not consistent with observations of enhanced leaf water potential (Saliendra *et al.* 1995) or stomatal closure at high VPD with concomitant lower transpiration (Farquhar 1978). The latter is called the 'feedward' response: both transpiration and stomatal conductance (g_s) decrease as the leaf-air VPD increases (Farquhar 1978). Monteith (1995) presented a hypothesis for reinterpretation of most observations of stomatal responses to leaf-air VPD, in which stomatal closure as VPD increase is attributed to increased transpiration. Monteith (1995) reviewed stomatal response to VPD in the context of the 'feedback' mechanism. However, Bunce (1996) demonstrated that varying leaf water potential by transpiration had no effects on the response of g_s conductance to VPD, contradicting the hypothesis of Monteith (1995).

In this study, we made a controlled-temperature experiment for a field-grown mature woody plant *Quercus liaotungensis,* a predominant species of deciduous broad-leaved forests in the warm-temperate region of Northern China. The plants are frequently subjected to interactive stresses of low temperature-strong irradiance in the early-spring and high temperature-strong irradiance in the midsummer. Is leaf temperature (T_l) really involved in the midday depression of photosynthetic CO_2/H_2O gas exchange? To what extent is the temperature effect involved? How does the stomatal/non-stomatal limitation for the CO_2/H_2O gas exchange appear in response to varying T_l? Our objective was to quantitatively elucidate the relationship between T_l and CO_2/H_2O gas exchange under high irradiance stress, finding the answers to the questions given above.

Materials and methods

Study site and plants: Field studies were conducted in the permanent forest plots at the Beijing Forest Ecosystem Station (40°00'-40°02'N, 115°26'-115°30'E, altitude 1 100 m), Chinese Academy of Sciences, which is located in the Dongling Mountains, approximately 100 km west downtown of Beijing. In the Dongling Mountain area, annual rainfall is about 600 mm and precipitation in July-August accounts for 60-80 % of annual rainfall. Mean annual air temperature is about 5 °C, reaching *ca.* 18 °C in July-August. Between 800 and 1600 m, oak (*Quercus liaotungensis*) forest and mixed deciduous broad-leaved forest with *Q. liaotungensis* are the dominant forest types. Small areas of forests are dominated by birch (*Betula platyphylla* Suk., *B. dahurica* Pall., *B. costata* Trautv., *B. chinensis* Maxim.), poplar (*Populus davidiana* Dode.), and walnut (*Juglans mandshurica* Maxim.). Measurements of the top canopy leaves of mature *Q. liaotungensis* (about 17 m height) were obtained by means of a 24-m high steel tower that was installed for meteorological observations.

Gas exchange: P_N, g_s, E, and C_i were determined using a portable, open gas exchange system (*CI-301PS, CID*, Vancouver, USA) at midday under clear sky conditions from July 29 to August 6, 1998. The attachments of the gas exchange system included a PAR sensor for measurement of photon flux density and an infrared temperature sensor for measurement of air/leaf temperature. Measurements were made on 6-9 mature leaves at the top of tree crown. T_l in the cuvette was set to 10, 15, 20, 25, 30, 35, 40, and 45 °C through heating and cooling by adjusting the temperature-controller attached to the cuvette. The T_l was set in descending order from 30 to 10 °C and in ascending order from 30 to 45 °C. When the temperature was close to 10 °C, condensation of water vapour occurred. A full range of temperature measurements was made with 2-3 similar leaves, and 7-10 min was allowed for the chosen leaf to acclimate to a new temperature. About five measurements were taken at each T_l. A biochemical model for C_3 plants (Farquhar and Caemmerer 1982) was used to calculate maximum carboxylation rate (V_{max}), an indicator of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity.

Statistical analysis: The effect of T_l on the physiological parameters studied was analysed with one-way ANOVA using *Excel 97* (*Microsoft*, USA).

Results

Experimental variation of T_l from 10 to 45 °C had large impacts on P_N, g_s, and E of *Q. liaotungensis* at high irradiance (about 1 800 µmol $m^{-2} s^{-1}$) around noon. P_N decreased significantly when T_l was either below 15 °C or over 30 °C, whereas it increased slowly as T_l increased from 15 to 30 °C (Fig. 1*A*). The optimal T_l for P_N was around 25-30 °C.

