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Eco-physiological modelling of leaf photosynthesis and adaptation analysis of Chinese ivy (*Hedera nepalensis* var. *sinensis*) in an evergreen broad-leaved forest in eastern China

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Abstract

The individual plant of Chinese ivy can produce three types of branches (creepy, climbing, and reproductive) during its development, which adapt to different environmental factors. An eco-physiological model was constructed to simulate leaf net photosynthetic rate (P_N) of Chinese ivy (*Hedera nepalensis* var. *sinensis*) in subtropical evergreen broad-leaved forest based on leaf physiological and mathematical analysis. The model integrated the rate-limiting biochemical process of photosynthesis and the processes of stomatal regulation. Influence of environmental factors (solar radiation, temperature, CO_2 concentration, vapour pressure deficit, *etc.*) on P_N was also considered in our model; its parameters were estimated for leaves on three types of branch in the whole growing season. The model was validated with field data. The model could simulate P_N of leaf on three types of branches accurately. Influence of solar radiation on leaf P_N of three types of branches in different seasons was analyzed through the model with numerical analysis.

Additional key words: CO_2 concentration; irradiance; simulation model; solar radiation; temperature; vapour pressure deficit.

Introduction

Irradiance is an important environmental factor that affects both plant morphology (such as shoot dry mass, shoot or internode length, leaf thickness, *etc.*), and leaf net photosynthetic rate, P_N (Yeh and Hsu 2004). Response of P_N to irradiance is influenced by transpiration through stomatal conductance (g_s), and transpiration rate (E) has obvious seasonal variation (Hauke and Schreiber 1998). P_N has seasonal differences (Da Matta *et al.* 1997, Ain-Lhout *et al.* 2004). Instantaneous P_N is the basis for calculating daily gross photosynthetic rate and growth rate of a plant. Therefore, it is very important to study the effects of photosynthesis on productivity and population regeneration. Only a few researches have dealt with the effect of irradiance on P_N in vines (Carter and Teramura 1988).

Modelling is necessary for understanding the mechanism of interaction among P_N, E, g_s, and environmental factors. A biochemical model for estimating P_N was proposed by Farquhar *et al.* (1980). This model was modified by many researchers (Caemmerer and Farquhar 1981, Collatz *et al.* 1991, Leuning 1995, Caemmerer 2000, Farquhar *et al.* 2001). These modifications do not undermine the Farquhar's model (Korzukhin *et al.* 2004) and make it more practical. The model has been applied to many plant species (Yu *et al.* 1998a, Mo *et al.* 2002, Jin *et al.* 2003, Zhang *et al.* 2004). However, species studied in these models are free-standing crops or trees and can get stable irradiance. Whether the model fits for non-free-standing vines is still unclear.

Vine plants cannot remain free-standing to appreciable height. Most forest vines have been described as "light hungry" (Putz 1984). In searching for high irradiance environment on top of canopy and at their edges, vines have developed a variety of climbing mechanics

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Abbreviations: C_i – intercellular CO_2 concentration; C_s – leaf surface CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_{max} – potential rate of CO_2 uptake per unit leaf area at photon saturation; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; Q_{10} – temperature sensitive coefficient of RuBPCO; R_D – respiration rate; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; T_a – air temperature; VPD – vapour pressure deficit; V_m – maximum carboxylation rate; α – quantum yield of photosystem; Γ – CO_2 compensation concentration; θ – parameters of the hyperbola.

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and associated characteristics (Castellanos *et al.* 1989). Climbing in vines is mainly constrained by support availability (Putz 1984), attachment success to the substrate (Penalosa 1982), and as a consequence of support attachment by photon availability. Vines have developed several strategies for "foraging" for photons and support, they grow horizontally and vertically across varying levels of resource availability (Penalosa 1983, Putz 1984). Exploitation of sites varying greatly in light and other available resources may be enhanced in vines by combining a number of physiological and morphological traits in their leaves (Putz and Mooney 1991). Furthermore, most vines exhibit significant changes in development from juvenile to adult stages—they are heteroblastic in Goebel's original sense of the term (Putz and Mooney 1991). The vine growth habit allows plants to live in the profound shade under vegetation, and then ascend to more direct exposure to sunlight (Putz and Mooney 1991).

