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PHOTOSYNTHETIC RESPONSE OF HIBISCUS PLANTS TO SHORT-TERM HUMIDITY CHANGE

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ZHANG, Y., XU H. L., DANSEREAU B. and GOSSELIN A. *Photosynthetic response of Hibiscus plants to short-term humidity change*. BIOTRONICS 25, 23–31, 1996. An experiment was conducted to examine the response of *Hibiscus* plants (*Hibiscus rosa-simensis* L.) to short-term change in air humidity. Photosynthetic capacity and quantum yield decreased when vapor pressure difference (VPD) of leaf to air increased from 0.8 to 1.5 kPa. Photosynthetic depression by high VPD was attributed to decreases in both leaf (g_L) and mesophyll (g_M) conductances. Under a high VPD as 2.5 kPa, net photosynthesis (P_N) showed oscillations with time. The amplitude of the cycle was decreased and the oscillation period was extended when the attached leaf was exposed to a lower light. The corresponding oscillation in g_L suggested that oscillation in P_N of *Hibiscus* in dry air was caused by the cyclic movement of stomata. The integrated results showed that hibiscus plants are sensitive to low air humidity.

Key Words : Photosynthesis ; leaf conductance ; mesophyll conductance ; humidity ; quantum yield ; oscillation.

INTRODUCTION

The humidity of the air surrounding a leaf affects photosynthesis by altering stomatal conductance (11, 14, 17, 20, 21, 30). In many species, stomata close in response to increased leaf-to-air vapor pressure difference (VPD), whereby CO_2 diffusion from the ambient air to intercellular space of the leaf decreases. However, a change in stomatal conductance does not necessarily affect photosynthesis to the same extent (3, 4, 12, 17). Usually, photosynthesis may be less affected than stomatal opening by low humidity if mesophyll conductance is not altered. Mesophyll conductance is the reciprocal of another resistance encountered by CO_2 diffusion from intracellular space to the carboxylation site (17). It has been argued whether or not mesophyll can be affected by low humidity (4, 14, 17, 30). Therefore, in this paper we involve the consideration of mesophyll conductance in response to low humidity. Moreover, the magnitude of humidity response of photosynthesis is dependent on species, growing conditions such as plant water status and light intensity (3, 4, 5, 10, 17, 30). Many researches have been conducted on humidity effect on photosynthesis and other physiological

processes (3, 4, 11, 12, 13, 16, 17, 20, 24, 30). However, few studies have been done on ornamental plants such as *Hibiscus*. In the present study, we introduced light into the relationship between photosynthesis and VPD and examined the photosynthetic responses of *Hibiscus* plants to the short-term alterations of these two environmental conditions. A phenomenon of photosynthetic oscillation, which is caused by cyclic changes in stomatal opening, is also discussed in the present work.

MATERIALS AND METHODS

Plant material and growth environment

Hibiscus plants (*H. rosa-sinensis* L.) were grown in 6-litre pots filled with a peat moss based substrate in a glasshouse during the summer of 1991. Air temperature was controlled at $23\pm2^{\circ}\text{C}$ during the day and $20\pm2^{\circ}\text{C}$ during night. Plants were watered every day and fertilized once a week with a nutrient solution of compound fertilizer (N : P : K = 20 : 20 : 20) at a concentration of 6 g per litre. Five months after the beginning of culture, when the plants developed with a height of about 40 cm, the recently expanded leaf was used for photosynthetic measurement in the laboratory.