A strong peak of E appeared at T_l of 30 °C (Fig. 1*B*). E decreased sharply when T_l was either below or above this critical temperature (30 °C).

The P_N *versus* C_i curve was used to assess mesophyll photosynthesis, which excludes stomatal effects (Terashima 1992). We plotted P_N/C_i against T_l to determine the effect of T_l on mesophyll photosynthesis (Fig. 1*C*): values close to the optimum for P_N/C_i were maintained at T_l as high as 35 °C, which is about 5 °C higher than the temperature optimum for P_N. This is consistent with the values of maximum carboxylation rate V_{max} (Fig. 1*D*). However, there was pronounced difference between the two parameters from T_l 35 to 40 °C: decrease in P_N/C_i was much greater than in V_{max}. There was a decrease in g_s in the T_l range of 10-20 °C, but g_s remained unchanged between T_l of 20 and 30 °C and then decreased at temperature above 30 °C (Fig. 1*E*). To analyse the changes in E and g_s, we plotted leaf-air vapour pressure deficit (VPD) against T_l (Fig. 1*F*). An exponential increase in VPD was found over the temperature range of 10-45 °C. C_i remained stable over T_l range of 10-30 °C but there was a marked drop in C_i in the T_l range of 30 to 35 °C, and subsequently a sharp increase at T_l between 40 and 45 °C (Fig. 1*G*).

The P_N/E ratio, an indicator of water use efficiency (WUE), showed a clear negative exponential decrease with increasing T_l (Fig. 1*H*). Thus, WUE was high at T_l between 15 and 10 °C, because E was low relative to photosynthesis within this T_l range. At T_l between 25 and 35 °C, WUE was low but constant, thereafter it declined towards zero at T_l range of 40-45 °C.

The effects of T_l on P_N, g_s, E, WUE, and P_N/C_i (mesophyll carboxylation) were analysed by one-way ANOVA (Table 1). The effects were highly significant (p<<0.001) for all parameters except g_s.

