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目　　录

1、　科研论文首页……………………………………………….……1

2、　教改论文首页……………………………….....................……13

New Phytologist

Research

The role of leaf water potential in the temperature response of mesophyll conductance

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Key words: carbon isotope, leaf water potential, mesophyll conductance, photosynthesis, rice, stomatal conductance, temperature, wheat.

Summary

- Variation in temperature (*T*) is usually accompanied by changes in leaf water potential (Ψ_{leaf}), which may influence mesophyll conductance (g_m). However, the effects of Ψ_{leaf} on g_m have not yet been considered in models of the g_m response to temperature.
- Temperature responses of g_m and Ψ_{leaf} and the response of g_m to Ψ_{leaf} were studied in rice (*Oryza sativa*) and wheat (*Triticum aestivum*), and then an empirical model of Ψ_{leaf} was incorporated into an existing g_m–*T* model.
- In wheat, Ψ_{leaf} was dramatically decreased with increasing *T*, whereas in rice Ψ_{leaf} was less sensitive or insensitive to *T*. Without taking Ψ_{leaf} into account, g_m for wheat showed no response to *T*. However, at a given Ψ_{leaf}, g_m was significantly higher at high temperature compared with low. After incorporating the function of Ψ_{leaf} into the g_m–*T* model, we suggest that the g_m–*T* relationship can be influenced by the activation and deactivation energy for membrane permeability, Ψ_{leaf} gradient between temperatures, and the sensitivity of g_m to Ψ_{leaf}, below a threshold ($\Psi_{leaf,0}$).
- The data presented here suggest that Ψ_{leaf} plays an important role in the g_m–*T* relationship and should be considered in future studies related to the temperature response of g_m and photosynthesis.

Introduction

The CO_2 diffusion capacity from the atmosphere to the carboxylation sites of Rubisco inside chloroplasts is one of the major limitations to photosynthesis. After diffusing from the atmosphere to intercellular air spaces through the boundary layer and stomata, CO_2 dissolves in the water-filled pores of the cell wall and then further diffuses in series across the cell wall, plasma membrane, cytosol, chloroplast envelopes, and stroma (Flexas *et al.*, 2008; Evans *et al.*, 2009). The CO_2 partial pressure at the Rubisco carboxylation sites (C_c) is dramatically lower than that in the atmosphere (Flexas *et al.*, 2008; Li *et al.*, 2009; Flexas *et al.*, 2012), due to a high diffusion resistance and the fixation of CO_2 by Rubisco. According to Fick's law, mesophyll conductance (g_m), the inverse of mesophyll resistance (r_m), is defined as the ratio of the photosynthetic rate (*A*) to $C_i - C_c$, the drawdown of CO_2 partial pressure from intercellular air spaces to the carboxylation sites.

Evidence is accumulating that g_m can vary over both short and long timescales in response to a suite of environmental variables, including light intensity, drought, salinity, temperature (*T*), and CO_2 concentration (Flexas *et al.*, 2008; Loreto *et al.*, 2009; Li *et al.*, 2012; Xiong *et al.*, 2015; Nadal and Flexas, 2018). Understanding the temperature response of g_m is important in photosynthesis models and in the prediction of crop production, especially in the context of global climate change. The temperature response of g_m has been experimentally examined in a number of studies, using both of the most widely applied g_m measurement techniques; namely, the Chl fluorescence method and the $\Delta^{13}C$ method (Bernacchi *et al.*, 2002; Yamori *et al.*, 2006; Evans & von Caemmerer, 2013; von Caemmerer & Evans, 2015; Huang *et al.*, 2017; Shrestha *et al.*, 2019). Thus far, three different types of g_m–*T* relationships have been documented: (1) g_m gradually increases with increasing temperature; (2) g_m is insensitive to temperature; (3) g_m initially increases with increasing temperature and then declines at supra-optimal temperature (Bernacchi *et al.*, 2002; von Caemmerer & Evans, 2015).

To date, there have been two main approaches to modeling the g_m–*T* response (Bernacchi *et al.*, 2002; Evans & von Caemmerer, 2013). The first, developed by Bernacchi *et al.* (2002), hypothesizes that the response of g_m to temperature is caused by temperature-dependent CO_2 permeability through proteins, such as aquaporins (AQPs), and lipid bilayers. However, this hypothesis does not seem compatible with the diverse range of observed g_m–*T* relationships, and is particularly problematic for species with limited or no response, as it is inconsistent with well-established properties of proteins (Lee *et al.*, 2012; Groszmann *et al.*, 2017).

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ORIGINAL ARTICLE

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Temperature responses of photosynthesis and leaf hydraulic conductance in rice and wheat

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Abstract

Studies on the temperature (T) responses of photosynthesis and leaf hydraulic conductance (K_{leaf}) are important to plant gas exchange. In this study, the temperature responses of photosynthesis and K_{leaf} were studied in Shanyou 63 (*Oryza sativa*) and Yannong 19 (*Triticum aestivum*). Leaf water potential (Ψ_{leaf}) was insensitive to T in Shanyou 63, while it significantly decreased with T in Yannong 19. The differential $\Psi_{leaf} - T$ relationship partially accounted for the differing g_m–T relationships, where g_m was less sensitive to T in Yannong 19 than in Shanyou 63. With different g_m–T and Ψ_{leaf}–T relationships, the temperature responses of photosynthetic limitations were surprisingly similar between the two lines, and the photosynthetic rate was highly correlated with g_m. With the increasing T, K_{leaf} increased in Shanyou 63 while it decreased in Yannong 19. The different K_{leaf}–T relationships were related to different Ψ_{leaf}–T relationships. When excluding the effects of water viscosity and Ψ_{leaf}, K_{leaf} was insensitive to T in both lines. g_m and K_{leaf} were generally not coordinated across different temperatures. This study highlights the importance of Ψ_{leaf} on leaf carbon and water exchanges, and the mechanisms for the g_m–T and K_{leaf}–T relationships were discussed.