Measurement of photosynthesis

Photosynthesis and transpiration were measured using two infra-red gas analyzers (ADC MK225, one for CO_2 and the other for vapor) in an open gas exchange system (22, 31). Leaf and air temperatures were measured using fine copper-constantan thermocouples pressed against the underside of the leaf blade and suspended under the leaf, respectively. An attached leaf was enclosed in an assimilation chamber, where the air temperature was $23\pm1^{\circ}\text{C}$ with fluctuations according to photosynthetic photon flux density (PPFD). The air in the leaf chamber was well circulated by a small fan to dissipate sensible heat from the leaf and provide uniform laminar air flow over the leaf surface. Dew points of the inlet air were controlled at 18 or 11°C , providing a VPD of 0.8 (control) or 1.5 kPa (low air humidity). Since the assimilation chamber was large (30 cm \times 25 cm \times 7 cm) and the enclosed leaf blade was small, VPD inside the chamber was only slightly higher than the inlet value despite the addition of vapor from leaf transpiration. The rate of air flow was set at 4200 ml min^{-1} . CO_2 concentration in air from the inlet of the chamber was 380 ppm. Light was supplied by two 1000 W high-pressure sodium vapor lamps suspended over a 15-cm deep water filter. PPF was increased from 0 through 170, 250 and 350 to 500 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for each measured leaf by changing the height of the lamps. At each PPF level the data were taken over fifteen min during which CO_2 concentration in the chamber stabilized. In cases to examine photosynthetic oscillations, the measurement lasted for over two hours at 2.5 kPa of VPD under a given PPF of either 550, 350 or 150 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Data of differences in CO_2 and water vapor concentration between inlet and outlet of the assimilation chamber, the leaf temperature and air temperature, and the PPFD were recorded once a minute by the computer.

After the photosynthetic measurement, leaf area was measured with a portable leaf area meter (Licor-3000). Photosynthetic rate and transpiration rate were calculated from these recorded data with leaf area. Leaf and mesophyll conductances were calculated from the data of photosynthesis, transpiration and vapor pressure difference of leaf to air (17, 29).

Analysis of photosynthesis light response curve

A rectangular hyperbolic equation (29) was used to fit the light-photosynthesis relation as follows.

$$P_N = P_C K_M I (1 + K_M I)^{-1} - R_D$$

Here, P_N is net photosynthetic rate; P_C is the theoretical saturation value of gross photosynthesis or photosynthetic capacity; K_M is the Michaelis-Menten constant, showing the reciprocal of the PPFD at which photosynthetic rate reaches half value of P_C . I is photosynthetic photon flux; R_D is dark respiration rate; and $P_C K_M$ shows the initial slope of the light-photosynthesis curve and is defined as quantum yield.

RESULTS

Effects of low humidity on photosynthetic light response curve and related variables

The light response curve of net photosynthetic rate (P_N) and corresponding curves of leaf conductance (g_L) and mesophyll conductance (g_M) are presented in Fig. 1. The photosynthetic variables from the analysis of the light response curve are presented in Table 1.

When VPD of the air surrounding the attached leaf increased from 0.8 to 1.5 kPa, P_N decreased by about 45–50% at all PPF levels (Fig. 1). Photosynthetic capacity shown by the value of P_C also decreased to the half value of the control (Table 1). At 1.5 kPa of VPD, g_L decreased by about 50% and g_M decreased by 40% at most PPF levels. This suggested that the photosynthetic depression by high VPD was attributed to decreases in both g_L and g_M although g_L was

Table 1. Photosynthesis-related variables for leaves of Hibiscus plants under different VPD in the leaf chamber. P_C is the photosynthetic capacity; P_{680} is the net photosynthetic rate at $680 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD; K_M , the Michaelis-Menten constant, showing the reciprocal of the PPFD at which photosynthetic rate reaches half value of P_C ; Y_Q , the maximum quantum yield; and R_D , the dark respiration rate

Variables	0.8 kPa	1.5 kPa	% Depression
P_C ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	17.9	10.1	44.4
P_{680} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	12.3	6.3	48.8
K_M ($10^{-3} \text{ m}^2 \text{s} \mu\text{mol}^{-1}$)	5.0	4.2	16.0
Y_Q ($10^{-2} \text{ mol CO}_2 \text{ mol}^{-1} \text{ PPF}$)	9.0	4.2	53.3
R_D ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.5	0.4	20.0