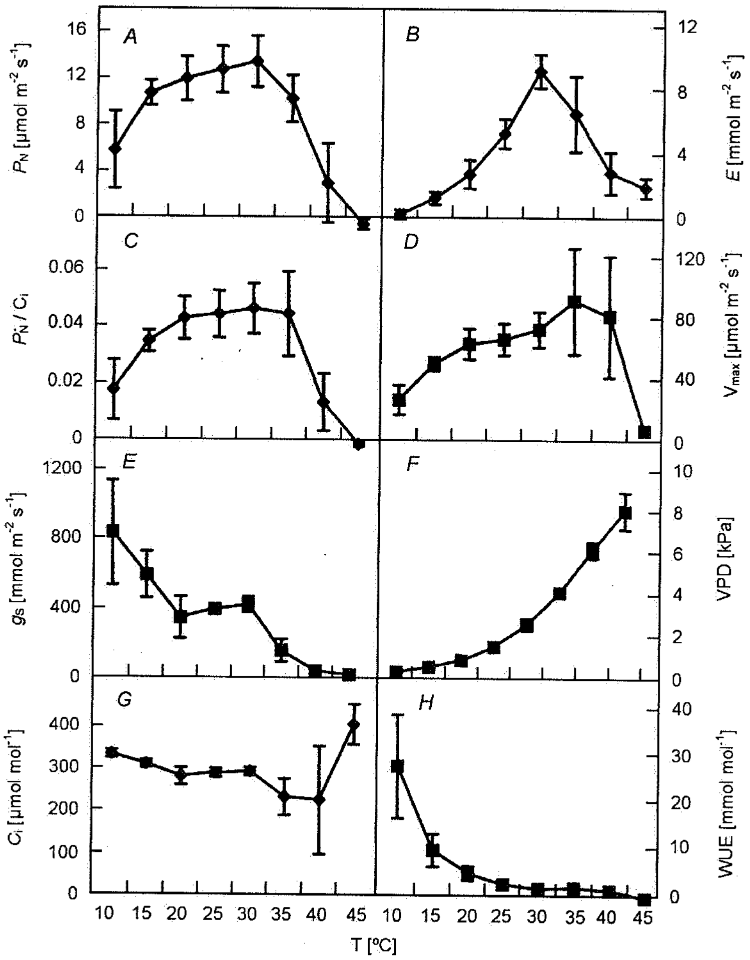

Fig. 1*A-H*. Effects of leaf temperature on net photosynthetic rate (P_N), transpiration rate (E), mesophyll carboxylation (P_N/C_i), maximum carboxylation rate (V_{max}), stomatal conductance (g_s), leaf-air vapour pressure deficit (VPD), intercellular CO_2 concentration (C_i), and water-use efficiency (WUE). The acclimation time at each leaf temperature was 7-10 min. The PFD during the measurements was 1 700-1 800 µmol m^{-2} s^{-1} at midday hours. Each point represents the mean and standard deviation of 3-7 repeated measurements.

Table 1. One-way ANOVA of net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), water use efficiency (WUE), P_N/PFD, and P_N/C_i in relation to different leaf temperature treatments (7-10 min). The PFD during the measurements was 1 700-1 800 μmol m^{-2} s^{-1} at midday hours. 3-7 repeated measurements at each leaf temperature. ***, $p<<0.001$; NS, not significant.

	Source of variation	SS	df	MS	F	P	F_{crit}
P_N	Leaf temperature (T)	1003.058	7	143.294	27.04303	1.87E-14***	2.211827
	Error	249.0409	47	5.298742			
E	Leaf temperature (T)	435.7873	7	62.25533	39.18942	1.59E-17***	2.211827
	Error	249.0409	47	5.298742			
g_s	Leaf temperature (T)	19322965	7	2760424	1.212071	0.315052 NS	2.211827
	Error	1.07E+8	47	2277444			
WUE	Leaf temperature (T)	12310.92	7	1758.703	25.19756	6.77E-14***	2.211827
	Error	3280.439	47	69.79658			
P_N/PFD	Leaf temperature (T)	0.000414	7	5.91E-5	27.13033	1.76E-14***	2.211827
	Error	0.000102	47	2.18E-6			
P_N/C_i	Leaf temperature (T)	0.01173	7	0.001676	9.149115	4.41E-7***	2.211827
	Error	0.008609	47	0.000183			

Discussion

Decreases in P_N at T_l above 30 °C resulted from either stomatal limitation or non-stomatal (biochemical) limitation. According to Farquhar and Sharkey (1982), the decreased P_N with simultaneously increased C_i in the T_l range 35-45 °C demonstrates that the decrease in P_N resulted from non-stomatal limitation. Such high T_l might inactivate photosynthetic enzymes, because both P_N/C_i (Fig. 1*C*) and V_{max} (Fig. 1*D*) decreased in this temperature range. Decrease in P_N resulting from biochemical limitation was also found in the T_l range of 15-10 °C as a result of inactivation of photosynthetic enzymes in response to low T_l. Based on the method of Farquhar and Sharkey (1982), if P_N and C_i decreases concomitantly, the criterion for assessing stomatal limitation or non-stomatal (biochemical) limitation rests on the changing direction of L (stomatal limitation): an increased L supports the conclusion that photosynthetic depression occurs in response to stomatal closure. Based on this criterion, the findings of concurrently decreased P_N (Fig. 1*A*), C_i (Fig. 1*G*), and sharply enhanced L (Fig. 2, L is calculated by the method of Berry and Downton 1982) indicate that the decrease in P_N in the T_l range of 30-35 °C is attributable to stomatal closure. Furthermore, we observed that V_{max} increased at T_l between 30 and 35 °C, whereas V_{max} decreased slightly at T_l between 35 to 40 °C. We therefore conclude that the decrease in P_N in the T_l range of 30-35 °C did not result from biochemical limitation.