Chinese ivy (*Hedera nepalensis* var. *sinensis*), a woody vine, is distributed widely in evergreen broad-leaved forest of Tiantong Mountain, Zhejiang province. An individual plant of Chinese ivy can produce three types of branches (creepy, climbing, and reproductive) during its development. These branches differ in morphology and growth behaviour. Creepy branch with few adventitious roots on node grovels along ground, usually distributing in the damp understory of forest. Climbing branch with a few adventitious roots, converted from creepy branch, climbs on or around trunk or branch of tree. Reproductive branch without adventitious root, transformed from climbing branch, extends horizontally outward. These different branches might adapt to different irradiances (weak, moderate, and intense) (Cai 1999). But till now no study analyzed the difference of physiological characteristics among them.

The aims of this study were: (*1*) to construct an ecophysiological model of photosynthesis of Chinese ivy in subtropical evergreen broad-leaved forest; (*2*) to estimate parameters for the model; (*3*) to model response of P_N to irradiance in whole growing season of leaves; (*4*) to analyze adaptation characteristics of Chinese ivy to environment.

Model description

The dependence of P_N on photosynthetically active radiation (PAR) [μmol m^{-2} s^{-1}] was modelled by Farquhar *et al.* (1980), Caemmerer and Farquhar (1981), Collatz *et al.* (1991), and Leuning (1995) by using the non-rectangular hyperbolic function. Essentially, their model can be presented as follows (Long *et al.* 1994):

$$\theta P^2 - (\alpha \mathrm{PAR} + P_{\max})\, P + \alpha \mathrm{PAR}\, P_{\max} = 0 \qquad (1)$$

P_N [μmol m^{-2} s^{-1}] is then given by:

$$P_N = P - R_D \qquad (2)$$

where α is quantum yield of whole-chain electron transport, θ is rate of bending toward the asymptote, $P_{\max}$ is the potential rate of CO$_2$ uptake per unit leaf area at photon saturation [μmol m^{-2} s^{-1}], and R_D is leaf respiration rate [μmol m^{-2} s^{-1}]. P in Eq. 2 is the smaller root of Eq. 1.

Variables used in the Eqs. 1 and 2 are calculated as follows:

Maximum quantum efficiency α is firmly depending on C_i (Ball *et al.* 1987), that is,

$$\alpha = \alpha_0\, (C_i - \Gamma)/(C_i + 2\,\Gamma) \qquad (3)$$

in which α_0 is potential quantum efficiency of CO$_2$ assimilation, C_i is intercellular CO$_2$ concentration [μmol mol^{-1}], Γ is CO$_2$ compensation concentration [μmol mol^{-1}], which is a function of temperature and can be computed as in Collatz *et al.* (1991) and Sellers *et al.* (1992):

$$\Gamma = 1.92 \times 10^{-4}\, O_2 \times 1.75^{(\mathrm{Ta}-25)/10} \qquad (4)$$

where O$_2$ is oxygen concentration [210×10^{3}μmol mol^{-1}] and T$_a$ is air temperature [°C].

