

Response of single leaf photosynthesis and transpiration to red light and UV-A radiation in two different plant-type rice cultivars (*Oryza sativa* L.)

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Abstract

The influence of red light and ultraviolet (UV)-A radiation on the single leaf photosynthesis and transpiration were investigated in two different plant-type rice cultivars: active tillering type, Hopumbyeo (HP) and low-tillering heavy panicle type, Shindongjinbyeo (SDJ) at maximum tiller number stage. An open photosynthesis measurement system was used to monitor CO₂ exchange rate, which was determined by decrement of CO₂ concentration at the out let of leaf chamber comparing with the concentration of incoming ambient air. The results suggested that CO₂ exchange rate increased linearly with increasing of red light up to 254 μmol m⁻²s⁻¹ in the two cultivars. This linear response rate was consistent even if UV-A was included or not. An effect of UV-A radiation was found only in transpiration; transpirations of both cultivars increased with increasing of UV-A level, and there was significantly difference of transpiration rate between two cultivars. The CO₂ exchange rate in single leaf was higher in SDJ than that in HP, whereas transpiration rate was higher in HP than that in SDJ. Considering higher CO₂ exchange rate together with lower transpiration in SDJ indicated that some other cultivars rice genetic resources could use to enhance rice yield potential and water use efficiency in an irrigated rice system.

Keywords: photosynthesis, red light, rice, transpiration, UV-A.

Abbreviations: PAR: Photosynthetically active radiation, PPFD: Photosynthetic Photon Flux Density, UV-A: Ultraviolet A radiation, WUE: water use efficiency.

Introduction

Rice (*Oryza sativa* L.) is the staple food of most Asian countries. The average irrigated rice yields must rise by 30% to about 7 t ha⁻¹ by 2020 to supply the increasing population of the world, and improved germplasm with a yield potential of 12 t ha⁻¹ in the dry season and 8-9 t ha⁻¹ in the wet season would become available within the next 10 years (Dobermann, 2000). Increase in yield is governed by the rate of net CO₂ assimilation, by available light energy, and by genetically determined properties such as light capture efficiency, conversion efficiency of intercepted light into biomass, and the proportion of biomass partitioned into grain (Cassman, 1994; Long et al., 2006; Murchie et al., 2009; Russell et al., 1989). The rate of biomass production is determined by the rate of canopy photosynthesis, which consists of single leaf photosynthesis, leaf area index, and light intercepting efficiency. Yield enhancement by conventional breeding has mainly resulted from improvement of plant type which is determined by the last two factors, leaf area index and light intercepting efficiency. The further improvement in canopy net photosynthesis by fine-tuning plant type is difficult because most high-yielding cultivars are close to the optimum canopy architecture. This suggests that increasing single leaf photosynthesis could be the only way to substantially enhance rice yield potential (Peng, 2000). A number of studies investigated the responses of plants to monochromatic light or combination of different lights, however, those concerning single leaf photosynthetic responses were still limited to such crops and light that included rice (Matsuda et al., 2004), wheat (Goins et al.,

1997) and bean (Maleszewski et al., 2001) under red and blue; lettuce under red, blue and green (Kim et al., 2004); cherry tomato under red, blue, yellow, green and white (Liu et al., 2011); cucumber under red, blue, UV-A and UV-B (Wang et al., 2007); *Lactuca sativa* under green (Johkan et al., 2012); five strains of benthic diatom under blue (Mercado et al., 2004) and the red alga *Porphyra leucosticta* under white, blue, green, yellow and red light (Korbee et al., 2005) revealing the necessity of investigation on the response of rice plants to different light conditions. Red light regulated the apical dominance via phytochrome, and favoured thallus expansion, cell division, carbon accumulation and its deposition in extensive cell walls and intercellular matrix formation in an expansive thallus with high photosynthetic efficiency (Figueroa et al., 1995). Therefore, red light is important for the development of the photosynthetic apparatus (Sæbø et al., 1995) and found to be the most effective for leaf photosynthesis in the short term (Paradiso et al., 2009). On the other hand, depletion of stratospheric ozone has led to a significant increase in ultraviolet (UV) radiation reaching the surface of the Earth (Mackerness, 2000; McKenzie et al., 1999; McKenzie et al., 2003). If the increase in UV radiation continues (Caldwell et al., 2007; McKenzie et al., 2003), it will damage plants (Du et al., 2011). Even relatively small increases in UV radiation can have serious impacts on human health and the biosphere (McKenzie et al., 1999), and have raised interest in the possible consequences of increased UV-B levels on plant growth and development and the mechanisms underlying