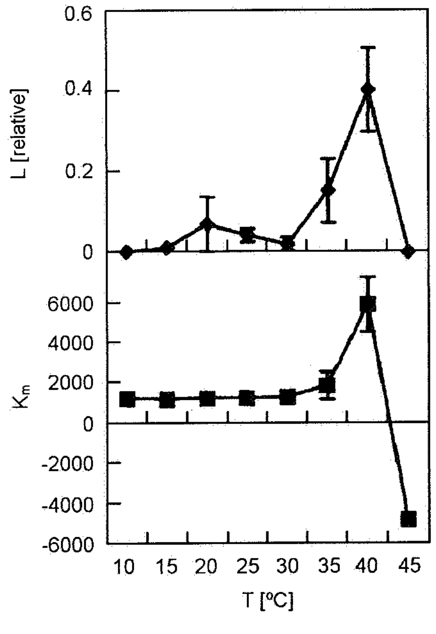

Fig. 2. Stomatal limitation (L) and Michaelis constant (K_m) as a function of leaf temperature. Each point represents the mean and standard deviation of 3-7 repeated measurements.

On a simple Michaelis-Menten approach we derive: $P_N = V_{max} C_i/(K_m + C_i)$, therefore, $K_m = C_i (V_{max} - P_N)/P_N$. K_m is the Michaelis constant and it is closely related to the structure of the RuBPCO. A sharp increase in K_m at T_l above 35 °C indicated that the structure of RuBPCO was transformed and the affinity between the enzyme and substrate decreased (Fig. 2, the negative value of K_m at 45 °C was due to the negative value of P_N). This was consistent with the concomitant decrease in P_N/C_i and V_{max} at T_l of 35-40 °C, suggesting that the decrease in P_N resulted from the biochemical limitation at this T_l range. V_{max} is proportional to the maximal enzyme-substrate concentration time, the rate constant K to the form of product as a function of temperature. The parameters V_{max} and K_m calculated by Farquhar and Caemmerer (1982) and Farquhar and Sharkey (1982) and Michaelis-

Menten's approaches refer only to the CO_2 concentration without considering other substrates such as ATP and NADPH. Therefore K_m and V_{max} are sensitive to the products of light reactions, ATP and NADPH. A mild heat treatment can transform active reaction centres into inactive ones, while a harder heat treatment can even inactivate the oxygen evolving complex, reducing electron transport and the synthesis of ATP and NADPH (Srivastava *et al.* 1997, Strasser *et al.* 2000), which may directly lead to drop in V_{max}.

A 'feedback' response of stomata to VPD was found over the T_{l} range of 30-45 °C, because both g_s and E decreased sharply with increasing VPD. Based on the method of Farquhar and Sharkey (1982), the above analysis of C_{i} and L also demonstrated that stomatal closure occurred in the T_{l} range of 30-35 °C.

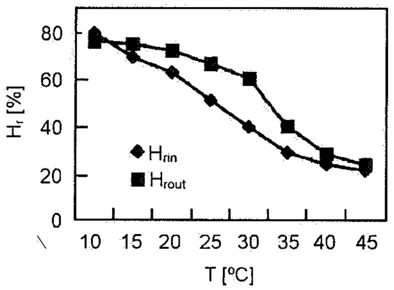

Fig. 3. Relative humidity difference ($H_{rout} - H_{rin}$) between cuvette outlet and inlet versus leaf temperature. The condensation occurred when leaf temperature was close to 10 °C.

Mott and Parkhurst (1991) concluded that stomata respond to transpiration rather than to VPD. This conclusion is consistent with the finding that over the T_{l} range of 30-20 °C, g_s remained almost constant although VPD changed (Fig. 1*E*), whereas E changed in parallel with VPD, indicating that E is affected by VPD when g_s is kept constant. For T_{l} from 20 to 10 °C, g_s was high, and C_{i} also remained high over the full range of T_{l} from 10 to 30 °C (Fig. 1*G*). This indicates that the decrease in E with decreasing T_{l} from 30 to 10 °C did not result from stomatal closure. Relative humidity of both inlet (H_{rin}) and outlet (H_{rout}) increased, as T_{l} decreased (Fig. 3). The difference in relative humidity between the outlet and inlet largely reflected the air stream trend in leaf transpiration (linear regression shown in Fig. 4, $r^2 = 0.8345$, $p < 0.001$). The difference in relative humidity between the outlet and inlet air stream reached a maximum at T_{l} of 30 °C, decreased gradually from T_{l} 30 to 10 °C, and decreased sharply from T_{l} 30 to 45 °C. From 30 to 35 °C, outlet relative humidity decreased by nearly 50 %. At T_{l} of 15 to 10 °C, although the stomata were open, the air in cuvette was nearly saturated with water vapour, so that the difference between the inter-cellular air moisture and air moisture in the cuvette was close to zero, and thus leaf E was very low.