KEYWORDS
leaf hydraulic conductance, leaf water potential, mesophyll conductance, photosynthetic limitations, temperature

1 | INTRODUCTION

Photosynthesis in C_3 plants is sensitive to a suite of environmental variations. Researches on the temperature (T) acclimation of photosynthesis and the related physiological and biochemical processes are of great importance to plant growth, especially in the context of global warming. In C_3 plants, photosynthesis is limited by stomatal conductance (g_s), mesophyll conductance (g_m) and leaf biochemical capacities, namely the maximum ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}) (Flexas et al., 2012; Tosens, Niinemets, Westoby, & Wright, 2012; von Caemmerer & Farquhar, 1981). Quantifying the partial limitations of these factors and studying the determinant factors to photosynthesis at different temperatures are critical to improve the temperature acclimation of photosynthesis. There are many researches in this field (Slot & Winter, 2017; Yamori, Noguchi, Hanba, & Terashima, 2006), but studies in rice and wheat, the two most important cereal crops for global food production, are rare. Moreover, the temperature response of g_m differs between the two crops. g_m in rice plants generally increases with temperature, while it is insensitive to temperature in wheat (Li, Song, Li, Salter, & Barbour, 2020; von Caemmerer & Evans, 2015). The different g_m–T relationships between the two crops may have some influence on the photosynthetic limitations. Thus, the first objective of this study was to quantify the photosynthetic limitations at different temperatures in rice and wheat.

Leaf transpiration rate (E) dramatically increases with temperature, because, with the increasing temperature, the leaf-to-air vapour pressure deficit (VPd) increases exponentially (Li et al., 2020) while the water viscosity decreases exponentially (Cochard, Martin, Gross, & Bogeat-Triboulot,

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RESEARCH PAPER

Increase rate of light-induced stomatal conductance is related to stomatal size in the genus *Oryza*

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Abstract

The rapid response of stomatal conductance (g_s) to fluctuating irradiance is of great importance to maximize carbon assimilation while minimizing water loss. Smaller stomata have been proven to have a faster response rate than larger ones, but most of these studies have been conducted with forest trees. In the present study, the effects of stomatal anatomy on the kinetics of g_s and photosynthesis were investigated in 16 *Oryza* genotypes. Light-induced stomatal opening includes an initial time lag (λ) followed by an exponential increase. Smaller stomata had a larger maximum stomatal conductance increase rate (SI_{max}) during the exponential increase phase, but showed a longer time lag and a lower initial stomatal conductance ($g_{s,initial}$) at low light. Stomatal size was, surprisingly, negatively correlated with the time required to reach 50% of maximum g_s and photosynthesis ($T_{50\%gs}$ and $T_{50\%A}$), which was shown to be positively correlated with λ and negatively correlated with $g_{s,initial}$. With a lower $g_{s,initial}$ and a larger λ, small stomata showed a faster decrease of intercellular CO_2 concentration (C_i) during the induction process, which may have led to a slower apparent Rubisco activation rate. Therefore, smaller stomata do not always benefit photosynthesis as reported before; the influence of stomatal size on dynamic photosynthesis is also correlated with λ and $g_{s,initial}$.

Keywords: Apparent Rubisco activation rate, flecked irradiance, *Oryza* genus, photosynthesis, stomatal response rate, stomatal size.

Introduction

Light intensity in a plant canopy inherently varies temporarily in magnitude (1–2000 μmol m^{-2} s^{-1}) and time (subseconds to minutes or longer) (Pearcy *et al.*, 1990; Barradas *et al.*, 1998; Leakey *et al.*, 2003; Smith and Berry, 2013). Leaves in the understory of a canopy obtain 10–90% of energy from these transient sunflecks (Pearcy *et al.*, 1990; Leakey *et al.*, 2003; Lawson *et al.*, 2012; Pearcy and Way, 2012), depending on forest type and plant age. The ability to utilize this energy varies significantly between species (Kaiser *et al.*, 2015, 2018), and improving the energy utilization efficiency of sunflecks is an attractive approach to increase canopy photosynthesis and food production. Simulation analysis showed that leaf cumulative CO_2 assimilation of wheat could potentially be improved by 21% by increasing the response rate of photosynthetic rate (*A*, see Table 1 for a list of abbreviations) to sunflecks (Taylor and Long, 2017). Plant biomass of transgenetic tobacco with an improved recovery rate of PSII under fluctuating light is 15% higher than that of the wild type (Kromdijk *et al.*, 2016).