these responses (Mackerness, 2000), as UV-B is much more biologically effective than UV-A at causing adverse effects (Vecchia et al., 2007). However, most UV-A radiation (315–400 nm) reaches the Earth's surface, whereas only about 10% of the UV-B radiation (280–315 nm) reaches the Earth, and UV-C (100–280 nm) is completely absorbed by atmospheric ozone, water vapor, and gases (WHO, 2003). An experiment investigating the effect of the different light quality on the growth characteristics of cucumber growing in solar greenhouse showed that UV-A and UV-B significantly enhanced leaf thickness, but reduced the fresh and dry weight, leaf area and chlorophyll content. UV-A inhibited fruit set, resulting in reduced number of fruits, probably due to an effect of UV-A on increased maleness of flowers or some direct effect on the growth of young fruit. The plant transpiration was markedly affected under different light quality. Red light had little effect on the transpiration rate compared to the control (white light), while the diurnal variation of transpiration rate under UV-A was much higher than under blue or UV-B light in cucumber (Wang et al., 2007). With increasing pressure on water availability, meanwhile, there is a need to increase water-use efficiency in irrigated rice system. Irrigation currently accounts for more than 60% of the world's fresh water consumption. The allocation of fresh water resources to agriculture needs to be reduced in order to ensure that future domestic needs are met (Zhou et al., 2011). With Food production and water use are closely linked processes. Of the different steps in water use in the crop production process, the most fundamental is water lost by transpiration for the assimilation of carbon dioxide (Steduto et al., 2007). Carbon dioxide and water exchange are typically coupled through the control of stomatal conductance (Lombardozi et al., 2012). Across species and under a variety of growth conditions, plants regulate their transpiration and photosynthetic rates in parallel, maintaining a balance between the stomata-mediated supply of CO₂ to the mesophyll chloroplasts and their photosynthetic demand for CO₂ (Baroli et al., 2008). Stomata optimize photosynthetic CO₂ uptake and minimize transpirational water loss from leaves. Stomatal opening is induced by low CO₂ concentrations, high light intensity, and high humidity, and closing is promoted by high CO₂ concentrations, darkness, drought, and the plant hormone abscisic acid (Outlaw, 2003). In an irrigation experiments with wetland rice (*Oryza sativa* L.) paddies, average evapotranspiration ranged from 7.4 to 9.2 mm day⁻¹ under continuous submergence and from 6.1 to 7.1 mm day⁻¹ under intermittent submergence (Tripathi et al., 1986). Evapotranspiration consists of three components: canopy transpiration through leaf stomata, canopy vaporation, and soil evaporation of the ground surface (Wang, 2008). Transpiration may differ depending on cultivars as large differences in maximum rates of net photosynthesis and transpiration were observed among twelve common bean (*Phaseolus vulgaris* L.) cultivars (Comstock and Ehleringer, 1993). This study was conducted to investigate varietal differences in two different plant type rice cultivars in terms of single leaf photosynthesis and transpiration under sole red light as well as sole UV-A radiation and under different combination of red light and UV-A.

Results

Response to red light and UV-A radiation alone

The influences of red light and UV-A radiation alone on photosynthesis and transpiration are shown in Fig. 1. Red light alone significantly affected the CO₂ exchange rate. In