In the non-rectangular hyperbola model of photosynthesis, C_i is assumed to be known, although in practice C_i is a continuously changing quantity with leaf surface CO$_2$ concentration C_s [μmol mol^{-1}], P_N, and g_s [μmol m^{-2} s^{-1}]. Based on the theory of gas transport, the following relationship was established:

$$C_i = C_s - P_N\, g_s^{-1} \qquad (5)$$

In stomatal conductance model proposed by Ball *et al.* (1987) and Leuning (1995), g_s has the following mathematical relation with P_N and C_s:

$$g_s = a_0 \frac{P_N}{(C_s - \Gamma)(1 + \mathrm{VPD}/\mathrm{VPD}_0)} + g_0 \qquad (6)$$

in which VPD is vapour pressure difference between air and leaf [Pa], and a_0, g_0, and VPD$_0$ are parameters. By setting $g_0 = 0$, we obtain the following formula:

$$C_i = C_s - (C_s - \Gamma)\,(1 + \mathrm{VPD}/\mathrm{VPD}_0)\, \alpha_0^{-1} \qquad (7)$$

Recall $P_{\max}$ in Eq. 1. It is determined by electron transport or end-product synthesis rates, and has the following mathematical relation with C_i:

$$P_{\max} = V_m \frac{(C_i - \Gamma)}{C_i + K_c(1 + o_i/K_0)} \qquad (8)$$

where o_i is the intercellular oxygen concentration [210×10^3 μmol mol^{-1}]; K$_c$ and K$_o$ are Michaelis coefficients for CO$_2$ and O$_2$, respectively. Following Sellers *et al.* (1992), $K_c = 300\times 2.1^{(\mathrm{Ta}-25/10)}$ μmol mol^{-1}, and $K_o = 300\,000\times 1.2^{(\mathrm{Ta}-25/10)}$ μmol mol^{-1}. V$_m$ is the maximum carboxylation rate [μmol m^{-2} s^{-1}] per unit leaf area when RuBP is saturated at T$_a$. For C$_3$ plants, V$_m$ is given by Collatz *et al.* (1991) and Bonan *et al.* (1993):

$$V_m = V_{m25}\, Q_{10}^{(Ta-25/10)}\, f(T) \qquad (9)$$

where V_{m25} denotes V_m at 25 °C, Q_{10} is temperature sensitive coefficient of RuBPCO, f(T) is temperature limitation factor, given as follows (Collatz *et al.* 1991, Bonan 1995):

$$f(T) = \left\{1 + \exp\left(\frac{-220\,000 + 710(T_a + 273)}{R(T_a + 273)}\right)\right\}^{-1} \qquad (10)$$

where R is the molar gas constant (8.314 J mol^{-1} K^{-1}).

Collatz *et al.* (1991) scaled R_D to the carboxylase content by:

$$R_D = 0.015\ V_m \qquad (11)$$

Simulation experiments

Study site: The field experiment was conducted in a subtropical evergreen broad-leaved forest in the National Forest Park of Tiantong Mountain (29º48′N, 121º47′E), Zhejiang province, south-east China. The mean annual temperature is 16.2 °C, the mean temperature being 28.1 °C in the warmest month (July) and 4.1 °C in the coldest month (January). The accumulated temperature ≥10 °C is 5 166.2 °C. The mean annual rainfall is 1 374.7 mm, of which 85 % is concentrated in the rainy reason from May to September (Song and Wang 1995).

Photosynthesis measurement: The experiment was conducted around 08:00 to 18:30 at about one-hour intervals during clear days in April, July, and October 2004. PAR, T_a, leaf temperature (T_l), air relative humidity (RH), C_i, C_s, vapour pressure difference (VPD) between air and leaf, P_N, E, and g_s were measured using portable photosynthesis system *HCM-1000*. The experiment design chose six individuals, and so six replications for each branch type were measured. The data were divided into two groups. One group was used to estimate parameters and the other one to validate the model.

Validations: The instantaneous P_N of leaves on three types of branches were computed, and then compared with field data to validate the model. The following three indexes were computed for each branch type to show the closeness of the estimated data to the measured ones: correlation coefficient (R), root mean square error (RMSE), and mean relative error (RE).

