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Review

Rubisco activity and gene expression of tropical tree species under light stress

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Tropical rain forests contain an ecologically and physiologically diverse range of vegetation and habitats. Sun-acclimated plants can be divided into two groups, shade-tolerant and shade-intolerant, according to the plant's physiological and genetic responses. Some tropical species have potential capacity for light damage in a shaded environment as well as shade-tolerance to compensate for the impaired light harvesting complex. In particular, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is regulated by the Calvin cycle, which participated in protein synthesis. Rubisco plays a role in CO_2 fixation, which helps supply the energy to regulate Rubisco for ribulose 1,5-bisphosphate (RuBP) reduction. Light intensity is associated with the photosynthetic rate and genetic response to moderate growth environments.

Key words: Gene expression, growth, light intensity, Rubisco activity.

INTRODUCTION

In many areas of tropical rain forests, the light associated with photosynthesis plays a key role in the physiological response (for example, photosynthetic rate, chlorophyll contents and Rubisco activity), growth and genetic response. Rubisco activity associated with photosynthesis and the molecular responses. Plants have high photon-harvesting capacity for photosynthesis, which involves the absorption of light energy from the sun and a transformation to chemical energy. Plants are affected by light stress with a sensitive response to the environment (for example, light, temperature, humidity) and light phase in vegetation affect genetic diversity. Copping work causes particularly decrease of vegetation and genetic divergence. In addition, plants gain usually photoinhibition and photodamage in high light intensity (Anderson et al., 2001; Chazdon et al., 1996; Deboeck et al., 2009; Jacquemyn et al., 2009).

The genetic response is also closely associated with the different light intensities. For example, in the case of C_3 plants, the nucleus receiving light energy from the sun exhibits different gene expression in the chloroplasts of plants according to the different light intensities. This function is affected by environmental stress or eco-physiological features in plants. Therefore, gene expression is closely associated with different light intensities. If light is excessive, the leaves begin to discolor and show damage due to oxidative stress. Proteomics analysis associated with gene expression of plants reveal a range of gene expression according to the light intensity. Thus, this study reviews the relationship between the physiological and Rubisco activity changes and gene expression under different light intensities.

STATUS AND DISTRIBUTION OF TROPICAL RAIN FORESTS

Tropical rain forests contain an ecologically and physiologically diverse range of vegetation and habitat. Wright (2005) examined the vegetation in Philippines. Hermann and Hugh (2010) studied the tropical species in the Rio de Janeiro region of Brazil. Humidity, soil moisture and photosynthetic efficiency were reported to vary according to elevation and seasonal changes. Great diversity of tropical species exists with *Leguminosae*

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Table 1. Shade tolerant plants in *legumes* family on light stress.

Degree of shade tolerance	Grass	Legume
High	*Axonopus compressus*	*Calopohonium caeruleum*
	Brachiaria milifomis	*Desmodium heterophyllum*
	Ischaemum aristaum	*Desmdium ovalifolium*
	Ottochla ndosa	*Flemengia congesta*
	Paspalum conjugatum	
	Stenotaphrum secundatum	
Medium	*Brachiaria brizantha*	*Calopogonium mucunoides*
	Brachiaria decumbens	*Centrosema pubescens*
	Brachiaria humidicola	*Desmodium triflorum*
	Digitaria setivalva	*Pueraria haseoloides*
	Lmperata cylindrical	*Desmodium intortum*
	Panicum maximum	*Leucaena leucocephala*
	Pennisetum purpureum	
	Setaria sphacelata	
Low	*Brachiaria mutica*	*Stylosanthes hamata*
	Cyndon plectostachyus	*Stylosanthes guianensis*
	Digitaria decumhens	*Zornia diphylla*
	Digitaria pentzii	*Macroptilium atropurpureum*

being the most dominant family and *Rubiaceae* and *Piperaceae* being important under shrubs. In a study of tropical rainforest trees, the physiological response, geographical distribution of tropical trees and growth is important for understanding the characteristics of tropical species.