the trend analysis, two coefficients of a linear and cubic response ($F < 0.0001$ and 0.0171) for HP, and a linear and quadric response ($F < 0.0001$ and 0.0503) in SDJ were significant. Therefore, a regression analysis and the test of fit for the regression model were carried out (Wildman-Pepe and Schott, 1991). A significant F-test for both cultivars ($F < 0.0001$ each) suggested that there were non-zero regression coefficients in the linear regression model, whereas nonsignificant (lack of fit) F values (0.4524 and 0.8125 for HP and SDJ, respectively) indicated that the deviations from the linear regression were entirely due to random error. Thus, linear regression was an adequate model to describe the CO₂ exchange response to red light by the two rice cultivars. Therefore, under the red light alone condition, the CO₂ exchange rate in both cultivars increased linearly with an increasing percentage of red light at the rate of 0.0337 and $0.0333 \mu\text{mol m}^{-2}\text{s}^{-1}$ (for HP and SDJ, respectively) for a 1% increase in red light. When ANCOVA was used to compare the regression coefficients of the two cultivars, the t-value was 0.04 but was insignificant ($p > |t| 0.9656$) (Table 2), indicating that the HP regression coefficient was not significantly different from that of SDJ. Therefore, the response to increasing red light percentage was more or less the same between the two cultivars (Fig. 1A). The cultivars possessed r^2 values of 0.4882 and 0.5368 for HP and SDJ, respectively, suggesting that only about 50% of the variation in CO₂ exchange rate could be explained by red light alone in the linear relationship. The coefficient of determination, r^2 , denotes the strength of the linear association between X and Y. The closer r^2 is to 1, the greater the degree of association between X and Y (Fonticella, 1998). However, a low coefficient of determination does not imply that a relatively flat line or a curve fits the data poorly (Barclay 1991). When the light was off (0% red light and 0% UV-A radiation), the CO₂ exchange rate was higher in SDJ ($0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$) than that in HP ($-0.475 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 1-B). On average of UV-A 0% (only red light), CO₂ exchange rates were not significantly different between HP and SDJ when average UV-A was 0% (1.59 and $2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, HP and SDJ, respectively). Therefore, under the single red light condition, both cultivars performed well, and their performances were equivalent; the CO₂ exchange rates of the two rice cultivars were not significantly different, they both responded similarly (positive linear response) to an increasing percentage red light, and their response rates (β_1) were not significantly different. CO₂ exchange rate did not differ with changes in UV-A within each cultivar. However, CO₂ exchange rates of the two cultivars differed depending on the UV-A percentage. Under low UV-A radiation (0–25%), the CO₂ exchange rate of SDJ was higher than that of HP. As the percentage of UV-A increased ($\geq 50\%$), they became similar (Fig. 1-B), but it was unknown whether this was due to a decrease in SDJ or an increase in HP. CO₂ exchange rates were significantly different between HP and SDJ with only UV-A light (-0.44 and $0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). Thus, UV-A radiation did not change the CO₂ exchange rate within a cultivar but caused cultivar difference in CO₂ exchange rate. The trend analysis for transpiration rate under red light showed both linear and cubic responses ($F < 0.0001$ and 0.0003) in HP, and linear and quadric responses ($F < 0.0001$ and 0.0001) in SDJ. A significant regression analysis ($F < 0.0001$ in both cultivars) suggested that there were non-zero regression coefficients in the linear regression model, whereas nonsignificant (lack of fit) F values (0.4524 and 0.8125 for HP and SDJ, respectively) indicated that the deviations from the linear regression were an adequate model to describe the transpiration response to red light alone by the

Table 1. Correlation coefficients among CO₂ exchange rate, transpiration rate, and photosynthetic photon flux density (PPFD) at each level of ultraviolet (UV)-A radiation.

UV-A	Variables	HP		SDJ	
		CO ₂ exchange	PPFD*	CO ₂ exchange	PPFD
0%	Transpiration	0.8876 ^{***}	0.5828 ^{***}	0.8795 ^{***}	0.6482 ^{***}
	CO ₂ exchange		0.6818 ^{***}		0.6945 ^{***}
25%	Transpiration	0.8722 ^{***}	0.5936 ^{***}	0.9148 ^{***}	0.6479 ^{***}
	CO ₂ exchange		0.8214 ^{***}		0.6516 ^{***}
50%	Transpiration	0.8569 ^{***}	0.5166 ^{***}	0.8724 ^{***}	0.5804 ^{***}
	CO ₂ exchange		0.7164 ^{***}		0.7070 ^{***}
75%	Transpiration	0.8296 ^{***}	0.5688 ^{***}	0.8243 ^{***}	0.5779 ^{***}
	CO ₂ exchange		0.7801 ^{***}		0.6518 ^{***}
100%	Transpiration	0.7698 ^{***}	0.4475 ^{***}	0.8279 ^{***}	0.5709 ^{***}
	CO ₂ exchange		0.6784 ^{***}		0.7033 ^{***}