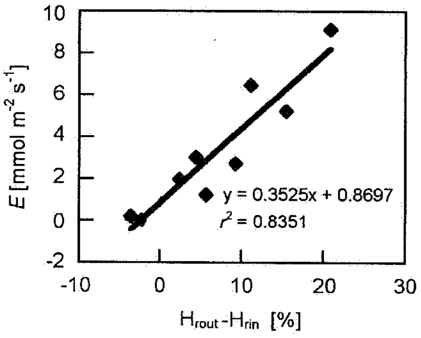

Fig. 4. Relationship between transpiration rate (E) and relative humidity ($H_{rout} - H_{rin}$) difference of cuvette outlet and inlet. The negative value means that condensation occurs when leaf temperature was close to 10 °C.

Stomatal closure can lead to a decrease of C_{i} from T_{l} of 30 to 35 °C when mesophyll cells maintain a relatively constant carboxylation capacity. We found a high carboxylation capacity (Fig. 1*C,D*) in the T_{l} range of 30-35 °C. The increase in C_{i} at T_{l} 40 to 45 °C might indicate that the stomata had reopened, which contradicts the values of E and g_s. According to P_N/C_{i} (Fig. 1*C*) and V_{max} (Fig. 1*D*), mesophyll carboxylation was almost completely inactivated when T_{l} were over 40 °C. At high temperatures the RuBPCO is favoured towards oxygenating reaction instead of carboxylating one because of the variations in temperature dependence of the solubility of CO_2/O_2 and the kinetic properties of RuBPCO decline at high temperature more in CO_2 solubility and K_O than in O_2 solubility and K_c. K_O and K_c are the Michaelis-Menten constants for carboxylation and oxygenation, respectively (Berry and Raison 1981, Brooks and Farquhar 1985, Lambers *et al.* 1998), which makes photorespiration proportionally dominant at high temperature. The optimal temperature range for leaf respiration exceeds that for photosynthesis by about 5 °C when subjected to high temperature stress (Pan and Dong 1995), which means that leaf photorespiration surpasses photosynthesis in its tolerance for high temperature (Sun and Sweet 1996). For T_{l} above 40 °C, carboxylation decreased substantially but photorespiration continued at a relatively high rate, so that the inactivation of mesophyll carboxylation in combination with photorespiration might contribute to the observed increase of C_{i} in this T_{l} range.

References

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

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.

Berry, J.A., Raison, J.K.: Responses of macrophytes to temperature. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology I. Pp. 277-338. Springer-Verlag, Berlin – Heidelberg – New York 1981.

Björkman, O., Demmig-Adams, B.: Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. – In: Schulze, E.-D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 17-47. Springer-Verlag, Berlin 1994.

Brooks, A., Farquhar, G.D.: Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas exchange measurements on spinach. – Planta **165**: 397-406, 1985.

Buckley, T.N., Farquhar, G.D., Mott, K.A.: Qualitative effects of patchy stomatal conductance distribution features on gas exchange calculations. – Plant Cell Environ. **20**: 867-880, 1997.

Bunce, J.A.: Does transpiration control stomatal responses to water vapour pressure deficit? – Plant Cell Environ. **19**: 131-135, 1996.

Demmig-Adams, B., Gilmore, A.M., Adams, W.W., III: *In vivo* functions of carotenoids in higher plants. – FASEB J. **10**: 403-412, 1996.

Farquhar, G.D.: Feedforward responses of stomata to humidity. – Aust. J. Plant Physiol. **5**: 787-800, 1978.

Farquhar, G.D., Caemmerer, S. von: Modelling of photosynthetic response to environmental conditions. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology II. Pp. 549-587. Springer-Verlag, Berlin – Heidelberg – New York 1982.

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

Havaux, M.: Effects of chilling on the redox state of the primary electron acceptor Q_A of photosystem II in chilling-sensitive and resistant plant species. – Plant Physiol. Biochem. **25**: 735-743, 1987.

