AcademicPres

Available online: www.notulaebotanicae.ro

Print ISSN 0255-965X; Electronic 1842-4309

Not Bot Horti Agrobo, 2016, 44(2):393-398. DOI:10.15835/nbha44210555

Notulae Botanicae Horti Agrobotanici Cluj-Napoca

Original Article

Effects of Light Quality on the Chlorophyll Degradation Pathway in Rice Seedling Leaves

Chang-Chang CHEN[1], Kuan-Hung LIN[2], Meng-Yuan HUANG[2], Wen-Dar HUANG[3]**, Chi-Ming YANG[4]*

[1]*Miaoli District Agricultural Research and Extension Station, Council of Agriculture, Gongguan township 36346, Miaoli County, Taiwan; cchen@mdais.gov.tw*

[2]*Chinese Culture University, Department of Horticulture and Biotechnology, 11114 Taipei, Taiwan; rlin@faculty.pccu.edu.tw; hmy6@ulive.pccu.edu.tw*

[3]*National Taiwan University, Department of Agronomy, Daan 10617, Taipei, Taiwan; wendar@ntu.edu.tw (**co-corresponding author)*

[4]*Academia Sinica, Biodiversity Research Center, Nankang 11529, Taipei, Taiwan; cmyang@gate.sinica.edu.tw (*corresponding author)*

Abstract

The objective of this study was to investigate the dynamics of chlorophyll (Chl), biosynthetic intermediates (protoporphyrin IX, magnesium protoporphyrin IX, and protochlorophyllide), degradation intermediates [chlorophyllide (Chlide), pheophytin (Phe), and pheophorbide (Pho)], and carotenoids (Car) in leaves of rice seedlings. Two rice varieties, 'Taichung Shen 10' ('TCS10') and 'IR1552', were grown under different light quality conditions controlled by light emitting diodes (LED). Lighting treatments for rice seedlings were included by red (R), blue (B), green (G), and red + blue (RB), with fluorescent lighting (FL) as the control and photosynthetic photon flux density being set at 105 μmol m^{-2} s^{-1}. The results show that lower levels of Chl and Car in leaves were detected under G lighting, and light quality did not mediate porphyrins in biosynthetic pathways. Rice seedling leaves took Chl→Phe→Pho and Chl→Chlide→Pho as the major and minor degradation routes, respectively. Furthermore, higher Phe/Chlide ratios were observed under G and FL lighting conditions, indicating that green-enriched environments can up-regulate the minor degradation route in leaves.

Keywords: biosynthesis and degradation pathways, light quality, rice

Introduction

Light is the photosynthetic energy source and used as an environmental factor that triggers plant morphogenesis and developments. Plant development is strongly influenced by light quality, which refers to the composition of spectrum or wavelengths reaching a plant (Johkan *et al*., 2010; Bian *et al*., 2015). Red and blue lights have the greatest impact on plant growth because they are the major energy sources for CO_2 assimilation in plant. It is well known that spectra have action maxima in the blue and red ranges (Kasajima *et al*., 2008). The quality, duration, and intensity of red light/far red light, blue light, UV-A (320-500 nm) or UV-B (280-320 nm) are related to plant hormone signaling pathways that have a profound influence on plant by triggering or halting physiological reactions and controlling the growth and development of plant (Clouse, 2001; Shin *et al*., 2008; Montgomery, 2016). The functions of green light on the morphogenesis, metabolism, and photosynthesis of plants have been investigated extensively (Kasajima *et al*., 2008; Zhang *et al*., 2011; Johkan *et al*., 2012).

