Effect of light intensity on partitioning of photosynthetic electron transport to photorespiration in four subtropical forest plants

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Abstract Photosynthetic rate (P_n) and the partitioning of noncyclic photosynthetic electron transport to photorespiration (J_o) in seedlings of four subtropical woody plants growing at three light intensities were studied in the summer time by measurements of chlorophyll fluorescence and CO_2 exchange. Except *Schima superba*, an upper canopy tree species, the tree species *Castanopsis fissa* and two understory shrubs *Psychotria rubra*, *Ardisia quinquegona* had the highest P_n at 36% of sunlight intensity. The total photosynthetic electron transport rate (J_F) and the ratio of J_o/J_F were elevated in leaves under full sunlight. J_o/J_F ratio reached 0.5—0.6 and coincided with the increasing of oxygenation rate of Rubisco (V_o), the activity of glycolate oxidase and photorespiration rate at full sunlight. It is suggested that an increasing partitioning proportion of photosynthetic electron transport to photorespiration might be one of the protective regulation mechanisms in forest plant under strong summer light and high temperature conditions.

Keywords: subtropical forest plants, photosynthetic electron transport, photorespiration, glycolate oxidase, ratio of oxygenation rate to carboxylation rate of Rubisco.

Photosynthetic noncyclic electron transport is the energy source of photosynthetic carbon metabolism[1]. Photorespiration is the by-pass electron flux induced by light and the main pool of producing reductants[2,3]. In recent years, it has been reported that the important physiological function of photorespiration may be as a mechanism to dissipate excess light energy, drive the operation of Calvin cycle, prevent photoinhibition and photooxidative damage in C_3 plants when the supply of CO_2 is limited[4,5]. One of the key points in photosynthetic control of electron transport is concerned with the partitioning of electron flow among carbon reduction cycle, carbon oxidation cycle, and the alternative O_2-dependent and NO_2-dependent photoreduction. The ratio of photosynthetic electron flowed to photorespiration depended upon the environmental factors and the kinetic characteristics of Rubisco[6,7]. To carry out the advanced study on the change of rates in different approaches of photosynthetic electron transport with a series of plant species and ecotypes exposed to various conditions is necessary for further understanding the feature, pattern and mechanism of photosynthetic control.

In the lower subtropical forest with a complex community structure consisting of vertical multiple layers of plant species and lifeforms, plants are located in different microenvironments.

The previous reports by Lin et al. showed that there are certain differences in leaf structure, contents of chlorophyll, photosynthetic rate and water status between plants located at upper and lower layers in Dinghushan natural forest, Guangdong Province[8,9]. The present paper focuses on the view of photosynthetic control to further study the feature of photosynthetic electron transport in the leaves of two trees and two shrub seedlings growing at different light intensities by using chlorophyll fluorescence and CO_2 exchange measurement.

1 Materials and methods

1.1 Plant material

Seedlings of tree species *Schima superba, Castanopsis fissa* and shrub species *Psychotria rubra, Ardisia quinquegona* in an evergreen broad-leaf forest in Dinghushan Biosphere Reserve of Guangdong Province were transplanted in pots in April, 1998. The seedlings were divided into three groups and grown under natural sunlight or shading shelf covered with black netting cloth. 30—40 pots were used for each light treatment. The soil, water and nutrition were provided by routine process. Light intensities in the two shading treatments were 36% and 16% relative to natural full sunlight. The 100% of incident photon flux density on leaf surface was about 873 μmol • m^{-2} • s^{-1} at 9:00 am and 1605 μmol • m^{-2} • s^{-1} at noon in sunny day of July. April—July in Southern China is a high temperature and raining season. The fully expanded matured leaves in the 3rd or 4th top position were selected as tested material.