* Photosynthetic photo flux density, *** Significant at $\alpha = 0.001$ level

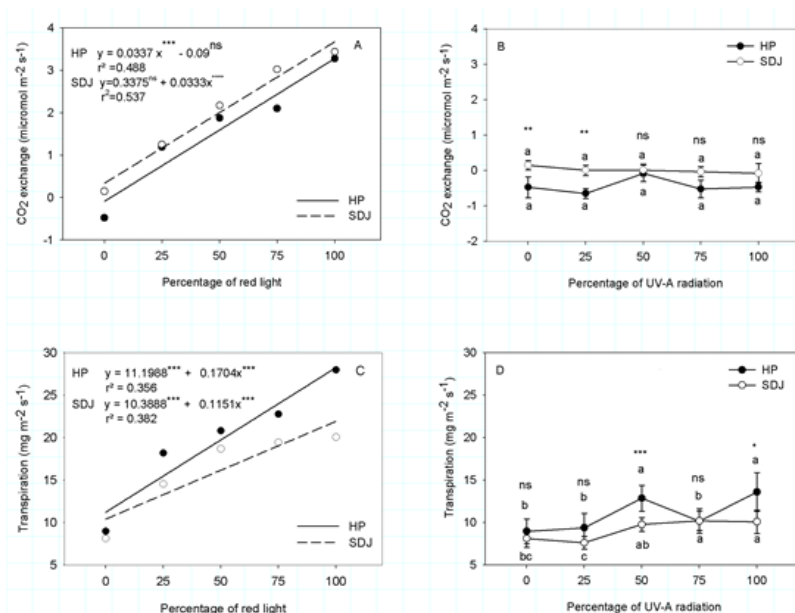


Fig 1. Influence of red light and ultraviolet (UV)-A radiation alone on CO₂ exchange rate (above) and transpiration rate (below) of two rice cultivars (The t-value was used to compare the regression coefficients (β_1) between the two equations. On the right panels, letters are used for the mean comparison within each cultivar. Different letters mean a significant difference within each line at $\alpha = 0.05$ level by Duncan's multiple range test. Asterisk show significant mean differences between cultivars; ns, nonsignificant, *significant at $P < 0.05$, **significant at $P < 0.01$, *** significant at $P < 0.001$).

two rice cultivars. Therefore, transpiration rates in both cultivars increased linearly with increasing red light percentage at the rate of 0.1704 and 0.1151 mg m⁻² s⁻¹ (for HP and SDJ, respectively) for a 1% increase in red light. The insignificant ($pr > |t| 0.2145$) t-value (1.25) showed that the regression coefficient for transpiration by HP was not significantly different from that of SDJ, indicating that the transpiration responses to increasing red light were not different between the two cultivars (Fig. 1C)(Table 2). Transpiration was higher in HP (19.718 mg m⁻² s⁻¹) than that in SDJ (16.145 mg m⁻² s⁻¹) under red light alone. UV-A significantly influenced transpiration rates within a cultivar as well as between cultivars (Fig. 1D). When no light was on, the transpiration rates of the two cultivars were not different (8.95 mg m⁻² s⁻¹ and 8.10 mg m⁻² s⁻¹, for HP and SDJ, respectively). However, transpiration rates of both cultivars increased with increasing UV-A radiation, although they did not show any significant pattern of response (linear, cubic, etc.). Furthermore, the two cultivars differed in transpiration rate depending on the UV-A level; transpiration was higher in HP than that in SDJ at 50% and 100% UV-A. Under UV-

A alone, transpiration was higher in HP (10.979 mg m⁻² s⁻¹) than that in SDJ (9.140 mg m⁻² s⁻¹). In short, under the single red light condition, the CO₂ exchange rates of the two rice cultivars responded similarly (positive linear response) to increasing red light percentage, but their response rates (β_1) were not significantly different. Similarly, under the red light alone condition, CO₂ exchange rates were not different, whereas under the UV-A alone condition, CO₂ exchange rates were significantly higher in SDJ than those in HP. However, transpiration was consistently higher in HP than that in SDJ either under red light alone or under UV-A alone.

Effect of UV-A radiation on photosynthesis at every red light level

A significant linear CO₂ exchange rate response to increasing red light was observed at each level of UV-A, as shown in Fig. 2. The model indicated that the linear regressions were good descriptions of the relationship between the dependent (CO₂) and independent (red light) variables for both cultivars

Table 2. Analysis of covariance comparing two regression lines.