SHADE TOLERANCE ABOUT PHOTOSYNTHESIS RESPONSE IN TROPICAL SPECIES

Depending on shade tolerance and shade intolerant species, photosynthetic response under different light intensities of tropical species was different according to plant growth, leaf anatomical characteristics, efficiency of light absorption, respiration rate, and photosynthetic efficiency. When sun leaves receive the amount of light, photosynthetic rate and leaf area ratio, and relative growth rate increase. Thickness of palisade cell layers and mesophyll tissue is also larger than shade leaves. As a result, light acclimation capacity and biomass in sun leaves increased. On the other hand, shade leaves showed delayed maturation of leaves and light acclimation (Ishii and Ohsugi, 2011). Table 1 show three tropical species groups according to shade-tolerance; strong, medium, and weak species. Shade intolerant species show limited biological productivity and nitrogen supply (Boardman, 1977; Thompson et al., 1992a, b; Jose et al., 2003; Chazdon et al., 1996; Kelvin, 2011; Monthomery et al., 2010).

THE INFLUENCE OF CO_2 CONCENTRATION ON PLANT GROWTH

The carbon dioxide (CO_2) concentration in the atmosphere has increased from approximately 200 to 379 μL L^{-1} in 2005 (IPCC, 2007) and is expected to rise to between 730 and 1020 μL L^{-1} by the year 2010 (IPCC, 2007). Plant growth was affected by variation of atmospheric CO_2 concentration as well as photosynthetic rate (P_N), stomatal conductance (*G*s) (Polley et al., 1992; Anderson et al., 2001; Maheraliet al., 2003; Long et al., 2004). Moreover, photosynthetic rate (P_N) and stomatal conductance (*G*s) decrease when plants have water insufficiency (Katul et al., 2010; Wang et al., 2010). For instance, light absorption into leaves induce rapidly stomatal opening in light environment, which urge plants to use light whereas light penetration through leaves in shade environment cause stomatal close (Katul et al., 2010).

In C_3 carbon fixation (C_3 plants) CO_2 concentration increases when photosynthetic rate (P_N) and stomatal conductance (*G*s) increase. When light intensity increase in sun leaves, photosynthesis and light acquisition capacity increase. Light compensation point (LCP) and light saturation point (LSP) also increase in sun leaves. Light compensation point includes CO_2 fixation and ATP generation for photosynthetic response. It means that sun leaves have potential light stress and shade tolerant capacity (Huang et al., 2011). Therefore, photosynthetic response plays a role in responses of the ecosystem to a change in CO_2 concentration. To elucidate this process, it is important to understand how ecosystems function, how plants adjust to environmental change (Bushand and Silman, 2004; Mayle et al., 2004; Beerling and Osborne, 2006; Choi and Lee, 2012), and how photosynthetic rate functions in carbon cycle budgets (Mayle and Beerling, 2004; Beerling and Mayle, 2006). Photosynthetic response is important in ecosystem, because photosynthesis is associated with global carbon budget, CO_2 assimilation, and carbon distribution. Photosynthesis affects generally carbon gain and ecosystem productivity for adjusting light environment (Zheng et al., 2011). Carbon gain in ecosystem has especially been an important factor in photosynthetic response because photosynthesis is responsible for plantation and plant resistance (Long et al., 1989; Zheng et al., 2011).

PHYSIOLOGICAL RESPONSES UNDER DIFFERENT LIGHT INTENSITY

Model of C_3 plant photosynthesis introduced by Farquahar et al. (1980) are accepted and used in many applications including CO_2 assimilation, light regime, leaf-age, and other physiological parameters. The amount of carbon absorbed into plants also decrease when the proportion of photosynthetic rate (P_N) and respiration (R_d) decrease, As a result, plants get stressed such as drought stress (Wolkerstorfer et al., 2011).