Chlorophylls (Chl) and carotenoids (Car) are photosynthetic pigments in plants. The Chl biosynthesis and/or degradation pathway influences Chl accumulation. Light induces the Chl biosynthesis pathway, and different spectrums influence the formation of photosynthetic pigments (Jilani *et al*., 1996; Hoober *et al*., 1999; Su *et al*., 2014). Blue light induces higher Chl *a*/*b* ratios (Rivkin, 1989; Demarsac *et al*., 1993; Chen *et al*., 2014; Hoffmann *et al*., 2015) and greater accumulations of Chl (Kurilčik *et al*., 2008; Poudel *et al*., 2008; Hoffmann *et al*, 2016). Red light inhibits Chl synthesis at lower concentrations of Chl and precursors like 5-aminolevulinic acid (Tanaka *et al*., 1998; Sood *et al*., 2005), protoporphyrin IX (PPIX), magnesium protoporphyrin IX (MGPP), and protochlorophyllide (Pchlide) (Fan *et al*., 2013). Moreover, the mole percentages of PPIX, MGPP, and Pchlide also respond to various physiological conditions and genotypes (Hsu *et al*., 2003; Hsu *et al*., 2011; Huang *et al*., 2014).

Chlorophyllase and Mg-dechelatase actions, which are responsible for the first steps in the Chl degradation pathway, are elicited by *Rhopalosiphum padi* and *Diuraphis noxia* (Ni *et*

Received: 07 Sep 2016. Received in revised form: 17 Nov 2016. Accepted: 19 Nov 2016. Published online: 14 Dec 2016.

al., 2002; Wang *et al*., 2004). Chlorophyllase 1 of *Arabidopsis thaliana,* encoded by *AtCLH1,* is indicated to be involved in plant damage control, and can modulate the balance between different plant defense pathways (Kariola *et al*., 2005). Previously, we found that the leaves of sweet potato (Hsu *et al*., 2003) and *Machilus thunbergii* (Yang *et al*., 2003) use Chl → pheophytin (Phe) → pheophorbide (Pho) as the major route for Chl degradation, whereas the leaves of banana might use Chl → chlorophyllide (Chlide) → Pho as the major route (Hsu *et al*., 2011). In addition, some biotic/abiotic factors also affect the degradation pathway (Hsu *et al*., 2003; Yang *et al*., 2003; Hsu *et al*., 2011; Huang *et al*., 2014). However, there are no reports describing the effects of LED lighting on the Chl degradation pathway. Our objective was to investigate Chl biosynthetic and degradation pathways in leaves of rice seedlings grown under different lighting spectra.

Materials and Methods

Plant materials and growth conditions

Rice (*Oryza sativa* L.) cultivars 'IR1552' with purple leaves and 'Taichung Shen 10' ('TCS10', green leaf), one of the most widely grown rice cultivars in Taiwan, were used in this study. Seeds were sterilized with 2% sodium hypochlorite for 20 min, washed extensively with distilled water, and germinated in Petri dishes on wetted filter paper at 37 °C in the dark. After 48 h of incubation, uniformly germinated seeds were selected and cultivated in a 150 ml beaker containing a half-strength Kimura B nutrient solution with the following macro and microelements: 182.3 μM $(NH_4)_2SO_4$, 91.6 μM KNO_3, 273.9 μM $MgSO_4{\cdot}7H_2O$, 91.1 μM KH_2PO_4, 182.5 μM Ca $(NO_3)_2$, 30.6 μM Fe-citrate, 0.25 μM H_3BO_3, 0.2 μM $MnSO_4{\cdot}H_2O$, 0.2 μM $ZnSO_4{\cdot}7H_2O$, 0.05 μM $CuSO_4{\cdot}5H_2O$, and 0.07 μM H_2MoO_4. Nutrient solutions (pH 4.7) were replaced every 3 d. Hydroponically cultivated rice seedlings were raised in growth chambers with the LED lighting at 30 °C and 25 °C for day and night, respectively, under a 12 h photoperiod.