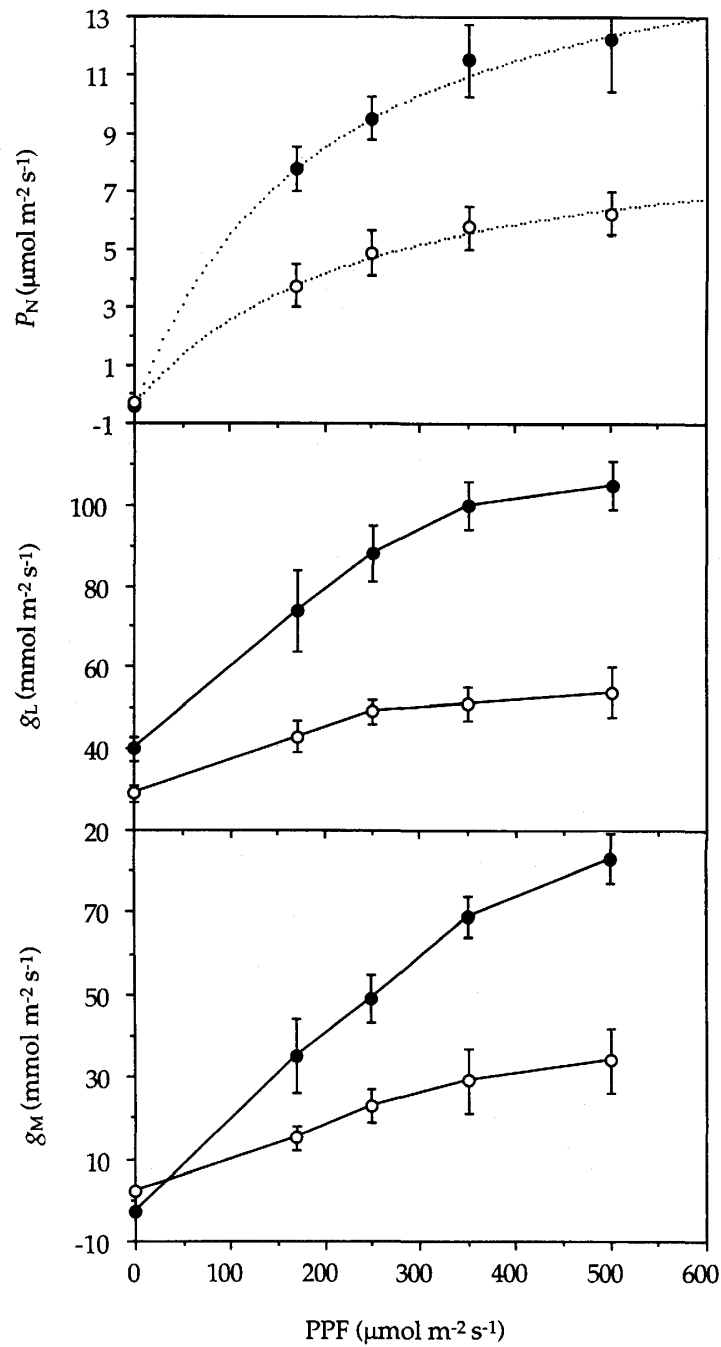


Fig. 1. Light response of net photosynthetic rate (P_N), leaf conductance (g_L), and mesophyll conductance (g_M), of *Hibiscus* leaves maintained at a VPD of 0.8 kPa (—●—) or 1.5 kPa (—○—). Each point shows the mean value of four samples with a vertical bar as standard error.

decreased more than g_M .

High VPD decreased the value of K_M to a small extent, in comparison with the effect on other photosynthetic variables (Table 1). However, quantum yield

or the maximum quantum use efficiency, shown by the value of $P_c K_M$, decreased by 53% by the high VPD. R_D was slightly lower under high VPD than under low VPD. The effect of high VPD on R_D was smaller than that on photosynthesis.

Photosynthetic oscillation induced by a high VPD

When VPD of the surrounding air of the attached leaf in the chamber was increased to 2.5 kPa, cyclic changes in P_N with time were observed. P_N increased gradually when the leaf was placed in the chamber and reached a maximum after about ten minutes and then started to decrease. Oscillation then occurred. The period of cycling was about 30 to 38, 40 to 50, and 32 to 40 min under PPF of 550, 350, and 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The amplitude of the oscillation varied with PPF. At 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, the amplitude was in the range of 9.7 to 10.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ without large fluctuation with time. The valley or