1.2 Methods

CO_2 exchange was measured using a LCA-4 portable photosynthesis system (ADC, England) in the field. The kinetics of chlorophyll fluorescence measurement was performed simultaneously with a PAM modulated fluorometer (Walz, Germany). The quantum yield of PSII dependent noncyclic electron transport (ϕ_{PSII}) is given by the equation $(F_m' - F_s)/F_m'$ [10]. Total electron transport rate of PSII (J_F) was calculated as described by Krall and Edward[2], $J_F = (\phi_{PSII})(I)(a)(f)$, where I = PFD incident on the leaf, a = percentage of light absorptance by leaf, the value is usually 0.8—0.84 (80%—84%), f = the absorptance by PSII divided by the absorptance of PSI + PSII, which is 0.5. The velocities of oxygenation (V_o) and carboxylation (V_c) by Rubisco, and the ratio of V_o/V_c were calculated according to Sharkey[11].

$$\Phi\ (\text{ratio}) = V_o / V_c = 2\Gamma^* / (CO_2), \tag{1}$$

$$V_o = (A + R_d)/(1/\Phi - 0.5), \tag{2}$$

$$V_c = A + 0.5V_o + R_d, \tag{3}$$

$$\Gamma^* = \Gamma^{*'} \times P, \tag{4}$$

$$\Gamma^{*'} = 42.7 + 1.68(T - 25) + 0.0012(T - 25)^2, \tag{5}$$

where A=net photosynthetic rate，R_d = respiratory rate, Γ^*= the compensation point in the absence

of respiration, $\Gamma^{*'} = \Gamma^*$ at a variety of temperature, (CO_2)=CO_2 concentration at the site of carboxylation = 0.6 Ca, P = atmospheric pressure.

Glycolate oxidase of leaves was extracted with Tris-HCl buffer 50 mmol/L, pH 7.6 containing $MgCl_2$ 10 mmol/L, EDTA 0.25 mmol/L, Cysteine 1 mmol/L. GAO activity was assayed by phenyldrazine hydrochloride[12].

Noncyclic electron transport to photorespiration (J_o) *in vivo* was calculated as

$$J_o = 2/3[J_F - 4(A + R_d)]^{[3,4]}.$$

2 Results

2.1 CO_2 exchange rate, the efficiency and rate of noncyclic electron transport of PSII

As illustrated in table 1, leaf temperature and respiratory rate declined in four woody plants at lower growing light intensity, but the changing trends of photosynthetic rate (P_n) corresponding with light were somewhat different among plant species. P_n value was similar in the leaves of a dominant tree species at upper canopy, *S. superba* growing under 36% and 100% of sunlight. However, at 36% sunlight condition, the P_n of shrubs *P. rubra*, *A. quinquegona* and another tree species *C. fissa* were respectively 12%, 14.2% and 31.4% higher than that at natural full sunlight, then they also dropped to different extents with the decreasing light intensity to 16%. It implied that the P_n of the latter three plants were inhibited by strong light, while that of *S. superba* was adaptable to natural sunlight.

Table 1 Changes of leaf temperature (T_L), photosynthetic rate (P_n) and respiratory rate (R_d) of four woody plants under varying growing light intensities

Species	Relative light intensity (%)	T_L/℃	P_n/μmol • m^{-2} • s^{-1}	R_d/μmol • m^{-2} • s^{-1}
(Tree)				
Schima	100	36.1±0.4	5.87±0.92	1.61±0.00
superba	36	35.0±0.6	5.79±0.59	1.00±0.15
	16	34.7±0.2	3.64±0.60	0.72±0.14
Castanopsis	100	36.7±0.7	4.17±0.36	2.42±0.52
fissa	36	35.0±0.6	5.48±1.76	1.02±0.31
	16	34.1±0.3	3.96±1.34	0.69±0.25
(Shrub)				
Psychotria	100	36.9±0.1	5.39±0.05	2.29±0.25
rubra	36	35.1±1.3	6.04±1.85	1.02±0.27
	16	34.6±0.2	2.94±0.07	1.05±0.13
Ardisia	100	37.2±0.8	6.76±0.32	1.92±0.01
quinquegona	36	34.5±0.4	7.72±0.96	0.82±0.10
	16	34.2±0.2	4.31±0.09	0.58±0.19