Light treatments

LED lighting systems with a digital controller designed by GRE Technology (Taipei, Taiwan) were used to control light quality. Spectral distributions of blue (peak at 460 nm), red (peak at 630 nm), and green (peak at 530 nm) were measured using a spectroradiometer (LI-COR1800, Lincoln, NE, USA) in the 300–800 nm range. Light treatments for rice seedlings, proliferation, and differentiation consisted of red LED (R), blue LED (B), green LED (G), a mixture of red plus blue LEDs (R:B = 4:1 by photon flux density; RB), and fluorescent lighting (FL, control). Photosynthetic photon flux density (PPFD) was uniformly set at 105 μmol m^{-2} s^{-1}. The experiment was independently performed three times under randomized growth conditions, and measurements representing the means of nine plants (three replications consisting of three plants each) were taken.

Pigment analysis

All hydroponic seedlings were collected on day 14 after reaching stage V2 or V3 according to Counce *et al*. (2000). The second fully expanded leaves of the seedlings were detached, frozen with liquid nitrogen, and extracted with 80% acetone. The concentrations of Car, less polar (LP) Car, more polar (MP) Car, and Chl-related compounds (*i.e*., PPIX, MGPP, Pchlide, Chl, Chlide, and Phe) were determined according to Yang *et al*. (1998) with a spectrophotometer (Hitachi U3010, Tokyo, Japan). The mole percent of individual porphyrin is defined as [(PPIX, MGPP or Pchlide) / (PPIX + MGPP + Pchlide)] x 100%. The values of phytylated and/or dephytylated pigments in samples were read directly at absorbances of 661 and 666 nm (A_{661} and A_{666} g^{-1} DW), respectively. The value of A_{661} cannot be transformed into individual content of Chl and Phe, however, it can be used to compare the relative content of total phytylated pigments (Shioi and Sasa, 1986). On the other hand, the value of A_{666} also can be used to compare the relative content of total dephytylated pigments (Chlide and Pho).

Statistical analyses

All measurements were evaluated for significance using an analysis of variance (ANOVA) followed by a least significant difference (LSD) test at the $p < 0.05$ level. All statistical analyses were conducted using SAS 9.3 (SAS Institute; Cary, NC, USA).

Results

Chl and Car

The dynamics of photosynthetic pigments in leaves of both cultivars under different lighting qualities are listed in Table 1. The concentrations of Chl and Car in leaves of 'IR1552' were higher than those of 'TCS10'. In both cultivars, the concentration of Chl was lower under G lighting, but Chl concentrations among B, BR, and FL treatments were not significantly different. A similar trend was observed in Car in the leaves of TCS10, but there were no significant differences with IR1552.

Concentrations of LP Car were dramatically reduced in leaves of both cultivars under G condition. A lower accumulation of LP Car was also observed in leaves of 'TCS10' under FL (369 μg g^{-1}DW). Significantly lower concentrations of MP Car were observed in leaves of 'TCS10' under G and R lightings. However, the effects of LED lighting were insignificant on MP Car in 'IR1552'. Light quality influenced LP Car/MP Car ratios in 'TCS10' strongly, but not in IR1552.

Porphyrins and their mole percentages

Porphyrins are the Chl biosynthesis intermediates. The accumulation of porphyrins in leaves of 'IR1552' was higher than those in 'TCS10' (Fig. 1). The concentration of porphyrins in TCS10 was not significantly different among all treatments (2.84 ~ 3.13 μmol g^{-1} DW). IR1552 showed a similar response, but the levels of porphyrins under B were lower than in other treatments. The percentages of PPIX and MGPP were insignificant among all lighting conditions for both cultivars (Fig. 2). The percentage of Pchlide in 'TCS10' was higher compared with other treatments, and it was irresponsive to lighting quality in 'IR1552'.