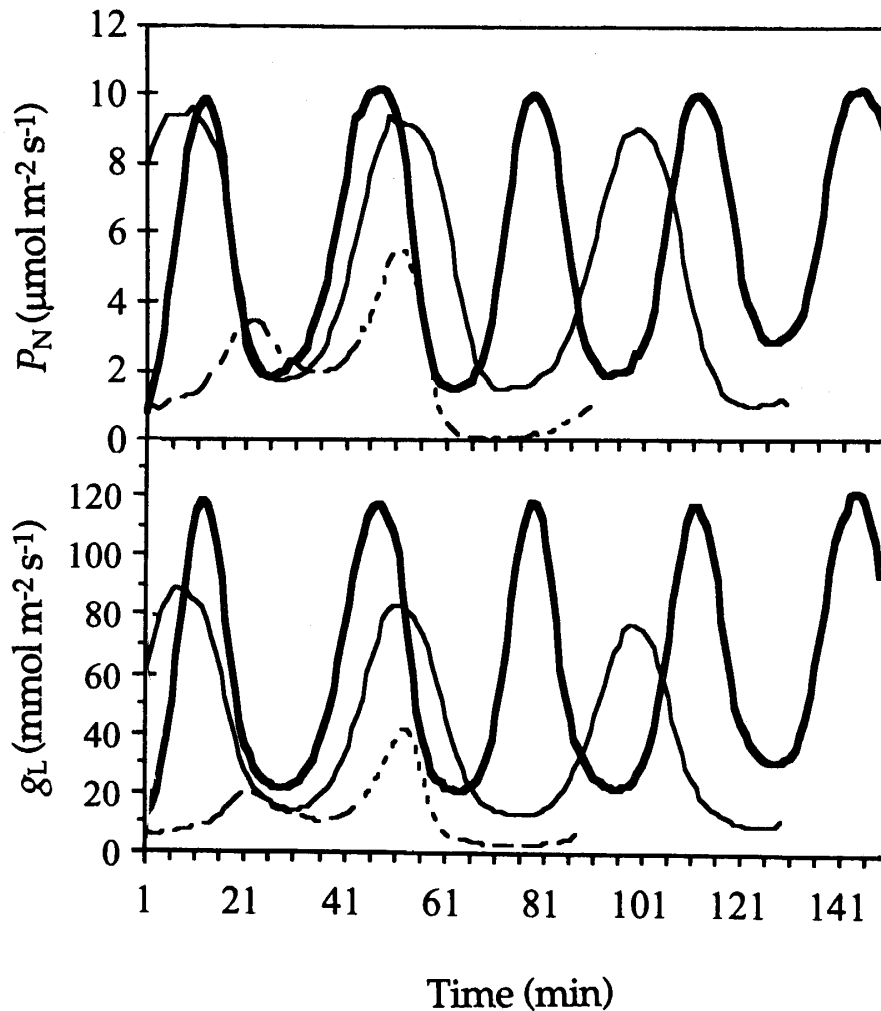


Fig. 2. Oscillation courses of net photosynthetic rate (P_N) and leaf conductance (g_L) of *Hibiscus* leaves maintained at a VPD of 2.5 kPa under PPF of 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (—), 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (— — —) and 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (---).

the minimum values of P_N increased with time from 1.6 to 3.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. There was a such large range of oscillation as about 8 to 10.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. When leaves were exposed to 350 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Fig. 2A), all of amplitude, valley and range decreased slightly. When PPF was as low as 150 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, the oscillation was much smaller than the above-mentioned two cases and irregular (Fig. 2, Table 2). Leaf conductance (g_L) showed similar oscillation patterns as P_N .

Table 2. Variables related to photosynthetic oscillation for leaves of Hibiscus plants at a VPD of 2.5 kPa under different PPF

Variables	$\mu\text{mol m}^{-2} \text{ s}^{-1}$ PPF		
	550	350	150
Plateau ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	10.2 \pm 0.5	9.3 \pm 0.7	4.1 \pm 1.2
Range ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	7.9 \pm 0.6	7.5 \pm 0.6	3.2 \pm 1.0
Valley ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	2.3 \pm 0.7	1.8 \pm 0.6	0.9 \pm 0.8
Period (min)	34 \pm 4	46 \pm 5	36 \pm 4