The quantum yield of electron flow through PSII (ϕ_{PSII}) and calculated total electron flow rate from fluorescence data (J_F) at varying light intensity are shown in fig. 1. ϕ_{PSII} depends on both the efficiency of excitation capture by PSII open centers (F_s/F'_m) and the proportion of PS Ⅱ open centers (q_p)[2, 10]. At 100% of sunlight intensity, ϕ_{PSII} of *P. rubra* was significantly lower than that at low light intensity and the values of other species at the same full sunlight. It indicated that strong

light induced the reduction in relative numbers of PSII center with charge separation and capacity of absorbed photon energy in leaves of *P. rubra*. The higher ϕ_{PSII} in *A. quinquegona* and *P. rubra* at 36% sunlight intensity compared with the cases at 100% or 16% sunlight was consistent with their higher P_n in table 1. J_F increased with the increasing light intensity. J_F levels of the four species were similar at each same light intensity except that of *P. rubra* at full sunlight. In comparison with full sunlight condition, J_F of the four plants with two shading treatments decreased to 41%—66% and 16%—25% of their corresponding control, respectively. Peterson reported that maximal rate of J_F in *Nicotiana tabacum* achieved higher level at high irradiance employed[7]. The present results suggested that the effect of light intensity on the level of J_F is evident, and plants exposed to full sunlight could generally produce more photosynthetic electrons in chloroplast with a rapid rate through noncyclic electron transport to supply energy for CO_2 fixation.

2.2 Photorespiratory rate, activity of glycolate oxidase and rate of oxygenation and carboxylation of Rubisco

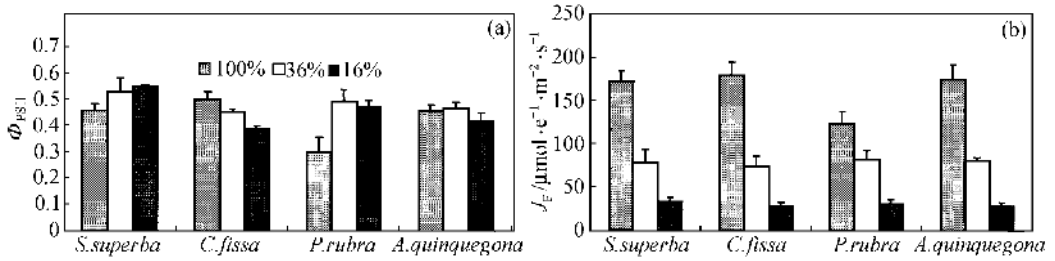

Fig. 1. Changes of noncyclic photosynthetic electron transport rate (J_F) and the quantum yield of electron flow through PSII (ϕ_{PSII}) in woody plants growing at different light intensities.

Within the light intensity employed, photorespiratory rate of *S. superba*, *C. fissa* and *A. quinquegona* declined at the reduced light intensity. It decreased 7%—10% and 32%—47% under 36% sunlight and 16% sunlight, respectively, but a slight increase of photorespiratory rate was found in *P. rubra* at 36% sunlight intensity (fig. 2(a)). In general, the levels of photorespiration depend on the activities of Rubisco oxygenase and glycolate oxidase (GAO). The activities of GAO related to light intensity in the four species showed two changing patterns (fig. 2(b)). Changes of GAO activity in *S. superba* and *A. quinquegona* were consistent with altering light intensity. The highest GAO activity was observed in the plants growing at full sunlight, while about 41% and 57% of reduction occurred in these two plants under 16% sunlight intensity. On the other hand, under 36% sunlight, GAO activities of *C. fissa* and *P. rubra* exhibited 5% and 13% larger than that from plants under full sunlight. Moreover, *C. fissa* and *P. rubra* could maintain 91%—98% of GAO activity when grown under 16% sunlight.

Effect of light intensity on the rate of Rubisco oxygenation (V_o) was similar to the changing trend of photorespiratory rate and GAO activity (fig. 2(c)). The Rubisco carboxylation rate (V_c) and V_o/V_c ratio are given in fig. 3. V_c of the four species decreased slightly (3%—10%) under 36% sunlight but significantly (31%—45%) under 16% sunlight. All the V_c values were higher than V_o