The response rate of *A* to a step increase of irradiance is predominantly determined by the stomatal opening rate and the

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Leaf density explains variation in leaf mass per area in rice between cultivars and nitrogen treatments

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- **Background and Aims** Leaf mass per area (LMA) is an important leaf trait; however, correlations between LMA and leaf anatomical features and photosynthesis have not been fully investigated, especially in cereal crops. The objectives of this study were (*a*) to investigate the correlations between LMA and leaf anatomical traits; and (*b*) to clarify the response of LMA to nitrogen supply and its effect on photosynthetic nitrogen use efficiency (PNUE).
- **Methods** In the present study, 11 rice varieties were pot grown under sufficient nitrogen (SN) conditions, and four selected rice cultivars were grown under low nitrogen (LN) conditions. Leaf anatomical traits, gas exchange and leaf N content were measured.
- **Key Results** There was large variation in LMA across selected rice varieties. Regression analysis showed that the variation in LMA was more closely related to leaf density (LD) than to leaf thickness (LT). LMA was positively related to the percentage of mesophyll tissue area (%mesophyll), negatively related to the percentage of epidermis tissue area (%epidermis) and unrelated to the percentage of vascular tissue area (%vascular). The response of LMA to N supplementation was dependent on the variety and was also mainly determined by the response of LD to N. Compared with SN, photosynthesis was significantly decreased under LN, while PNUE was increased. The increase in PNUE was more critical in rice cultivars with a higher LMA under SN supply.
- **Conclusions** Leaf density is the major cause of the variation in LMA across rice varieties and N treatments, and an increase in LMA under high N conditions would aggravate the decrease in PNUE.

Key words: Leaf density, leaf mass per area, leaf photosynthesis, leaf thickness, photosynthetic N use efficiency, rice.

INTRODUCTION

The leaf is the primary organ for photosynthesis and mediates resources and energy fluxes in the ecosphere. Leaf mass per area (LMA) is an important leaf trait that is strongly correlated with leaf functional, biochemical and structural traits. Recent work has demonstrated that LMA together with other traits, such as vein length per leaf area (VLA), mass-based leaf nitrogen (N) content (N_{mass}), leaf photosynthetic rate (A) and leaf hydraulic conductance (K_{leaf}), scale with each other (Wright *et al.*, 2004; Sack *et al.*, 2013). A well-known generalization is that fast-growing species tend to have a lower LMA, a higher mass-based leaf photosynthesis (A_{mass}) and a higher N_{mass}, but a shorter leaf life span relative to slow-growing species (Wright *et al.*, 2004).

Leaf mass per area can be considered as the product of two physical properties: leaf density (LD) and leaf thickness (LT). The LT ranges between 100 and 700 µm, and LD ranges between 0·1 and 0·6 g cm^{-3} across a range of species (Poorter *et al.*, 2009). However, it is not known what the dominant factor that drives the variation in LMA across species and/or genotypes is. An early study proposed that variation in LMA among species is mainly driven by variation in LT (Vile *et al.*, 2005). In contrast, Poorter *et al.* (2009) claimed that LD and LT explained 80 and 20 % of the differences in LMA, respectively, across a wide range of plant species, and they also found that LMA did not correlate with LT, but was closely related to LD within grasses, herbaceous dicots, deciduous or evergreen woody species groups. More details are needed to reveal the contribution of LT and LD to LMA.

Variation in LMA among species and genotypes can also be obtained by considering LMA as the sum of the dry mass per unit area of different leaf tissues (Roderick *et al.*, 1999). The leaf vein is an important type of anatomical feature; leaves from different cultivars and species exhibit enormous diversity in VLA (Sack *et al.*, 2012). There are two contradictory opinions on the contribution of VLA to LMA. Castro-Díez *et al.* (2000) reported a tight correlation between LMA and the proportion of leaf vein tissue among 52 European woody species. Furthermore, Blonder *et al.* (2011) recently showed that a high VLA can result in a high LMA, and proposed that VLA was the ‘origin’ of LMA. In contrast, Sack *et al.* (2013) re-analysed

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The inhibition of photosynthesis under water deficit conditions is more severe in flecked than uniform irradiance in rice (*Oryza sativa*) plants

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Abstract. Water deficit is considered the major environmental factor limiting leaf photosynthesis, and the physiological basis for decreased photosynthesis under water deficit has been intensively studied with steady irradiance. Leaves within a canopy experience a highly variable light environment in magnitude and time, but the effect of water deficit on photosynthesis in fluctuating irradiance is not well understood. Two rice cultivars with different drought tolerance, Champa and Yangliangyou 6 (YLY6), were hydroponically grown under well-watered, 15% (m/v) and 20% PEG (polyethylene glycol, 6000 Da) induced water deficit conditions. The inhibition of steady-state photosynthesis in Champa is more severe than YLY6. The maximum Rubisco carboxylation capacity (V_{cmax}) and maximum electron transport capacity (J_{max}) were decreased under 20% PEG treatment in Champa, whereas less or no effect was observed in YLY6. The induction state (*IS*%, which indicates photosynthesis capacity after exposure of low-light period) of both leaf photosynthetic rate (A) and stomatal conductance (g_s) was highly correlated, and was significantly decreased under water deficit conditions in both cultivars. Water deficit had no significant effect on the time required to reach 50 or 90% of the maximum photosynthetic rate ($T_{50\%,\mathrm{A}}$ and $T_{90\%,\mathrm{A}}$) after exposure to high-light level, but significantly led to a greater decrease in photosynthetic rate in the low-light period under flecked irradiance ($A_{\mathrm{min\text{-}fleck}}$) relative to photosynthetic rate in the same light intensity of continuously low-light period (A_{initial}). The lower *IS*% of A and more severe decrease in $A_{\mathrm{min\text{-}fleck}}$ relative to A_{initial} will lead to a more severe decrease in integrated CO_2 fixation under water deficit in flecked compared with uniform irradiance.

Additional keywords: dynamic photosynthesis, induction state, simulated sunflecks, steady-state photosynthesis, stomatal conductance, water deficit.