Chl degradation intermediates

The concentration of Phe was higher than Chlide for both cultivars (Fig. 3). Leaves of rice seedlings took Chl → Phe→ Pho as the major degradation route, but Chl → Chlide → Pho as the

Table 1. Effects of light quality on the levels of Chl (express in mg g^{-1} DW), Car, LP Car, MP Car (expressed in μg g^{-1}DW), and their ratios in seedling leaves collected from 14-d seedlings under different lighting environments

Variety	Light treatment*	Chl	Car	LP Car	MP Car	LP/MP
'TCS10'	FL	12.08 c	4.55 cd	369 de	575 a	0.64 c
	R	10.6 d	4.2 de	400 cde	377 b	1.06 a
	G	9.67 d	3.88 e	342 e	348 b	0.98 ab
	B	12.96 bc	4.88 bc	394 de	544 a	0.79 bc
	RB	12.75 c	4.63 c	446 cd	518 a	0.90 abc
'IR1552'	FL	15.01 a	5.49 a	593 a	604 a	0.99 ab
	R	14.16 ab	5.23 ab	554 ab	541 a	1.02 ab
	G	12.63 c	4.93 bc	486 bc	500 a	0.97 ab
	B	14.27 a	4.95 bc	543 ab	511 a	1.06 a
	RB	15.35 a	5.2 ab	613 a	584 a	1.05 ab

Within columns, means followed by the same letter are not significantly different according to LSD ($p < 0.05$)
Chl - chlorophyll; Car - carotenoids; LP - less polar; MP - more polar; R - red; B - blue; G - green; RB - mixture of red plus blue; FL - fluorescent lighting

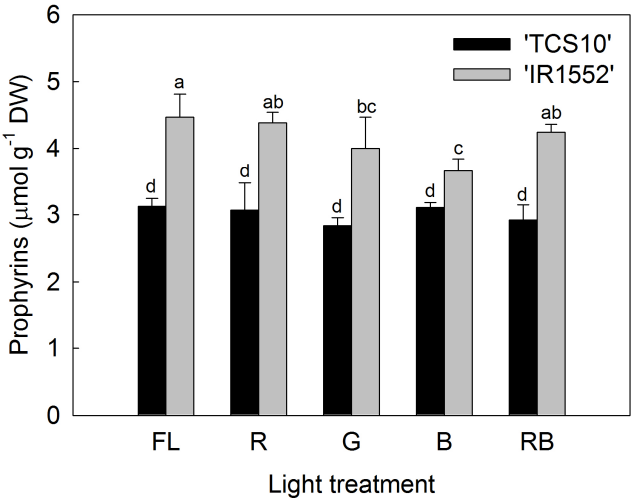

Fig. 1. Means ±SE of prophyrins of leaves collected from 14-d seedlings under different lighting environments. The values followed by the different letter show statistically significant differences at $p < 0.05$. R - red; B - blue; G - green; RB - mixture of red plus blue; FL - fluorescent lighting