Under different light intensities, Chloroplast CO_2 concentration (C_c) show the maximum rate of carboxylation of ribulose bisphosphate carboxylase (V_{cmax}) and the maximum rate of photosynthetic electron transport (J_{max}). It was associated with the initial slope of the response of the assimilation rate (A) to chloroplast CO_2 concentration (C_c). Photosynthetic rate was determined by Rubisco kinetics. This is because the amount of Rubisco increased in leaves, carbon assimilation on photosynthesis also increased (Yamori et al., 2006a, b). In addition, intercellular stomatal conductance into CO_2 and temperature of leaves affect the photosynthesis response. When photosynthesis occurs, CO_2 is diffused into the atmosphere and stomatal opening causes mesophyll cell to have resistance between chloroplast of leaf and atmosphere (Warren and Dreyer, 2006). Measurements of stomatal conductance at high temperatures are often confounded by high water vapor pressure deficits. When water vapor pressure is avoided, stomatal conductance can increase with temperature above the optimum temperature for photosynthesis (Raschke, 1970; Hall et al., 1976; Katul et al., 2010) and C_c may increase with temperature (Bunce, 1998; Zhou et al., 2011).

Rubisco ACTIVITY UNDER DIFFERENT LIGHT INTENSITIES

Rubisco activity included RuBP carboxylation and RuBP regeneration in photosynthetic response. Carbon assimilation ability on leaf depends on increase of carboxylation on Rubisco enzyme. For instance, RuBP (Ribulose bisphosphate) regeneration need photosynthesis electron transport and photophosphorylation because of producing adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate-oxidase (NADPH) under low light intensity (Seemann et al., 1988; Mi et al., 2012). Rubisco activation rate increase in dark reaction because of acquiring more carbon before photosynthesis in leaf occurs (Woodrow and Mott, 1989; Zou et al., 2011). Rubisco activation is achieved by carbon gain process in dark reaction. A capacity of RuBP regeneration limited CO_2 assimilation to maintain higher CO_2 concentration in the Calvin cycle under light stress condition. In addition, RuBP regeneration played a role in making NADPH and ATP synthesis for yielding photosynthetic response (Yamori et al., 2011). Rubisco kinetics differs from species to species because of different environment (Galmés et al., 2005).

In aspect of temperature on plant growth, when the temperature of plant growth lows, ribulose 1, 5-bisphosphate carboxylase/oxygenase was accumulated in leaves for photosynthetic response. And also, the amount of carbon on photosynthesis increased in the low temperature (Yamori et al., 2006b).

Rubisco activity shows the main factors controlling photosynthesis in terrestrial C_3 plants, particularly under dark reactions and CO_2 concentrations (Farquhar et al., 1980; Farquhar and Sharkey, 1982; Woodrow and Berry, 1988; Quick et al., 1991; Busch et al., 2012). Rubisco has double functions that Rubisco catalyze carboxylation of RuBP (ribulose 1, 5-bisphosphate) and Rubisco oxygennates RuBP in photo-respiration (Busch et al., 2012). Consequently, Rubisco enzyme plays a role in assimilating into carbon oxide from oxygen in photo-environment (Busch et al., 2012). In addition, the Rubisco activity is controlled by RuBP and the CO_2 concentration (carbamylation of Lys-201 on the large subunit and binding of a magnesium ion to the carbamate). Magnesium (Mg^{2+}) helps Rubisco activation because change of carbamylation at Rubisco active site helps activation of stomatal conductance and CO_2 supply in light environment (Farquhar et al., 1980; Huffaker, 1982; Cleland et al., 1998; Galmés et al., 2011). Since the CO_2 concentration in leaves is regulated by stomatal opening, the stomata actually control the availability of the substrate for Rubisco. Upon illumination, magnesium ions required for Rubisco activation are translocated from the thylakoid lumen to the chloroplast stroma.

Chloroplast membrane plays an important role in light synthesis in photosynthesis (Ishida and Marjenah, 1999; Kamal et al., 2012). Most anions, such as sulphate, inorganic phosphate, several phosphorylated sugars, and NADPH, modulate the Rubisco activity by elevating the activation level and by competition with the RuBP substrate (Badger and Andrews, 1974; Igamberdieva and

Rousselb, 2012). CO_2 fixation shows a good type in the case of Rubisco activity. The role of the Calvin cycle is to fix CO_2. In a complex system in the Calvin cycle, CO_2 plays a role in the direction of carbon. In the Calvin cycle, CO_2 focuses on the amount of ribulose 1, 5-carboxylase/ oxygenase and 3-phosphoglycerate aldehyde. Ribulose-1, 5-biphosphate (RuBP) catalyze RuBP carboxylase/oxygenase (Rubisco) which produce glycerate-3-phosphate (3-PGA) in Calvin cycle (Sánchez-Rodríguez et al., 2011). For example, the amount of RuBP and 3-phosphoglycerate aldehyde (3PGA) is decreased when a water deficit response occurs in plants (Von Caemmerer and Farquhar, 1981; Sánchez-Rodríguez et al., 2011).