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Introduction

Studies of photosynthesis are mostly conducted under steady-state conditions. However, steady-state conditions are rare in nature, and growth environments, especially irradiance, are inherently heterogeneous in time and space within canopies (Pearcy *et al*. 1990; Lawson *et al*. 2012). At any given level in the canopy, gaps between the leaves in the layer above produce sunflecks that may change rapidly in size and photosynthetic photon flux density (PPFD) because of the wind (Pearcy *et al*. 1990; Timm *et al*. 2002; Lawson *et al*. 2012). Involving many subprocesses, photosynthesis cannot respond linearly to changing irradiance. Therefore, in order to understand photosynthesis in natural conditions, it is important to investigate in conditions of fluctuating irradiance, namely, dynamic photosynthesis.

Previous studies on dynamic photosynthesis have focussed on the influences of changing irradiance on photosynthetic subprocesses, including electron and proton transport, non-photochemical quenching, RuBP regeneration, activation of Calvin cycle enzymes, and stomatal opening (Lawson *et al*. 2012; Kaiser *et al*. 2015). The effect of environmental factors on dynamic photosynthesis is less well known; only a handful of studies have focussed on the influence of elevated CO_2 concentration, leaf temperature, and air humidity on dynamic photosynthesis (Leakey *et al*. 2002, 2003; Cui *et al*. 2009). The lack of knowledge in this area will restrict the understanding of photosynthesis in natural conditions, because plants are usually grown under suboptimal conditions.

Water deficit is considered the major environmental factor limiting plant growth and productivity, because it decreases leaf

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Intraspecific variation in photosynthetic nitrogen-use efficiency is positively related to photosynthetic rate in rice (*Oryza sativa* L.) plants

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Abstract

To explore the natural variation in leaf photosynthesis and investigate its relations with leaf nitrogen (N) status, 121 rice cultivars were pot-grown and their leaf photosynthetic rate (P_N) and N content were measured on the flag leaves at heading stage before anthesis. The results showed that there were substantial natural variations in P_N, leaf N content based on leaf area and leaf mass, and photosynthetic N-use efficiency (PNUE). P_N ranged between 15.4 and 32.6 μmol m^{-2} s^{-1}; P_N and PNUE of four widely grown cultivars in China were significantly lower than P_N and PNUE of the cultivar Nancay PA, which possessed the highest values for P_N and PNUE. Moreover, PNUE was positively related to P_N across cultivars, the high PNUE was related to high stomatal conductance, high transpiration, and low leaf mass per area. We concluded that intraspecific variation in PNUE is positively related to P_N in rice plants.

Additional key words: CO_2 diffusion conductance; leaf anatomy; leaf hydraulic conductance.

Introduction

Improvements in crop management and genetic gain in harvest index lead to a dramatic increase in crop yields, which have more than doubled since 1960 (Long *et al*. 2015). Although the yields continue to increase in most growing areas on a global scale, the yield improvements are stagnating or even moving in reverse at about 24–39% of the growing areas for maize, rice, wheat, and soybean crops (Ray *et al*. 2012, Long 2014). Ray *et al*. (2013) found that the global yields of these four major crops are now increasing at a rate of 1.6, 1.0, 0.9, and 1.3% per year, respectively, which is far less than the rate of 2.4% per year required to double global production by 2050. Therefore, a second Green Revolution is needed to boost crop production and to meet the rising demand.

Over the past 50 years, intercepted radiation and the harvest index have been largely improved, but the conversion efficiency of visible solar energy, which is related to photosynthesis and respiratory loss, has not been improved (Long *et al*. 2015). Thus, increasing energy conversion efficiency can promote the yield. Many researches have aimed to select genotypes for high photosynthesis and were successful in identifying such cultivars (Moss and Musgrave 1971, Austin *et al*. 1982, Shibles *et al*. 1987), but most of these cultivars could not reach the higher crop yield (Moss and Musgrave 1971, Ford *et al*. 1983). The main reason is the complexity of relations between instantaneous assimilation rate of a single leaf and the biomass/yield at the level of a crop canopy. The yield formation is a complex process, the relationship between yield and photosynthesis of a single leaf may be influenced by many factors, such as respiration rate, transportation, *etc*. In addition, Sinclair *et al*. (2004) illustrated that the impact of factors that underlie crop yield can be diminished when scaling up to a higher level, *e.g*., a 50% increase in mRNA synthesis for Rubisco carboxylase finally increases (or even decreases) yield by up to 6% depending on the level of nitrogen accumulation. Therefore, though many previous researches showed weak relations between the yield and net photosynthetic rate (P_N), improving P_N and ascertaining its mechanism is necessary for future breeding work.

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Abbreviations: E – leaf transpiration rate; EFM – evaporative flux method; f_{ias} – fraction of intercellular air space; g_m – mesophyll conductance to CO_2; g_s – stomatal conductance to H_2O; HPFM – high pressure flowmeter method; K_{leaf} – leaf hydraulic conductance; K_{ox} – out-of-xylem hydraulic conductance; K_x – leaf hydraulic conductance inside xylem; LES – leaf economic spectrum; LMA – leaf mass per area; N_{area} – leaf nitrogen content based on leaf area; N_{mass} – leaf nitrogen content based on leaf mass; P_N – net photosynthetic rate; PNUE – photosynthetic nitrogen-use efficiency; RKM – rehydration kinetics method; S_c – surface area of chloroplasts exposed to intercellular airspaces per leaf area; S_m – mesophyll cell wall surface area exposed to intercellular airspace per leaf area; SSNM – site-specific nitrogen management; VPM – vacuum pump method.