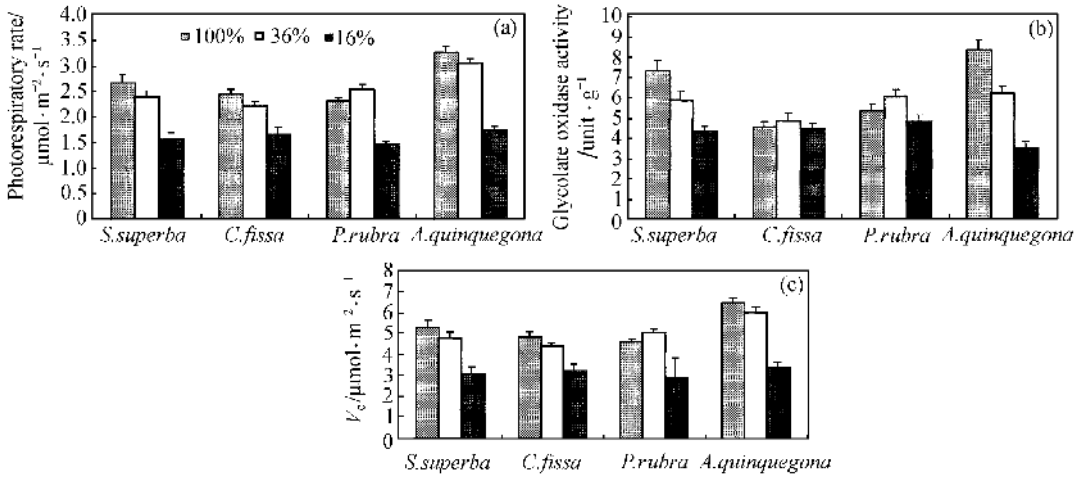

Fig 2. Effect of growing light intensity on photorespiration, activity of glycolate oxidase (GAO) and rate of Rubisco oxygenation (V_o).

in the four species at varying light intensity. However, both of the changing range in V_o and V_c were nearly the same under low light condition, so the V_o/V_c ratios were approximate at the three tested light intensities. The fact of no obvious difference of V_o/V_c ratio among the four woody plants showed that these species maintained the compatible efficient adjusting capacity for the rates of Rubisco oxygenation and carboxylation at the light intensity used.

2.3 Partitioning of noncyclic photosynthetic electron transport to photorespiration

J_o represents the rate of total electron flow transported to respiration and J_o/J_F reflects the

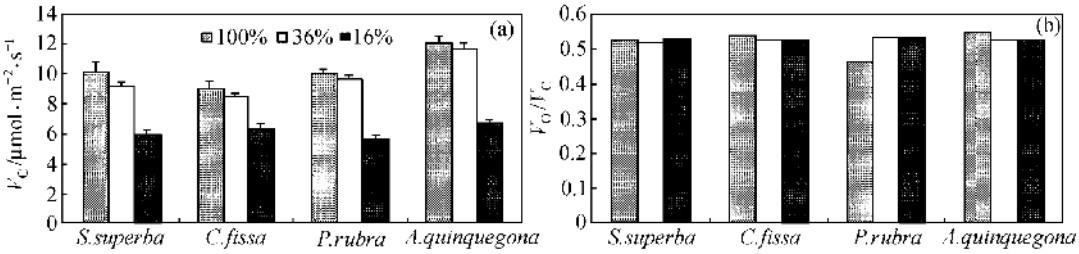

Fig. 3. Effect of growing light intensity on the rate of Rubisco carboxylation (V_c) and the ratio of oxygenation to carboxylation (V_o/V_c).

proportion of total electron flow devoted to photorespiration (oxygenation of Rubisco). Fig. 4 shows the variation in J_o and J_o/J_F of the four species at varying light intensity. It is evident that J_o and J_o/J_F depended on light intensity. Both of the two parameters were elevated by strong light. The J_o/J_F reached the highest value of 0.5—0.6 under the full sunlight and declined gradually to 0.39—0.47 under 36% sunlight and 0.21—0.33 under 16% sunlight, respectively. Photorespiration was induced by light and regulated by leaf temperature [13, 14]. Therefore, the high irradiation and the high leaf temperature up to 37℃ during summer growing season in the present experiment