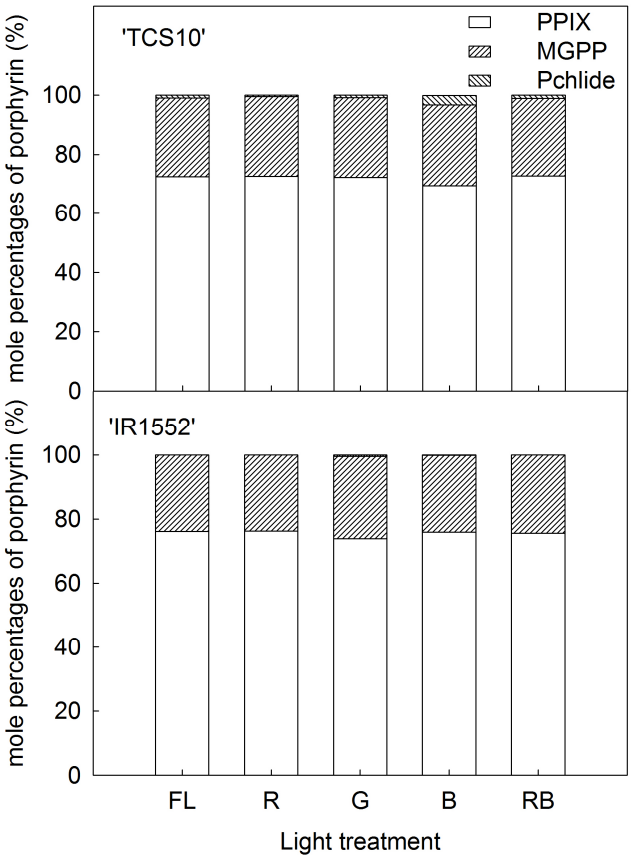

Fig. 2. The mole percentages of protoporphyrin IX (PPIX), magnesium protoporphyrin IX (MGPP), and protochlorophyllide (Pchlide) in leaves collected from 14-d seedlings of 'TCS10' and 'IR1552'under different lighting environments. R - red; B - blue; G - green; RB - mixture of red plus blue; FL - fluorescent lighting

minor degradation route. In both cultivars, the concentrations of Phe under G were lower than in other treatments, and the highest concentration of Phe was under RB. The concentration of Chlide under FL was greater than in other treatments. The Phe/Chlide ratios of 'IR1552' under G and FL were lower than other treatments (insignificant at $p < 0.05$). A similar trend was observed in 'TCS10', with the exception of G. The results of phytylated and dephytylated pigments and their ratios were also shown a similar trend to the Phe/Chlide ratio (Fig. 4).

Discussion

Plant pigments have specific wavelength absorption patterns known as absorption spectra. Biosynthetic wavelengths for the production of plant pigments are referred to as action spectra (Wang *et al*., 2009). Chls have high light absorptions at 400-500 and 630-680 nm, and Cars have high light absorptions at 400-500. Meanwhile, both Chls and Cars have low light absorption at 530-610 nm. Previous studies (Nhut *et al*., 2003; Lee *et al*., 2007; Johkan *et al*., 2010; Guo *et al*., 2011; Lin *et al*., 2011; Liu *et al*., 2011; Fan *et al*., 2013, Hoffmann *et al*., 2015; Hoffmann *et al*., 2016) have demonstrated that blue light induced the synthesis of Chl and Car. In our study, the concentrations of Chl and Car were greater under FL, B, and RB treatments, with the exception of

IR1552 under B lighting, and were lower under G lighting (Table 1). However, our previous study showed that Car levels were not responsive to light quality (Chen *et al*., 2014). These different results under the same experimental conditions, including light quality and rice variety, might be due to the change in light irradiance with higher light irradiance (160 μmole m^{-2} s^{-1}), resulting in insignificant differences in Car levels. MP and LP Car levels respond to different aging and senescent conditions (Hsu *et al*., 2003). MP Car levels decrease as LP Car levels increase during the maturation/ageing process. Our results show that MP and LP Car levels were also mediated by light quality; including the possibility that green light inhibited LP Car synthesis.

Light is an important environmental signal and induces chlorophyll biosynthesis (Jilani *et al*., 1996). Chl reduction was observed under red light as a result of a decrease in aminolevulinic acid (Tanaka *et al*., 1998; Sood *et al*., 2005), PPIX, MGPP, and Pchlide (Fan *et al*., 2013). In our study, porphyrin levels were not reduced by red light (Fig. 1). The mole percentages of PPIX, MGPP, and Pchlide are responsive to maturing/aging in sweet potato leaves (Hsu *et al*., 2003), and tissues infected by disease/insects (Hsu *et al*., 2011; Huang *et*