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Studies

STUDIES

High leaf mass per area *Oryza* genotypes invest more leaf mass to cell wall and show a low mesophyll conductance

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Abstract

The intraspecific variations of leaf structure and anatomy in rice leaves and their impacts on gas diffusion are still unknown. Researches about the tradeoff between structural compositions and intracellular chemical components within rice leaves are still lacking. The objectives of the present study were to investigate the varietal differences in leaf structure and leaf chemical compositions, and the tradeoff between leaf structural tissues and intracellular chemical components in rice leaves. Leaf structure, leaf anatomy, leaf chemical composition concentrations and gas exchange parameters were measured on eight *Oryza sativa* L. genotypes to investigate the intraspecific variations in leaf structure and leaf anatomy and their impacts on gas exchange parameters, and to study the tradeoff between leaf structural compositions (cell wall compounds) and intracellular chemical components (non-structural carbohydrates, nitrogen, chlorophyll). Leaf thickness increased with leaf mass per area (LMA), while leaf density did not correlate with LMA. Mesophyll cell surface area exposed to intercellular airspace (IAS) per leaf area, the surface area of chloroplasts exposed to IAS and cell wall thickness increased with LMA. Cell wall compounds accounted for 71.5 % of leaf dry mass, while mass-based nitrogen and chlorophyll concentrations decreased with LMA. Mesophyll conductance was negatively correlated with LMA and cell wall thickness. High LMA rice genotypes invest more leaf mass to cell wall and possess a low mesophyll conductance.

Keywords: Cell wall; leaf anatomy; leaf chemical compositions; leaf mass per area; *Oryza sativa* L.; tradeoff.

Introduction

Under current ambient conditions (around 400 μmol CO_2 mol^{-1} air), CO_2 diffusion conductance from the air to the sites of carboxylation is regarded as one of the most important limiting factors for photosynthesis in C_3 plants (Evans *et al.* 2009; Li *et al.* 2009; Yamori *et al.* 2011; Flexas *et al.* 2012; Adachi *et al.* 2013).

After reaching substomatal cavities, CO_2 needs to further diffuse through the mesophyll cell to reach the carboxylation sites (Terashima *et al.* 2011). The CO_2 diffusion resistance from the substomatal cavities to the carboxylation sites is called mesophyll resistance (r_m), and the reciprocal of r_m is mesophyll conductance (g_m). g_m is determined by both anatomical and biochemical components (e.g. aquaporins and carbonic anhydrase etc.) (Nakhoul *et al.* 1998; Uehlein 2003, Evans *et al.* 2009). There are many anatomical properties relating to mesophyll conductance, including the fraction of intercellular airspace (f_{ias}), the mesophyll cell wall surface area exposed to intercellular airspace per leaf area (S_m), the surface area of

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Nitrogen Can Alleviate the Inhibition of Photosynthesis Caused by High Temperature Stress under Both Steady-State and Flecked Irradiance

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Nitrogen is one of the most important elements for plants and is closely related to photosynthesis. High temperature stress significantly inhibits photosynthesis under both steady-state and flecked irradiance. However, it is not known whether nitrogen can affect the decrease in photosynthesis caused by high temperature, especially under flecked irradiance. In the present study, a pot experiment was conducted under two nitrogen (N) supplies with rice plants, and the steady-state and dynamic photosynthesis rates were measured under 28 and 40°C. High temperature significantly increased leaf hydraulic conductance (K_{leaf}) under high N supply (HN) but not under low N supply (LN). The increased K_{leaf} maintained a constant leaf water potential (Ψ_{leaf}) and steady-state stomatal conductance ($g_{\text{s,sat}}$) under HN, while the Ψ_{leaf} and $g_{\text{s,sat}}$ significantly decreased under high temperature in LN conditions. This resulted in a more severe decrease in steady-state photosynthesis (A_{sat}) under high temperature in the LN conditions. After shifting from low to high light, high temperature significantly delayed the recovery of photosynthesis, which resulted in more carbon loss under flecked irradiance. These effects were obtained under HN to a lesser extent than under LN supply. Therefore, it is concluded that nitrogen can alleviate the inhibition of photosynthesis caused by high temperature stress under both steady-state and flecked irradiance.

Keywords: dynamic photosynthesis, high temperature, leaf hydraulic conductance, nitrogen, steady-state photosynthesis

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INTRODUCTION

Global warming is threatening crop yields. Lobell and Asner (2003) estimated that each 1°C increase in growing season temperature can result in up to 17% decrease in corn and soybean yield. Experimental data in rice production showed that rice yield decreases by 10% for each 1°C increase in the minimum temperature of the growing-season (Peng et al., 2004). Photosynthesis is important for crop growth and production, and it is very sensitive to temperature. Photosynthesis usually peaks at ~30°C in rice plants, with a significant decrease in CO_2 assimilation for additional increases in temperature (Yamori et al., 2011).

The intrinsic mechanisms for reduced photosynthesis under high temperature stress have been intensively studied. First, ribulose-bisphosphate carboxylase/oxygenase (Rubisco) is a bifunctional enzyme, and Rubisco activity can be substantially restrained under supra-optimal temperature

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ORIGINAL ARTICLE

Rice (*Oryza sativa* L.) hydraulic conductivity links to leaf venation architecture under well-watered condition rather than PEG-induced water deficit