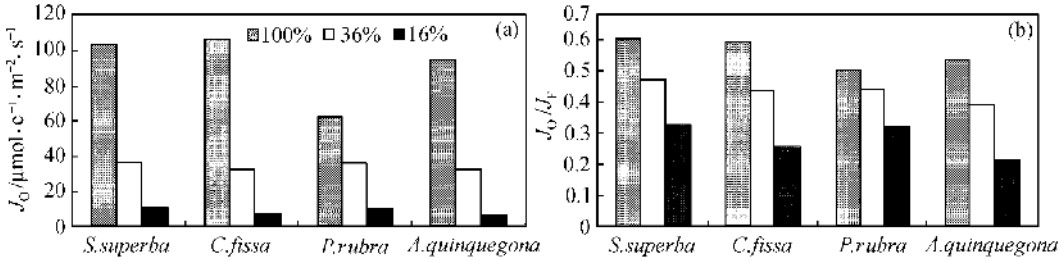

Fig. 4. The partitioning proportion from noncyclic photosynthetic electron transport to photorespiration at different intensities.

were considered to be the main reason for high J_o/J_F and high photorespiratory rate in the plants growing under full sunlight.

Two tree species showed a higher J_o/J_F ratio than two understory shrub species growing under full sunlight, probably because the difference of metabolic regulation adapted to strong light intensity and the location in the forest between two types of lifeform.

3 Discussion

Valentini et al. reported that the increase of total electron flow in Turkey oak in a day was paralleled with the enhancement of irradiation[3]. Peterson also observed the maximum rate of total electron transport (J_F) at high light intensity[7]. Our results with the four woody plants from a lower subtropical forest showed that the magnitude of J_F and the carboxylation rate of Rubisco (V_c) were closely related to growing light intensity, and it was limited obviously by low light intensity and promoted by full sunlight. Hence, light intensity seems to be an important limited factor influencing photosynthetic electron transport and carbon assimilation of these woody plants.

The function of light is not only to activate and regulate the activity of Rubisco, but also to drive more electron flows participating in CO_2 reduction. It may provide more NADPH by activating NADP-MDH and increase electron flux through PSII and PSI[1]. The low photosynthetic rate of the four species under 16% sunlight might be mainly interpreted as their low values of J_F and V_c. At 36% sunlight intensity, V_c and ϕ_{PSII} still remained at high level, J_F (74—82 μmol • m^{-2} • s^{-1}) was smaller than that under full sunlight, but it was compatible to the maximum electron flow rate (73—80 μmol •m^{-2} •s^{-1}) calculated from CO_2 exchange data in *Malus sp*. and *Nauclea diderrichii*[15].

Photorespiration is an essential physiological process for C_3 plant surviving in the air. Photorespiration could drive electron transport even in the absence of net photosynthesis[5]. Photorespiration can be a major sink for electron from noncyclic electron flow[2]. It has been reported that there is about 40% of total electron flow diverting to photorespiration (R_L) in leaves of Turkey oak under saturated irradiance, and the R_L/P_n ratio ranged from 0.15 to 0.70 with the mean value of 0.56; it could reach 0.8—0.9 under stress condition[3]. The results of our experiment illuminated that at varying light intensity, R_L/P_n ratio was 0.39—0.59 (data not shown) which is

within the ranges reported by Valentini et al., and J_o/J_F was 0.21—0.60. About 50%—60% of J_F was transported and partitioned to photorespiration when the tested plants were grown under full sunlight, while the J_o/J_F decreased at limited light intensity. The changes in J_F and J_o/J_F at three light intensities indicated that the regulation of light on photorespiration is evident for forest plant. The reason for such a high photorespiratory rate under full natural light might be the promotion of J_o/J_F, V_o and GAO activity by strong light. Therefore, the effect of light intensity on photosynthesis could change the partitioning fraction of electron transport through different accepting approaches, except its regulative effect on the activities of some key enzymes in PCR and PCO cycles.

The increasing J_o/J_F ratio and photorespiratory rate in several woody plants at high summer temperature under strong light were considered one of the efficient protective mechanisms of metabolic adjustment by dissipating excess light energy to maintain the balance between the process of light reaction and carbon fixation during photosynthesis, in order to avoid photodamage of photosynthetic apparatus. The similar changing trend in properties of photosynthetic electron transport, kinetics of Rubisco and the V_o/V_c ratio with varying light intensity among the four tested woody species implied that they all had certain adjustable ability adaptable to different light environment during summer active growth season. However, the problem of whether the evident difference does occur among species and lifeforms at low temperature during dry winter time with varying light intensity remains to be further studied.

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