Results

Parameters estimation: Six parameters have to be estimated in Eqs. 1–11: θ, α_0, a_0, VPD_0, V_{m25}, and Q_{10}. With the measured T_a, C_i, C_s, and VPD, Γ was computed directly, and then the values of a_0 and VPD_0 were estimated through the nonlinear least square method using the *Statistica 6.0* computer program. By using the measured values of T_a, C_i, PAR, and P_N, parameters θ, α_0, V_{m25}, and Q_{10} in Eqs. 1–4 and Eqs. 8–11 were estimated. V_{m25} ranged from 1 to 100 (supposed lower and upper limit of V_{m25}) using the same method as for a_0 and VPD_0 (see Table 1).

Table 1. Estimated parameters in the model of leaf photosynthetic rate for Chinese ivy. For symbols see the text.

Season	Branch type	θ	α_0	a_0	VPD_0	V_{m25} [μmol m^{-2} s^{-1}]	Q_{10}
April	creepy branch	0.9	0.055	2.00	143.18	3.7	2.0
	climbing branch	0.9	0.039	2.05	119.47	5.3	1.1
	reproductive branch	0.9	0.041	1.87	169.22	7.5	0.9
July	creepy branch	0.7	0.061	3.69	153.17	5.1	3.5
	climbing branch	0.9	0.073	2.01	141.45	7.6	2.5
	reproductive branch	0.9	0.088	2.08	116.44	9.5	2.4
October	creepy branch	0.7	0.088	2.46	141.88	10.6	2.2
	climbing branch	0.8	0.098	2.29	168.48	14.5	3.6
	reproductive branch	0.9	0.094	2.44	123.29	15.9	3.7

Instantaneous photosynthesis simulation: Fig. 1 compares the estimated and measured instantaneous P_N of three types of branches during the daytime in different seasons. Since usually tens of measurements were made during the day, the measured and estimated P_N values are averages of these measurements and simulations.

The estimation of the instantaneous P_N with the model was close to the measured one (in Fig. 1). It was validated when the model was assessed by correlation coefficient, root mean square error, and mean relative error. For the three types of branches in different seasons, the estimated instantaneous P_N values were well correlated with the measured ones, root mean square error (RMSE) ranging from 0.238 to 1.158, and mean relative error (RE) from 0.100 to 0.595 % (Table 2).

As Fig. 1 shows, P_N of creepy branch was the lowest of the three branch types at early stage (April) of Chinese ivy. At the middle stage (July), leaf P_N of the three