Havaux, M.: Short-term responses of Photosystem I to heat stress. – Photosynth. Res. **47**: 85-97, 1996.

Havaux, M., Lannoye, R.: Effects of chilling temperatures on prompt and delayed chlorophyll fluorescence in maize and barley leaves. – Photosynthetica **18**: 117-127, 1984.

Havaux, M., Strasser, R.J.: Protection of photosystem II by light in heat-stressed pea leaves. – Z. Naturforsch. **45c**: 1133-1141, 1990.

Havaux, M., Strasser, R.J.: Antagonistic effects of red and far-red lights on the stability of photosynthesis II in pea leaves exposed to heat. – Photochem. Photobiol. **55**: 621-624, 1992.

Krivosheeva, A., Tao, D.-L., Ottander, C., Wingsle, G., Dube, S.L., Öquist, G.: Cold acclimation and photoinhibition of photosynthesis in Scots pine. – Planta **200**: 296-305, 1996.

Lambers, H., Chapin, F.S., III, Pons, T.L.: Plant Physiological Ecology. – Pp. 10-95. Springer-Verlag, New York 1998.

Lyons, J.M.: Chilling injury in plants. – Annu. Rev. Plant Physiol. **24**: 445-466, 1973.

Mamedov, M., Hayashi, H., Murata, N.: Effects of glycinebetaine and unsaturation of membrane lipids on heat stability of photosynthetic electron-transport and phosphorylation reactions in *Synechocystis* PCC6803. – Biochim. biophys. Acta **1142**: 1-5, 1993.

Monteith, J.L.: A reinterpretation of stomatal responses to humidity. – Plant Cell Environ. **18**: 357-364, 1995.

Mott, K.A.: Effects of patchy stomatal closure on gas exchange measurements following abscisic acid treatment. – Plant Cell Environ. **18**: 1291-1300, 1995.

Mott, K.A., Parkhurst, D.F.: Stomatal responses to humidity in air and helox. – Plant Cell Environ. **14**: 509-515, 1991.

Nash, D., Miyao, M., Murata, N.: Heat inactivation of oxygen evolution in Photosystem II particles and its acceleration by chloride depletion and exogenous manganese. – Biochem. biophys. Acta **807**: 127-133, 1985.

Pan, R., Dong, Y.: Photosynthesis and respiration. – In: Pan, R., Dong, Y.: Plant Physiology. 3rd Ed. Pp. 67-143. Higher Educational Press, Beijing 1995. [In Chin.]

Pastenes, C., Horton, P.: Effect of high temperature on photosynthesis in beans. – Plant Physiol. **112**: 1245-1251, 1996.

Powles, S.B., Björkman, O.: Photoinhibition of photosynthesis: effect on chlorophyll fluorescence at 77K in intact leaves and in chloroplast membranes of *Nerium oleander*. – Planta **156**: 97-107, 1982.

Saliendra, N.Z., Sperry, J.S., Comstock, J.P.: Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. – Planta **196**: 357-366, 1995.

Schreiber, U., Berry, J.A.: Heat-induced changes of chlorophyll fluorescence in intact leaves correlated with damage to the photosynthetic apparatus. – Planta **136**: 233-238, 1977.

Srivastava, A., Guissé, B., Greppin, H., Strasser, R.J.: Regulation of antenna structure and electron transport in photosystem II of *Pisum sativum* under elevated temperature probed by the fast polyphasic chlorophyll *a* fluorescence transient: OKJIP. – Biochim. biophys. Acta **1320**: 95-106, 1997.

Strasser, R.J., Srivastava, A., Tsimilli-Michael, M.: The fluorescence transient as a tool to characterize and screen photosynthetic samples. – In: Yunus, M., Pathre, U., Mohanty, P. (ed.): Probing Photosynthesis: Mechanism, Regulation and Adaptation. Pp. 445-483. Taylor & Francis, London – New York 2000.

Sun, O.J., Sweet, G.B.: Genotypic variation in light and temperature response of photosynthesis in *Nothofagus solandri* var. *cliffortioides* and *N. menziesii*. – Aust. J. Plant Physiol. **23**: 421-428, 1996.

Terashima, I.: Anatomy of non-uniform leaf photosynthesis. – Photosynth. Res. **31**: 195-212, 1992.