GENETIC RESPONSES UNDER DIFFERENT LIGHT INTENSITY

In C_3 plants, chloroplasts are responsible for producing carbonate and oxygen in the photosynthesis cycle as well as photorespiration in chloroplast for photoprotective mechanism (Robert et al., 1989; Ditmarová et al., 2009). In addition, plant cells synthesize starch in large granules, so the plant cells have the essential function according to the light mechanism (Ophir and Ben-Shaul, 1974; Appenroth et al., 2011). Chloroplasts involve the transcription and translation of many genes. Gene expression is the RNA polymerase type that is associated with the photosynthesis proteins. On the other hand, plants have limited genetic, physiological and biochemical responses to environmental stress. Rubisco, glyceraldehyde 3-phosphate dehydronase and fructose 1, 6-bisphosphate enzyme show the gene expression in biosynthesis. These enzymes play a role in the nucleus and produce proteins. The genetic response contributes to the production of valuable timber.

In the molecular biological response, reverse transformation polymerase chain reaction (RT-PCR) is a useful technique for examining gene expression encoded at the mRNA level. In particular, RT-PCR can clarify the various proteins about gene expression. In C_3 plants, light is closely associated with gene expression. The role of light in carbon fixation in C_3 plants involves an interaction of light with the palisade mesophyll and spongy mesophyll within the cell (Gutschik, 1984; Terashima, 1989; Fukshansky and Remisowsky, 1992; Evans, 1988; Tosens et al., 2012; Zell et al., 2010). Mesophyll diffusion conductance influences photosynthetic response because the mesophyll diffusion conductance is related to leaf age and light intensity (Tosens et al., 2012). In addition, C_3 plants depend on the photoautotroph with light energy. Specifically, light helps enable the plant to control the photoperiod, seasonal environment and the regeneration of plant species in terms of the genetic response. The light signals are mediated by highly specialized information-transducing photoreceptors. For example, *Arabidopsis thaliana* has genome sequences for a proteomic response.

Proteomics has been studied at different light intensities. In Legumes, *Medicago truncatula* was studied on proteomic proteins. Two-dimensional (2D) gel- electrophoresis can identify proteins according to their mass (Paul and Philip, 2004). For both sun-grown and shade-grown plants, 2D gel-electrophoresis was used to quantify the proteins. The accumulation of proteins revealed the technical methods and difference at the molecular levels between the sun and shade environment. The results suggest that tropical species can respond to the environment or light stress through a genetic response. In addition, 2D gel proteomic analysis can be used to obtain the score and queries-matched (%) association with the function of the proteomic response.

PROSPECT

Based on physiological and genetic response, photosynthesis, Rubisco activity, and genetic response of tropical plants under different light intensities, has already been progressed in C_3 plants. Some experiment in plant light intensity has been achieved by some plants (Chaves et al., 2009). To understand photosynthetic and genetic response under different light intensity, we have to study gene expression and physiological characteristics, including Rubisco activity of Calvin cycle on light stress in plants. There are a number of photosynthetic responses under different light intensity related to genetic response. Through complex response to light intensity, we have to specifically find physiological metabolism of plants on photosynthesis. On the light response, we also study resistant capacity of plants under different light intensity. It suggests that studying light response would be interesting to find plant's potential stress on the light.

CONCLUSION

In the shading environment, some tropical species had shade-tolerance because of the potential light harvest capacity and photoprotective activity in the thylakoid membrane. The decrease in photosynthesis capacity, Rubisco activity and growth in shading environment means that capacity of carbon storage and CO_2 supply regarding the Calvin cycle was not active. This indicates that the Rubisco activity is influenced by the Calvin cycle. In the Calvin cycle, Rubisco helps fix CO_2 as the dark response to transfer light energy. Therefore, ATP and NADPH help supply the energy. On the other hand, in a shading environment, there is less carbonate accumulation due to light stress and shade intolerance.

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