Parameter	UV 0%		UV 25%		UV 50%		UV 75%		UV 100%	
	t Value	Pr> t	t Value	Pr> t	t Value	Pr> t	t Value	Pr> t	t Value	Pr> t
Photosynthesis										
Intercept	1.04	0.3029	0.38	0.7071	0.66	0.5086	1.15	0.2529	0.29	0.7748
HP	-0.93	0.3558	-0.75	0.4536	-0.04	0.9697	-1.30	0.1963	-0.44	0.6609
Red	6.27	<.0001	6.45	<.0001	7.09	<.0001	5.84	<.0001	6.18	<.0001
Red*HP	0.04	0.9656	0.64	0.5248	-0.59	0.5572	1.04	0.3003	0.32	0.7471
Transpiration										
Intercept	5.44	<.0001	4.33	<.0001	4.64	<.0001	5.01	.0001	4.41	<.0001
HP	0.30	0.7653	1.00	0.3209	1.19	0.238	0.27	0.7852	1.22	0.2272
Red	3.69	0.0004	3.29	0.0015	3.02	0.0035	2.30	0.0243	2.86	0.0054
Red*HP	1.25	0.2145	1.44	0.1526	1.08	0.2821	1.85	0.068	0.39	0.6943

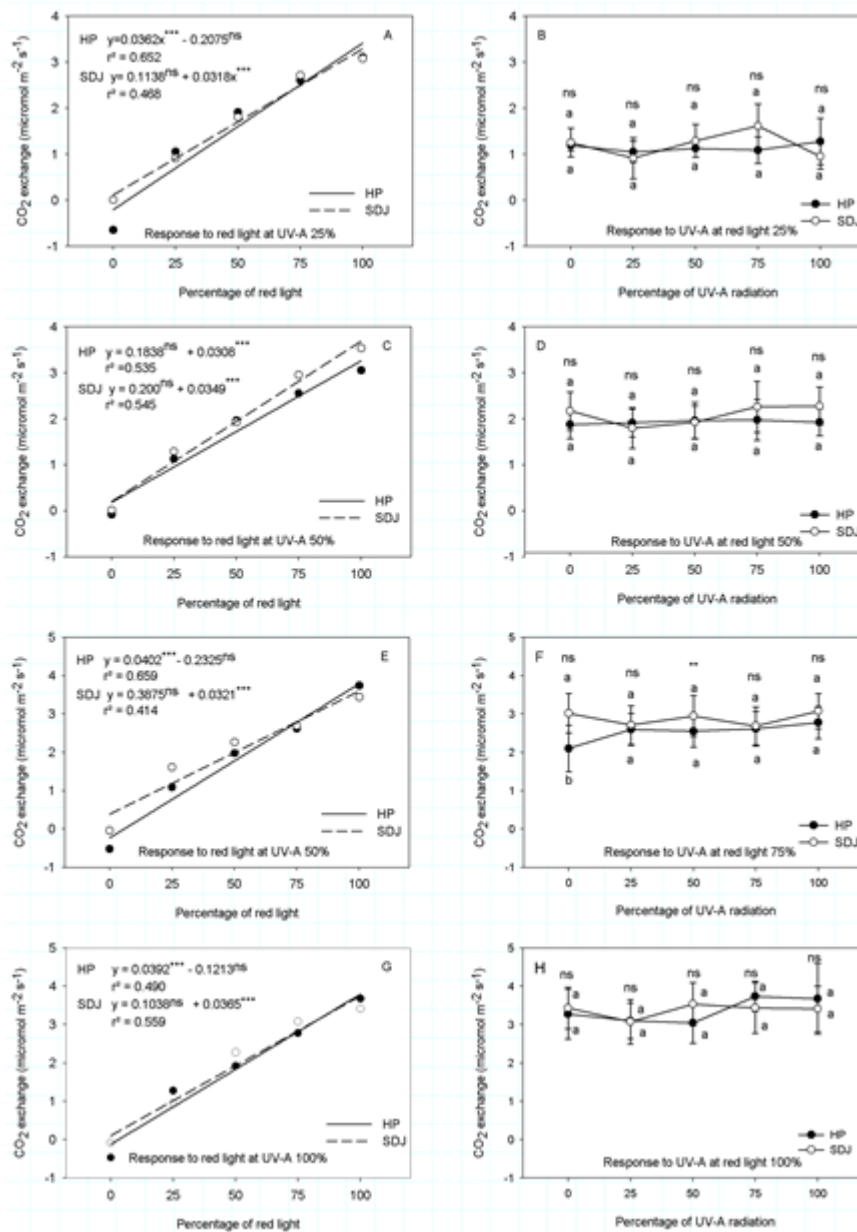


Fig 2. Response in CO₂ exchange rate to red light and ultraviolet (UV)-A by two rice cultivars (The t-value was used to compare the regression coefficients (β_1) between the two equations). On the right panels, letters are used for the mean comparison within each cultivar. Different letters indicate a significant difference within each line at $\alpha = 0.05$ level by Duncan's multiple range test. Asterisks on the figure showed significant differences in the means between cultivars ns, nonsignificant, * significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$).