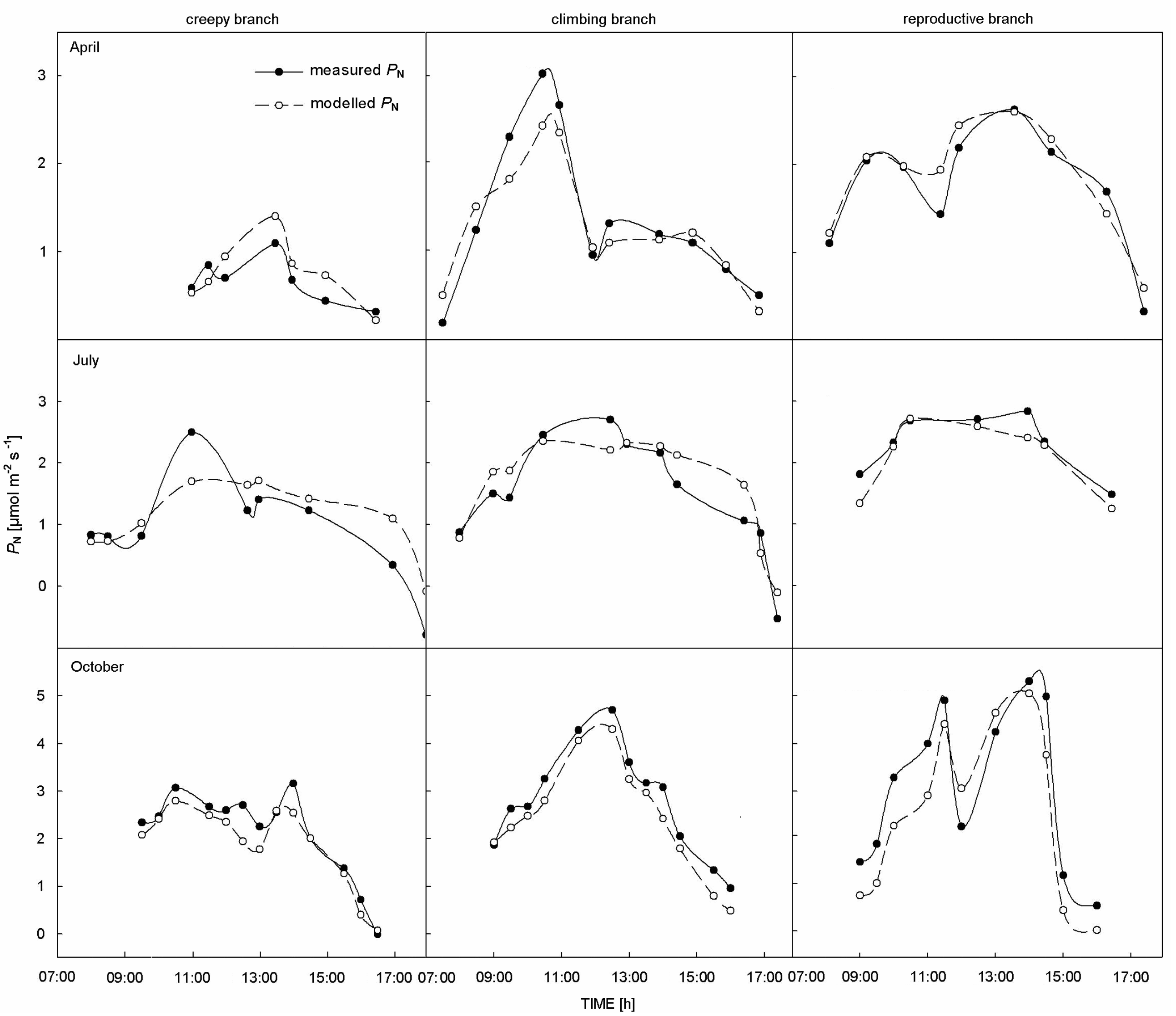

Fig. 1. Comparison of measured and estimated instantaneous net photosynthetic rate (P_N) among three types of branches of Chinese ivy.

Table 2. Validation analysis by comparing the estimated and measured net photosynthetic rates of Chinese ivy. Cre = creepy branch, Cli = climbing branch, Rep = reproductive branch.

	April			July			October		
	Cre	Cli	Rep	Cre	Cli	Rep	Cre	Cli	Rep
Number of samples	134	142	141	181	122	184	175	139	169
R	0.810	0.871	0.832	0.845	0.859	0.871	0.896	0.835	0.892
RMSE	0.238	0.432	0.386	0.542	0.480	0.436	0.492	1.158	1.023
RE	0.515%	0.451%	0.454%	0.595%	0.221%	0.190%	0.100%	0.249%	0.271%

branch types did not differ significantly, except that leaf P_N values of the creepy branch and climbing branch were slightly lower than that of the reproductive branch in the morning and evening. At the late stage (October), maximum leaf P_N of the reproductive branch was larger than that of the climbing branch, which was again larger than that of the creepy branch. Surprisingly, the order of change of P_N was opposite. In addition, with the growth of Chinese ivy the P_N change range in one day tended to increase during the season in the same branch.