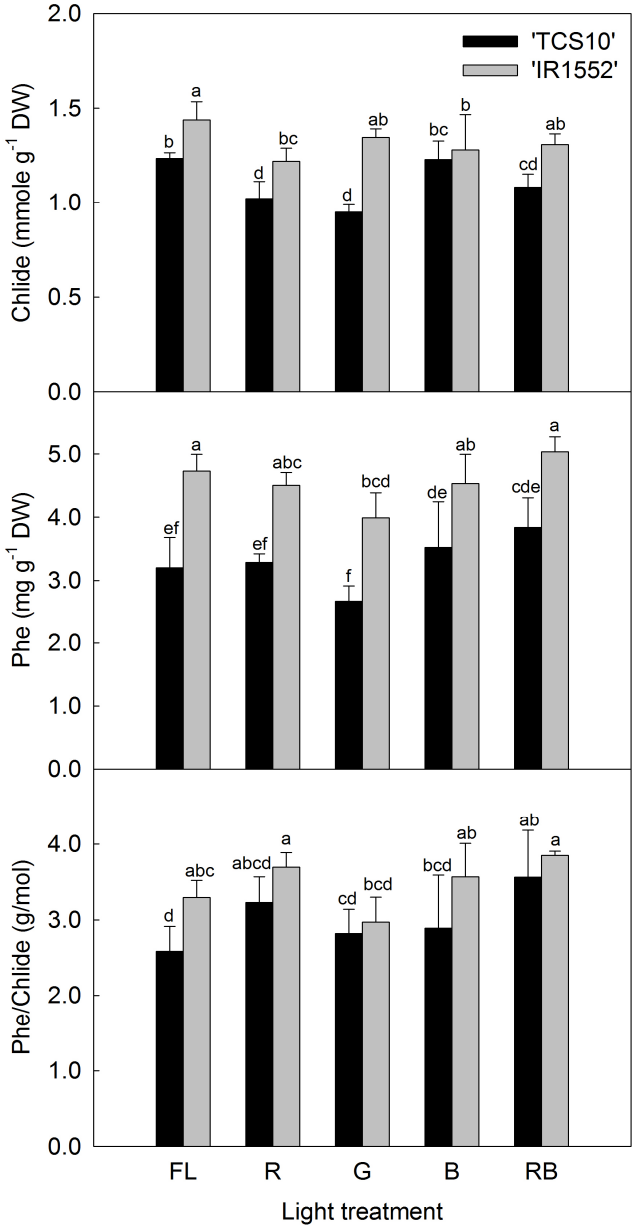

Fig. 3. Means ±SE of chlorophyllide (Chlide), pheophytin (Phe), and their ratios in 14-d seedling leaves under different lighting environments. The values followed by the different letter show statistically significant differences at $p < 0.05$. R - red; B - blue; G - green; RB - mixture of red plus blue; FL - fluorescent lighting