at every UV-A level (Fig. 2A, C, E, and G). The regression coefficients were not significantly different among different UV-A radiation conditions within each cultivar or between the two cultivars at each UV-A radiation condition (Fig. 3), indicating that both cultivars responded similarly to increasing red light percentage at every UV-A radiation condition, and within cultivars. CO₂ exchange response to increasing red light was similar (linear) and constant (same β_1) between the two cultivars at each UV-A level (Fig. 2A, C, E, G), and among UV-A levels in each cultivar (Fig. 3). The contrast analysis between 0% UV-A (red light alone) and UV-A radiation also indicated that the regression coefficients were not different ($P > F$, 0.6452 for HP and 0.5955 for SDJ). These results suggest that CO₂ exchange rate responded linearly to red light at a constant rate, regardless of whether UV-A radiation was included or not, and that the response rate was the same as that found under red light alone. In contrast, the CO₂ exchange rates of both cultivars did not differ with changes in UV-A radiation at each red light percentage (Figs. 2B, D, F, H, and 4), although they increased linearly with increasing red light percentage (Fig. 2B, D, F, H). Cultivar differences in CO₂ exchange rates were not observed within each red light percentage in response to UV-A (Fig. 2B, D, F, H).

Effect of UV-A radiation on transpiration at every red light level

Transpiration rate increased with increasing red light percentage at every UV-A level. A linear regression was adequate to describe the relationship between the dependent (transpiration rate) and independent (red light) variables for both cultivars at each UV-A level. The regression coefficients (β_1) of every UV-A radiation level within each cultivar suggested that transpiration rates increased linearly with an increase in red light intensity. The regression coefficients were not different among different UV-A levels within cultivars at each UV-A level (Fig. 5A, C, E, G). The contrast analysis between 0% UV-A (red light alone) and the UV-A radiation levels also indicated that the regression coefficients were not different, suggesting that the transpiration response to red light was consistent with or without UV-A. Transpiration rates within each cultivar differed significantly with changes in the percentage of UV-A at every red light percentage in response to UV-A radiation; they increased with increasing UV-A percentage; however they did not show any statistically significant trend (Fig. 5B, D, F, H). The transpiration rate of HP was significantly higher than that of SDJ at every level of UV-A radiation. Table 1 presents the relationship among CO₂ exchange, transpiration, and PPFD in the two rice cultivars at each UV-A level. The table shows a significant positive relationship among the three variables and suggests that when PPFD of red light increased at each level of UV-A radiation, CO₂ exchange and transpiration rates increased accordingly. Similarly, an increase in transpiration could increase CO₂ exchange, and vice versa. However, it was noticed that the correlation coefficient between CO₂ exchange and transpiration seemed to decrease, particularly for HP, when the percentage of UV-A radiation increased.

Overall response to a combination of red light and UV-A

Figure 6 shows the overall response (the average of all UV-A at each red light level, and the average of all red light at each UV-A level) of the two cultivars to red light and UV-A. CO₂ exchange rate increased with increasing red light intensity

(Fig. 6A) but did not change with changes in UV-A (Fig. 6B). As the CO₂ exchange rate of SDJ tended to be slightly higher than that of HP at each red light and UV-A level (Fig. 6-A, B), the overall average of CO₂ exchange rate, i.e. the average of the combination of all red light and UV-A radiation, was higher in SDJ (1.91 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than that in HP (1.71 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Overall transpiration rate increased with increasing red light percentage (Fig. 6-C), as well as with increasing UV-A (Fig. 6D). HP transpiration rate was significantly higher at every level of red light (Fig. 6C) and at every level of UV-A (Fig. 6D) than those of SDJ. The transpiration response to red light was similar between the two cultivars up to 75% red light; at 100% red light, transpiration of SDJ tended to drop slightly, but not significantly. Likewise, the overall WUE of the two cultivars increased with increasing percentage of red light (Fig. 6E), however WUE was not affected by UV-A (Fig. 6F). Either under red light or UV-A radiation, the overall WUE was significantly higher in SDJ than in HP, except under 25% red light.