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Abstract Higher plant hydraulic conductivity (K_{plant}) is vital for plant growth, especially under PEG-induced water deficit stress (PEG-IWDS). Leaf venation architecture is a key determinant of leaf hydraulic conductivity (K_{leaf}) and K_{leaf} is a major component of K_{plant} across different plant species. However, there is little information about (1) varietal difference in leaf vein development in cereal crops, such as rice plants; (2) the effects of PEG-IWDS on leaf vein development; (3) the coordination between leaf venation architecture and K_{plant} as well as K_{leaf} under PEG-IWDS. In the present study, widely cultivated eight rice cultivars were grown hydroponically under well-watered condition (WWC) and PEG-IWDS, simulated by adding 15 % (w/v) PEG6000. Leaf venation architecture, including total longitudinal leaf vein number, leaf vein numbers per unit width (LVNW), vein thickness and leaf mass per area, as well as K_{plant} and K_{leaf} were measured to address above-mentioned questions. The results showed that leaf venation architecture exhibited significant varietal differences and PEG-IWDS significantly increased LVNW while decreased vein thickness. PEG-IWDS suppressed both K_{plant} and K_{leaf} but the decrease was much higher in K_{plant} than K_{leaf}. There was a significant and positive correlation observed between LVNW and K_{leaf} under both WWC and PEG-IWDS but the correlation between LVNW and K_{plant} was only significant under WWC. K_{leaf} was significantly and positively correlated with K_{plant} under WWC but not under PEG-IWDS. It is concluded that K_{leaf} is a major determinant for K_{plant} under WWC but not under PEG-IWDS; therefore, breeding or selecting rice cultivars with high LVNW can improve shoot water supplement under WWC but not under PEG-IWDS condition.

Keywords Rice · PEG-induced water deficit stress · Leaf vein numbers per unit width · Plant hydraulic conductivity · Leaf hydraulic conductivity · Leaf thickness

Introduction

Leaves are the primary loci for plants to convert sun energy and carbon resources into photosynthates. Many leaf morphological and functional traits, such as leaf mass per area (LMA), leaf photosynthesis, leaf nitrogen content, and

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RESEARCH ARTICLE

Varietal difference in the correlation between leaf nitrogen content and photosynthesis in rice (*Oryza sativa* L.) plants is related to specific leaf weight

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Abstract

Increasing leaf photosynthesis per area (*A*) is of great importance to achieve yield further improvement. The aim of this study was to exploit varietal difference in *A* and its correlation with specific leaf weight (SLW). Twelve rice cultivars, including 6 *indica* and 6 *japonica* varieties, were pot-grown under two N treatments, low N (LN) and sufficient N (SN). Leaf photosynthesis and related parameters were measured at tillering stage. Compared with LN treatment, *A*, stomatal conductance (g_s), mesophyll conductance (g_m), leaf N content (N_{area}), and chlorophyll content were significantly improved under SN treatment, while SLW and photosynthetic N use efficiency (PNUE) were generally decreased. Varietal difference in *A* was positively related to both g_s and g_m, but not related to N_{area}. This resulted in a low PNUE in high N_{area} leaves. Varietal difference in PNUE was generally negatively related to SLW. Response of PNUE to N supply varied among different rice cultivars, and interestingly, the decrease in PNUE under SN was negatively related to the decrease in SLW. With a higher N_{area}, *japonica* rice cultivars did not show a higher *A* than *indica* rice cultivars because of possession of high-SLW leaves. Therefore, varietal difference in *A* was not related to N_{area}, and SLW can substantially interfere with the correlation between *A* and N_{area}. These findings may provide useful information for rice breeders to maximize *A* and PNUE, rather than over reliance on N_{area} as an indicator of photosynthetic performance.

Keywords: specific leaf weight, leaf nitrogen content, leaf photosynthesis, mesophyll conductance, photosynthetic nitrogen use efficiency, stomatal conductance

1. Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops in the world, and is a staple food source for more than a third of the world's population (Khush 1997). More than 90% of the world's rice is planted in Asia, where about 35–60% of the calories consumed by three billion people are taken from rice. Rice is also the staple food for more than 65% of the population of China (Peng *et al*. 2009). With a rapidly growing population, improving rice productivity within

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Nitrogen can improve the rapid response of photosynthesis to changing irradiance in rice (*Oryza sativa* L.) plants

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To identify the effect of nitrogen (N) nutrition on the dynamic photosynthesis of rice plants, a pot experiment was conducted under two N conditions. The leaf N and chlorophyll levels, as well as steady–state photosynthesis, were significantly increased under high N. After the transition from saturating to low light levels, decreases in the induction state (*IS*%) of leaf photosynthesis (*A*) and stomatal conductance (g_s) were more severe under low than under high N supply. After the transition from low to flecked irradiance, the times to 90% of maximum *A* ($T_{90\%A}$) were significantly longer under low than under high N supply. Under flecked irradiance, the maximum *A* under saturating light ($A_{max\text{–}fleck}$) and the steady–state *A* under low light ($A_{min\text{–}fleck}$) were both lower than those under uniform irradiance (A_{sat} and $A_{initial}$). Under high N supply, $A_{max\text{–}fleck}$ was 14.12% lower than A_{sat}, while it was 22.80% lower under low N supply. The higher *IS*%, shorter $T_{90\%A}$, and the lower depression of $A_{max\text{–}fleck}$ from A_{sat} under high N supply led to a less carbon loss compared with under a low N supply. Therefore, we concluded that N can improve the rapid response of photosynthesis to changing irradiance.

Photosynthesis is one of the most important biochemical processes in the world, and it is mostly studied under controlled and steady-state conditions. However, steady-state conditions are rare in nature, and growth environments, especially irradiance, are intrinsically heterogeneous in time and space within canopies[1]. Leaves within a canopy experience a highly variable light environment in magnitude (1–2000 μmol m^{-2} s^{-1}) and time (seconds to minutes or longer) over the course of a day due to changes in the incoming solar irradiance, cloud cover, wind, self-shading of the upper leaves[2,3]. Sunflecks—relatively brief but high-intensity patches of light—have been recognised as an important energy source. It is reported that leaves, especially in the understory of the canopy, obtain 10–90% of the total photosynthetic photon flux density (PPFD) from sunflecks during 10% of the time in a day, which drives up to 65% of the total daily photosynthesis[3–5].