DISCUSSION

In our experiment, when VPD of the air surrounding the attached leaf increased from 0.8 to 1.5 kPa, photosynthesis at all PPF levels decreased to the half value of the control. This suggested that there was no interactive effect of PPF was added to that of high VPD. Here, the response of *Hibiscus* photosynthesis to low air humidity is different from most cases of other plants, where low air humidity shows additive effect with other environmental stresses on photosynthesis (3, 5, 21, 24, 28, 30). The photosynthetic depression by high VPD was attributed to decreases in both g_L and g_M . That was why photosynthesis was depressed to such an extent as 45–50%. Here, g_M shows the CO_2 diffusion speed from the mesophyll surface to the carboxylation. It is determined by the carboxylation activity, which affects diffusion by removing CO_2 from the path end, and the turgidity of mesophyll and chloroplast, which determines diffusion path length of CO_2 from the mesophyll surface to the carboxylation site. For most plants, a short-term VPD high as 1.5 kPa cannot depress photosynthesis very much because carboxylation is not inhibited by such a VPD (12, 17). However, from our results it is suggested that P_N in *Hibiscus* plants was reduced by high VPD in two ways: 1) stomata partially closed at high VPD, resulting in a decreased CO_2 diffusion through stomata; 2) CO_2 diffusion from the intracellular space to carboxylation site was reduced, which might be due to water deficit in mesophyll tissues. The results of the present study demonstrated that photosynthesis of *Hibiscus* plants are sensitive to low humidity in aspects of both stomatal function and non-stomatal activities. Moreover, quantum yield decreased 53% by the high VPD, suggesting that the activity of light

reaction was also inhibited by the high VPD in *Hibiscus* plants. The decrease in quantum yield might be another account for photosynthetic depression by high VPD.

In our experiment, the phenomenon of photosynthetic oscillation was also observed. When VPD in the chamber increased to 2.5 kPa, photosynthetic oscillation was observed. Oscillation is an abnormal photosynthetic response phenomenon that photosynthetic rate declines for a while, recovers to some extent and drops again, showing cyclic changes (1, 8, 15, 30). It is dynamics of water balance in response to changes in leaf water status. Previous studies suggested that in the case of a very high evaporation demand oscillation occurs to adjust the balance between water uptake and transpirational water loss (5, 12, 13, 16). When water uptake cannot balance the transpired water loss, leaf tissue loses its water and subsequently leaf turgor is reduced, and stomata close. Transpiration decreases when stomata close and water uptake surpasses transpiration water loss and leaf tissue stores excess water. When the stored water is much enough to rehydrate the leaf, stomata open again (30). This mechanism causes stomatal oscillation. Because oscillation occurs when transpiration demand is high, both high light and low humidity conditions may contribute to the cyclic change in net CO₂ assimilation. In our experiment, the range of the cycle, which shows the extent of oscillation, increased as PPF increased. This suggests that light intensity contributes to photosynthetic oscillation. Leaf conductance (g_L) showed similar oscillation patterns as P_N . This suggests that photosynthetic oscillation was mainly attributed to the cyclic changes in stomatal opening. Since there was no limitation in substrate water supply in this experiment, stomata aperture recovered well from closing when the leaf was rehydrated from the root. Therefore large oscillations in P_N were observed under 550 and 350 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD. The coordination between P_N and g_L demonstrated a stomatal control over this photosynthetic cycling. Cyclic changes in P_N have been observed in many plant species, such as cotton (10, 12, 27), soybean (3, 6), rice (26), oats (18), orange (19), peanut (15), rose (25) and tomato plants (30). For soybean plants (5), oscillation occurs at a VPD between 2.8 and 3 kPa, at 1.1 kPa for peanut leaves (15) and between 1.5 to 2.5 kPa for greenhouse grown roses (25). Results of the synchronized movement of P_N and g_L in many species have suggested that the oscillation in P_N is caused by oscillation in g_L , which is induced by dynamics of turgor in guard and subsidiary cells as affected by leaf water balance. Further studies are needed to determine if oscillations in P_N and g_L are related to some mechanisms other than water balance such as hormonal responses (2, 7, 9, 23).

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