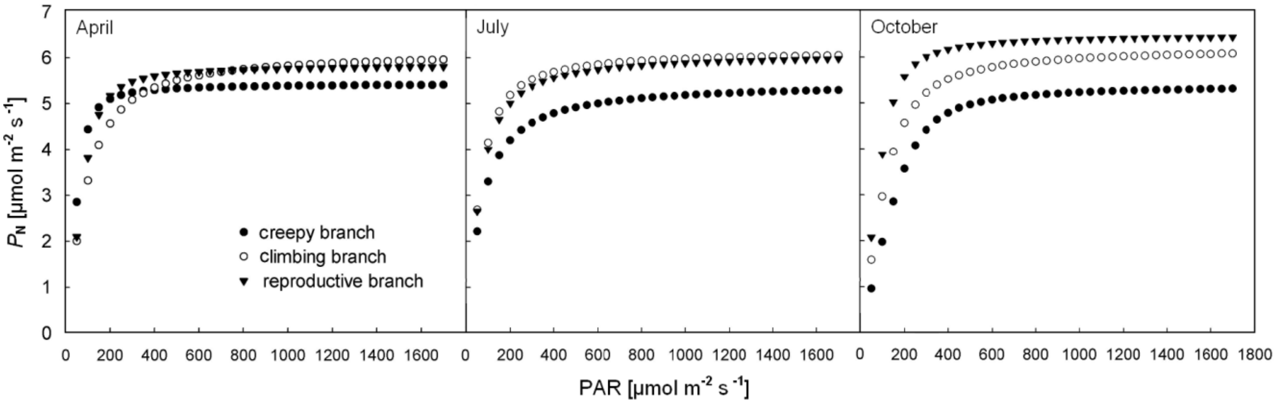

Fig. 2. Response of net photosynthetic rate (P_N) of three types of branches of Chinese ivy to photosynthetically active radiation (PAR).

Responses of P_N on irradiance of the three types of branches during the season were analyzed by setting T_a to 26 °C, VPD to 22 Pa, and C_s to 400 µmol mol^{-1}. The photosynthesis-irradiance (PI) curves behaved like non-rectangular hyperbolae and the season affected the pattern of P_N in the three types of branches (Fig. 2). The differences of P_N among the branch types became larger as the seasons changed. There was no difference in April except that P_N of the climbing and reproductive branches were a little higher than the one of the creepy branch. In July, the P_N values of the climbing and reproductive branches were much higher than the one of the creepy branch, but there was no difference in P_N between the climbing and reproductive branches. In October, leaf maximum P_N of climbing branch remained the same, however, leaf maximum P_N of the climbing branch decreased to 5.3 µmol m^{-2} s^{-1} and reproductive branch increased to 6.4 µmol m^{-2} s^{-1}, so the difference among the three branch types enlarged further. Actual ambient daily integrated PAR at the branch types also showed a distinct seasonal pattern similar to PI curves (Table 3).

Table 3. Seasonal changes in daily-integrated PAR of three types of branches of Chinese ivy. Data from the field measurements at about 08:00 to 17:00.

Season	Branch type	PAR [µmol m^{-2} s^{-1}] mean	minimum	maximum
April	creepy branch	58.64	11.0	267.0
	climbing branch	185.83	23.3	317.0
	reproductive branch	156.33	45.0	294.0
July	creepy branch	171.28	22.0	953.0
	climbing branch	239.07	15.0	931.0
	reproductive branch	254.0	31.0	936.0
October	creepy branch	133.63	3.0	691.0
	climbing branch	201.50	9.0	731.0
	reproductive branch	295.98	9.0	1012.0