Plants have the ability to acclimate their growth to their light environment, from whole-plant morphological changes to the differences in stoichiometry of the photosynthetic apparatus observed in leaves grown under sun and shade conditions[3,6]. However, this acclimation occurs over a timescale of days and weeks. In addition to this, the dynamic response of photosynthesis to rapidly changing irradiance is a quick response over a timescale of seconds to minutes, but leaf photosynthesis responds non-linearly to changes in light levels. Several minutes of low light levels will down-regulate Calvin cycle enzyme activity, and stomatal aperture; photosynthesis will thus be limited before a full induction of these photosynthesis processes occurs during a transition from low to high light levels[3,7–9], and non-photochemical quenching (NPQ), a photoprotective mechanism to photosynthesis organs, will be improved. As a consequence, carbon loss is evident in flecked irradiance compared with uniform conditions, especially under abiotic stresses, for example high-temperature stress[5,10]. Moreover, photoinhibition would be occur when protective processes are either saturated or themselves damaged.

It is reported that daily carbon gain can be reduced by as much as 40% under flecked irradiance compared with uniform irradiance[10,11]. Similarly, plant biomass can be severely depressed under flecked irradiance[11],

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Influence of leaf vein density and thickness on hydraulic conductance and photosynthesis in rice (*Oryza sativa* L.) during water stress

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The leaf venation architecture is an ideal, highly structured and efficient irrigation system in plant leaves. Leaf vein density (LVD) and vein thickness are the two major properties of this system. Leaf laminae carry out photosynthesis to harvest the maximum biological yield. It is still unknown whether the LVD and/or leaf vein thickness determines the plant hydraulic conductance (K_{plant}) and leaf photosynthetic rate (*A*). To investigate this topic, the current study was conducted with two varieties under three PEG-induced water deficit stress (PEG-IWDS) levels. The results showed that PEG-IWDS significantly decreased *A*, stomatal conductance (g_s), and K_{plant} in both cultivars, though the IR-64 strain showed more severe decreases than the Hanyou-3 strain. PEG-IWDS significantly decreased the major vein thickness, while it had no significant effect on LVD. *A*, g_s and K_{plant} were positively correlated with each other, and they were negatively correlated with LVD. *A*, g_s and K_{plant} were positively correlated with the inter-vein distance and major vein thickness. Therefore, the decreased photosynthesis and hydraulic conductance in rice plants under water deficit conditions are related to the decrease in the major vein thickness.

Photosynthesis is an important physiological process that is very sensitive to abiotic stresses[1,2]. Diffusive (stomatal or mesophyll conductance) and biochemical impairments are considered two major responses that decrease photosynthesis under drought conditions[3,4]. Stomatal conductance (g_s) is a fundamental process required for CO_2 acquisition and is regulated by stomatal opening and closing[5,6]. A decreasing leaf turgor pressure and an increasing vapor pressure deficit (VPD) closes the stomata rapidly in response to water deficit condition[7]. Thus, stomatal limitation is a key cause of the decrease in *A* that occurs under water-limited conditions[7,8].

The water transportation capacity of plants is known as the plant hydraulic conductance[9,10], which is determined by the root, stem and leaf hydraulic conductance (K_{leaf})[11]. The root contribution ranges from one-third to one-half of the internal plant resistances[12,13]. The transpiration rate (*E*) or stomatal conductance exhibit significant and linear correlations with K_{plant} in a number of higher plants and rice plant[14–18]. Therefore, the capacity of water transport system controls the plant growth as it maintains the hydraulic link between the roots and leaves[19].

The leaf hydraulic architecture is the key location for gas exchange between the plant and its environment[20,21], and extra-vascular resistance imposes one-quarter or higher resistance ($\geq$30%) in K_{leaf}[22,23]. A decrease in K_{leaf} leads to stomatal closure, which reduces photosynthesis[24,25]. Therefore, a strong correlation has been observed between g_s and K_{leaf}[22,23,26]. The leaf venation architecture is a perfect illustration of a highly efficient irrigation structure[27,28]. Veins are made up of phloem and xylem vessels implanted in parenchyma, rarely in sclerenchyma, that are wrapped in bundle sheath cells. Leaf veins in monocots of the *Poaceae* family are divided into three categories (major, minor and transverse veins) in addition to the leaf midrib, and are different in sizes and

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慕课时代下高校《植物生理学》教学模式面临的机遇和挑战

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摘要:提高《植物生理学》的教学质量对于培养高水平植物生产类专业和生物专业人才具有重要意义。文章就慕课的特点、问题和解决途径进行了简要的探讨,并结合《植物生理学》课程分析慕课和传统课堂有机结合的方法,希望能够为其他教育工作者提供一定的参考和借鉴。

关键词:《植物生理学》;慕课;传统教学
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《植物生理学》是研究植物生命活动规律及其与外界环境相互关系、揭示植物生命现象本质的一门科学,是生命科学尤其是植物生产类专业、生物专业人才培养的重要专业基础课。提升《植物生理学》教学水平对于夯实高等农业院校学生的基础知识水平,培养高水平植物生产类和生物专业人才和提高农业院校教学与研究水平具有重要的意义[1]。然而,植物生命活动非常复杂,植物与外界环境的关系又涉及很多机理、机制和生化反应过程,在教学过程中如果不能合理地运用各种教学方法,我们很难将复杂的植物生理学知识非常清楚地、有条理地讲授出来,学生在学习过程中也难免会感到枯燥乏味,也很难取得良好的教学效果。传统的教学方法是以PPT讲授为主、板书为辅的“填鸭式”教学,是“课堂传授知识,课后完成作业”的讲授方式,学生在学习过程中是一种被动地接受知识的过程,学生在学习过程中的积极性和主动性没有被充分调动出来。