Discussion

This experiment was carried out to determine light quality effects on CO₂ exchange and transpiration rates in two rice cultivars. Two types of light (UV-A and red), both alone and combined and at different percentages were provided to two rice cultivars at the maximum tiller number stage. The results indicated that both rice cultivars responded to UV-A and red light not only alone but together. When both UV-A radiation and red light were provided together, net photosynthesis rate (i.e., CO₂ exchange rate) increased with an increasing percentage of red light, whereas the transpiration rate increased with an increasing percentage of both red light and UV-A radiation. The plants responded differently to red light alone and to UV-A alone. CO₂ exchange rates of both cultivars increased linearly with increasing red light percentage at the rate of 0.0337 and 0.0333 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (HP and SDJ) for 1% increases in red light. The lack of significant differences between regression coefficients (β_1) (Wildman-Pepe and Schott, 1991) indicated that both cultivars responded at the same rate to red light alone. Under UV-A radiation alone, neither cultivar showed a response to increasing UV-A radiation, i.e., their CO₂ exchange rates did not change with changing UV-A radiation, but the two cultivars differed at lower UV-A radiation levels, though they were not different at $\geq 50\%$ UV-A radiation. A similar pattern was observed for transpiration rate. Transpiration rate increased with increasing red light alone in both cultivars, but the response rates (β_1) were not significantly different. It was opposed to the finding of Wang et al. (2007): they observed that red light had little effect on the transpiration rate of cucumber. Different result would be due to the use of different kinds of crops, because transpiration differs by varieties (Hartmann, 2010), and may differ depending on cultivars within the same species as found in common bean (Comstock and Ehleringer 1993). Under UV-A radiation alone, both cultivars showed the potential to increase transpiration rate with increasing UV-A; however, no significant response pattern was observed. A cultivar difference was found at 50% and 100% UV-A radiation alone. Thus, a significant linear response of the CO₂ exchange rate under combined light (UV-A radiation and red) could be due to the effects of red light alone, because UV-A alone did not show any significant responses. However, both red light and UV-A radiation contributed to increase transpiration rate. Enhanced UV radiation has deleterious effects on the growth and development of higher plants: UV exposure results in

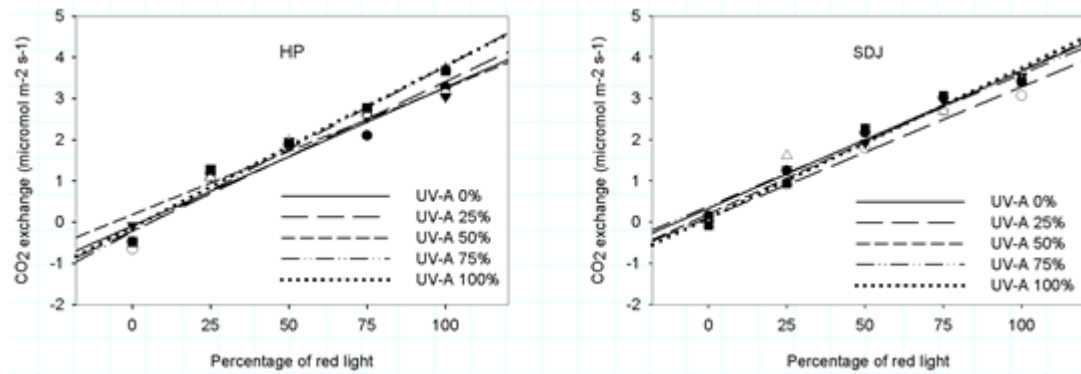


Fig 3. Relationship between CO₂ exchange rate and red light within each ultraviolet (UV)-A radiation (● = 0% (only UV-A), ○ = 25%, ▼ = 50%, △ = 75% , and ■ = 100% UV-A)