Discussion

Photosynthesis is a physiological process that is affected by environment. Most models of photosynthesis have been designed to simulate P_N in the scaling of canopy (Chen *et al.* 1999, Dai *et al.* 2003). Some of them are not suitable for simulating the instantaneous P_N (Dewar *et al.* 1999, Hikosaka 2003, Jin *et al.* 2003) because P_N is calculated as a function of content of leaf N per leaf area (n_L) (Hikosaka 2003) or of leaf protein (Dewar *et al.* 1999), whose changes are not easy to measure within a very short time. Moreover, some of these models were so complex that they required considerable input of data and computer time. Hence it was necessary to develop a simpler model. We developed a photosynthesis model for Chinese ivy in which leaf P_N is a function of PAR, T_a, C_s, and VPD. These variables are key factors affecting photosynthesis and can be easily measured and calculated. A single parameter had a limited value in previous model studies (Tuzet *et al.* 2003). However, our model complies with the fact that the parameters vary with the change of seasons, for some key parameters of photosynthesis such as α_0 or V_{m25} are not invariable during plant growth (Urban *et al.* 2006). These slight seasonal differences in physiological parameters of photosynthesis also suggest a plastic response of this species to environment. The effect of nitrogen on photosynthesis is ignored in our model. This might contribute to some errors in the simulation. Fortunately, the errors are usually small, as photosynthesis of shaded leaves within the canopy is usually limited by absorbed PAR (Wang and Leuning 1998). Leuning (1995) numerically demonstrated that total photosynthesis of shaded leaves is relatively insensitive to N distribution within the canopy for a given amount of total canopy N.

A clear midday depression of P_N was shown at noon in October in the reproductive branch, but it was unclear in April and July for the other two types of branches

(Fig. 1). Midday depression of P_N is mainly caused by two factors. One is a stomatal factor, the other a non-stomatal factor, that is, the activities of RuBPCO and fructose bisphosphatase, and photosynthetic electron transport in the reaction centre of photosystem 2 (Krause and Weis 1991). These two factors can operate simultaneously, but hold different positions under different conditions. In consideration of precipitation decrease, while temperature and irradiance are still high from July to October, it was concluded that high VPD value caused by low humidity and high temperature were the basic factors that result in the midday decline of photosynthesis in reproductive branch (Raschke and Resemann 1986, Xu 1990, Yu *et al.* 1998b). The phenomenon is similar to that in jujube (Su and Liu (2005).

In natural environment, photosynthesis depends on environmental factors and photon utilization efficiency. Daily P_N of Chinese ivy changed with environmental factors, especially PAR (Table 3). With the growth of Chinese ivy, both the leaf P_N and its diurnal change were different among the three branch types and the difference of P_N change in the same branch tended to increase in one day. This may be a result of physiological adaptation of Chinese ivy to environment. As the season changed, the coverage of the forest increased and then the differences of environmental factors among branches (especially irradiance) became larger.

Numerical analysis of response of P_N to irradiance showed that maximum P_N of Chinese ivy ranged from 5.3 to 6.4 μmol m^{-2} s^{-1} in different seasons, which is a little higher than that of lichen (4 μmol m^{-2} s^{-1}) (Segovia and Figueroa 2003) and far lower than that of species that can get direct and stable irradiation, such as soybean (14 μmol m^{-2} s^{-1} – Zheng and Wu 2001), winter wheat (17.5 μmol m^{-2} s^{-1} – Liu *et al.* 2004), maize (32 μmol m^{-2} s^{-1} – Liu *et al.* 2002), and tea (24.3 μmol m^{-2} s^{-1}) (Huang *et al.* 1999). As Chinese ivy grew, the differences of maximum leaf P_N among the three different branches became larger and maximum leaf P_N in climbing and reproductive branches tended to increase with time. There are some possible reasons which can specifically lead to this phenomenon: (*1*) adult leaves have higher photosynthesis capacity than young leaves; (*2*) the centre of vegetative growth changes from growth to reproduction (Zhang 2003) along with the development of Chinese ivy, and then the physiological function (mainly photosynthesis) of plant adapts to different irradiances, low-irradiance leaves show limited photosynthetic capacity, whereas high-irradiance leaves are not limited by photosynthesis. This adaptation can also be found in the activity of non-photochemical quenching pathways, which are associated with xanthophyll cycle activity (Ralph and Gademann 2005).

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