一、慕课的定义、特点和问题

慕课(Massive Open Online Course)是大规模开放在线课程,是互联网时代下产生的新兴的教学模式。传统的课程教学对人数有明显的限制,课程只能有几十到上百人,只能针对本校相关专业的学生在特定的时间、特定的地点进行课堂讲授。慕课具有开放和在线两大特点,对参与人数和学生来源都没有限制。一门慕课的选课人数可以高达成千上万个,同时打破了时空的限制,学生可以在全国各地甚至世界范围的高校内选择自己感兴趣的课程进行自主学习,并通过网络与教师进行互动。慕课的推广有利于实现教育均衡发展,促进教育公平化,缩小地区间教育水平的差异。

以慕课为基础发展起来的翻转课堂,是以学生自主学习为主、教师指导解答为辅的教学模式[2]。在翻转课堂模式下,学生在课前自主观看教学视频,查阅资料,完成课前预习。在课堂上,教师与学生进行面对面的交流,组织和参与小组讨论,并针对学生提出的学习难点和重点进行针对性的解答。翻转课堂将学习的主动权交给学生,学生自主决定如何学习、什么时候学习,是一种能够激发学生自主学习的有效模式。

但是,慕课在高校教学中的运用中也存在很多问题和挑战。(1)慕课要求学生具备基本的信息技术应用能力,具备熟练使用各种多媒体资料和网络交流平台的能力[3]。(2)慕课要求学生拥有一台计算机,至少在图书馆等学校公共资源中能够非常容易地借用或租用相关硬件和软件资源。尽管我国现在的经济发展水平得到了显著提升,但是由于地区发展不平衡等,目前每个高校都有一批家庭条件比较贫困的学生。学校在推广慕课的同时,应该充分考虑这一部分学生的困难并进行定向帮扶。(3)慕课对学生的自学能力和自控能力具有很高的要求。在具体实施过程中,经常发现有些学生打开慕课课程,但并未真正学习。(4)网络资源的学习都是在课下进行,因为没有上课时的氛围和紧迫感,所以学习效率一般较差,学生也很难把握课程的重点和难点。

针对上述问题,在实际教学中应该注意以下几点:(1)在网络资源的学习前,教师可以提供相应的开放性题目引导学生自学,让学生带着问题有的放矢地去学习,从而提升学习质量和学习效率。(2)在学习结束后,教师可以提供一些检验性题目,让学生自检学习质量,同时监督学生是否真正自主学习。(3)在课程开始前,详细了解学生的学习状况,掌握学生学习的难点并结合教学重点有针对性地讨论和解答问题。

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大学植物生理学教学中细胞信号转导的教学设计

——以华中农业大学植物保护专业为例

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摘　要：在高等农业院校，植物生理学是很多专业必修的一门专业课。本文介绍了植物细胞信号转导一章的教学设计，希望对激发学生学习兴趣、提高学生自主学习能力、进一步提升教学效果有所帮助。

关键词：植物生理学；细胞信号转导；教学设计

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Teaching Design of Cell Signal Transduction in College Plant Physiology Teaching

—Taking Plant Protection Major of Huazhong Agricultural University as an Example

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Abstract: Plant physiology is a required professional course for many majors in agricultural colleges and universities. In this paper, in order to stimulate students’ interest in learning, improve students’ autonomous learning ability, and further improve the teaching effect, the teaching design of cell signal transduction was introduced.

Key words: Plant physiology; Cell signal transduction; Teaching design

一　引言

植物生理学（plant physiology）是研究植物生命活动规律及其与环境相互关系、揭示植物生命现象本质的科学。高等植物的生命活动主要包括生长发育与形态建成、物质与能量代谢、信息传递与信号转导等方面。植物体内信息传递和信号转导在植物生命活动过程中占据着举足轻重的地位，一旦植物体内信息传递和信号转导机制在分子水平上得以认识和调控，许多尚未揭示的植物生命现象的本质将会展现出来。因此，植物生理学课程中植物细胞信号转导部分的教学非常重要。在现有的教学环节中，关于课件的美化和信息化手段的使用都有了很大的提升，但教学效果仍不尽人意。往往学生考完试以后，就把教师课堂上讲的统统忘记了。究其原因，学生还是以应付考试为主，我们的教学并未真正触及到学生的兴趣点，未激发出学生的求知欲。

教学设计是根据课程标准的要求和教学对象的特点，将教学诸要素有序安排，确定合适的教学方案的设想和计划。一般包括教学目标、教学重难点、教学方法、教学过程、时间分配、板书设计等环节。一个好的教学设计，是提高教学效率和教学质量，使学生在单位时间内能够学到更多的知识，更大幅度地提高学生各方面的能力的基础。本文结合笔者多年来的植物生理学教学实践，针对高等农业院校植物保护专业的学生，提出以下教学设计供大家参考。

二　课程目标与专业培养目标

（一）课程目标

通过植物生理学的教学，要求学生掌握植物生命活动的基本原理、规律和过程及其与环境的相互关系；注重培养学生应用知识和创新思维的能力；引导学生应用

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