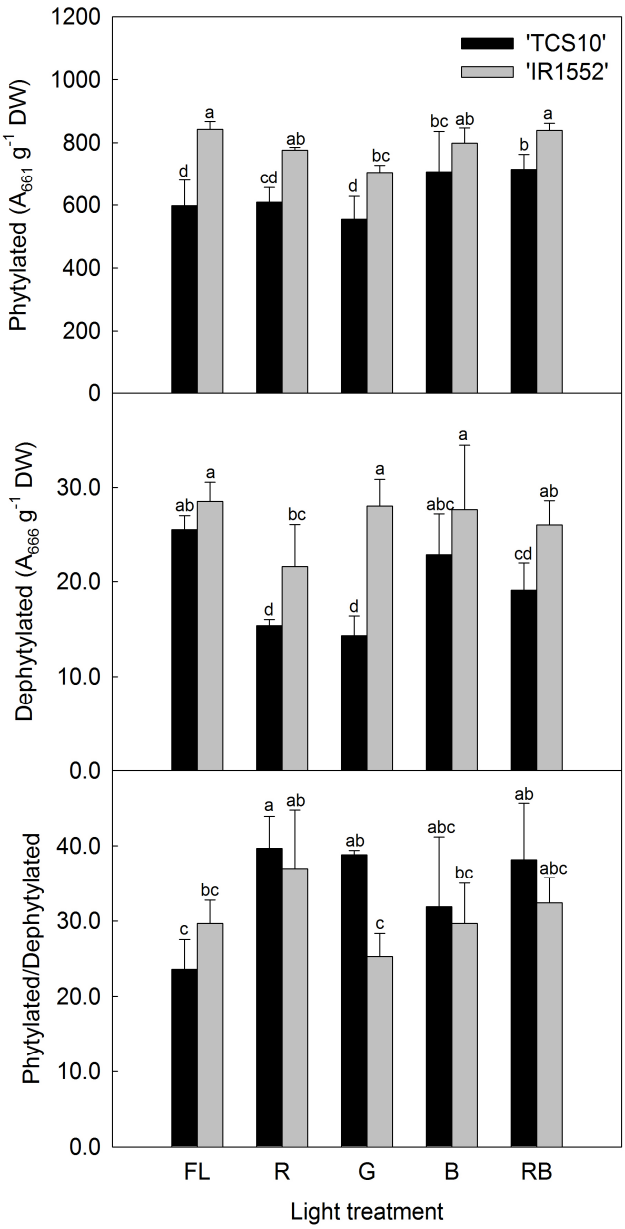

Fig. 4. Means ±SE of phytylated (expressed in A_{661} g^{-1} DW) and dephytylated (expressed in A_{666} g^{-1} DW) pigments and their ratios in 14-d seedling leaves under different lighting environments. The values followed by the different letter show statistically significant differences at $p < 0.05$. R - red; B - blue; G - green; RB - mixture of red plus blue; FL - fluorescent lighting

al., 2014). Light quality also influences the mole percentages of these three precursors. According to Fan *et al*. (2013), green light increases the mole percentage of PPIX but decreases the mole percentage of MGPP and Pchlide. Nevertheless, our results demonstrate that the mole percentages of the three precursors were insignificant among all treatments except for 'TCS10' under B, and Chl biosynthetic intermediates under light quality did not affect the Chl biosynthetic pathway (Fig. 2). The removal of Mg or the phytol chain, catalyzed by Mg-dechelatase and chlorophyllase, respectively, are the two possible routes in the initial period of Chl degradation. Their products are Chlide and Phe, respectively, which are further converted into Pho and continue to degrade into even smaller molecules (Matile *et al*., 1996). The four products in the initial period of Chl degradation can be divided into two categories according to their chemical structures. The first category contains phytylated pigments, such as Chl and Phe, all of which contain a phytol chain in their structure, but the first example contains Mg while the second does not. The other category contains dephytylated pigments, including Chlide and Pho, but the first contains Mg while the second does not (Matile *et al*., 1996).

Sweet potato, rice, and *Machilus thunbergii* use Chl→Phe→Pho and Chl→Chlide→Pho as the major and minor routes for chlorophyll degradation, respectively (Hus *et al*., 2003; Huang *et al*., 2014). Some physiological conditions, such as aging (Hsu *et al*., 2003), disease (Hsu *et al*., 2011), and infestation by insects (Huang *et al*., 2014), are important factors for mediating the ratio between these two routes and phytylated and dephytylated pigments. In our study, rice seedlings also took Chl→Phe→Pho as the major route (Fig. 3). A lower Phe/Chlide ratio under G lighting was observed among three mono-spectrum lighting conditions, and the ratio under FL was also lower between the two poly-spectrum lighting conditions. Furthermore, higher levels of Chlide were generally apparent under G and FL in the study. Phytylated/dephytylated ratios showed similar trends (Fig. 4). These results suggest that a green light-enriched environment might promote the minor route for Chl degradation. This phenomenon warrants further investigation.

Conclusions

Light quality not only influences the accumulation of photosynthetic pigments, but also mediates the Chl degradation pathway in rice seedling leaves, possibly promoting the minor route of Chl degradation in rice seedling leaves.

Acknowledgements

We thank Dr. Su-Jein Chang (Miaoli District Agricultural Research and Extension Station) and Dr. Zhi-Wei Yang (Taoyuan District Agricultural Research and Extension Station) for donation of 'IR1552' and 'TCS10' seeds.

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