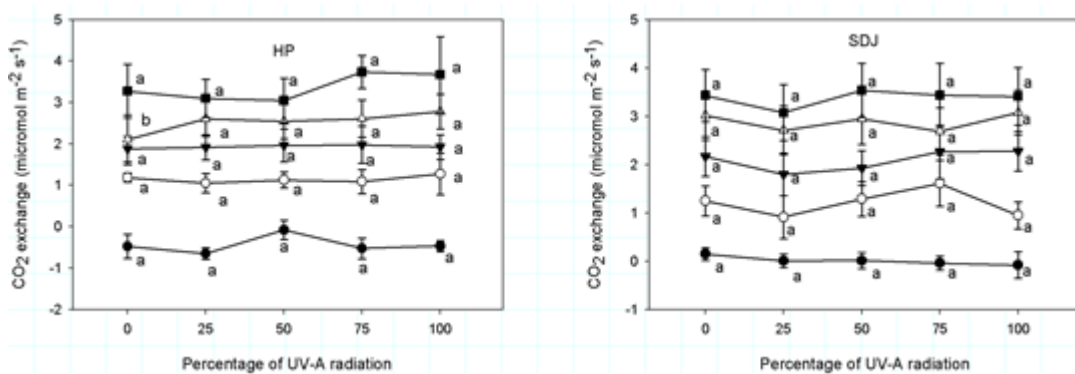


Fig 4. CO₂ exchange rates of the two rice cultivars at five red light levels in response to ultraviolet (UV)-A radiation (● = 0% (sole red), ○ = 25%, ▼ = 50%, △ = 75% , and ■ = 100% f red light)^{(ns, nonsignificant; *significant at $\alpha = 0.05$ level by Duncan's multiple range test).}

light brown patches on leaves, the accumulation of UV-absorbing compounds (including flavonoids and other phenolic pigments) differential protein expression; decreased lipid peroxidation, net photosynthetic rate (Du et al., 2011) and plant height, fresh leaf masses, shoots, roots and leaf area (Zuk-Golaszewska et al., 2003), tiller number, grain size (Kumagai et al., 2001), and changes in the expression of a large number of genes (Brosché and Strid, 2003). However, in the present study, CO₂ exchange rate was not affected by UV-A radiation, but transpiration rate increased. The unaffected CO₂ exchange rate and increasing transpiration could have been due to the development of a protective mechanism against UV stress within the plant, such as enhancement of the antioxidant system (Brosché and Strid, 2003) and accumulation of UV-absorbing compounds (Brosché and Strid, 2003; Frohnmeyer and Staiger, 2003), such as carotenoids and flavonoids, which are involved in plant UV-B photoprotection (Middleton and Teramura, 1993). Therefore, photosynthetic tissue is protected from UV radiation by UV-absorbing compounds (e.g., flavonoids) (Middleton and Teramura, 1993), and, consequently, chlorophyll content shows no significant decrease during UV stress, which is consistent with no chlorotic symptoms on leaves (Du et al., 2011). As chlorophyll *a* is the primary sensitizer in photosynthesis (Emerson and Rabinowitch, 1960; Govindjee and Rabinowitch, 1960), absorption of light by chlorophyll *a* is fully sufficient for photosynthesis (Govindjee and Rabinowitch, 1960). Therefore, moderate levels of UV-A enhance photosynthesis and growth rates in

some algae (Xu and Gao, 2010). We found that transpiration rate and net photosynthesis (i.e. CO₂ exchange rate) increased with increasing percentages of red light alone as well as combined with UV-A in both rice cultivars. As UV-A did not affect CO₂ exchange rate within cultivars, the changes in CO₂ exchange rate were due to red light alone. The increase in CO₂ exchange rate under red light could be explained by the presence of the photoreceptor-phytochromes in leaves. Phytochromes, which absorb wavelengths of 300–800 nm with maximum absorption in the R region (600–700 nm) and peak absorption at 660 nm and in the FR region (700–800 nm) with peak absorption at 730 nm (Cerny et al., 2000) are more sensitive to red than blue, and phytochrome B enhances photosynthesis and transpiration (Boccalandro et al., 2009). Therefore, plants can complete their life cycle under red LEDs alone (Britz and Sager, 1990). The linear increase in both CO₂ exchange and transpiration rate with increasing red light could have been due to either increasing light intensity (i.e. PPFD), which was associated with increasing percentage of red light, or an increase in the R:FR ratio, which was the result of increasing the percentage of red light or both. The presence of a significant positive relationship between CO₂ exchange rates, transpiration, and PPFD (Table 1) confirmed the role of light intensity (PPFD) on CO₂ exchange rate and transpiration. As plants respond to light intensity (Takemiya et al., 2005), and light intensity increases photosynthesis (Dionisio-Sese et al., 2001), changes in the photosynthetic capacity of rice were the result of a response to radiation intensity (Murchie et al., 2002). Therefore, net

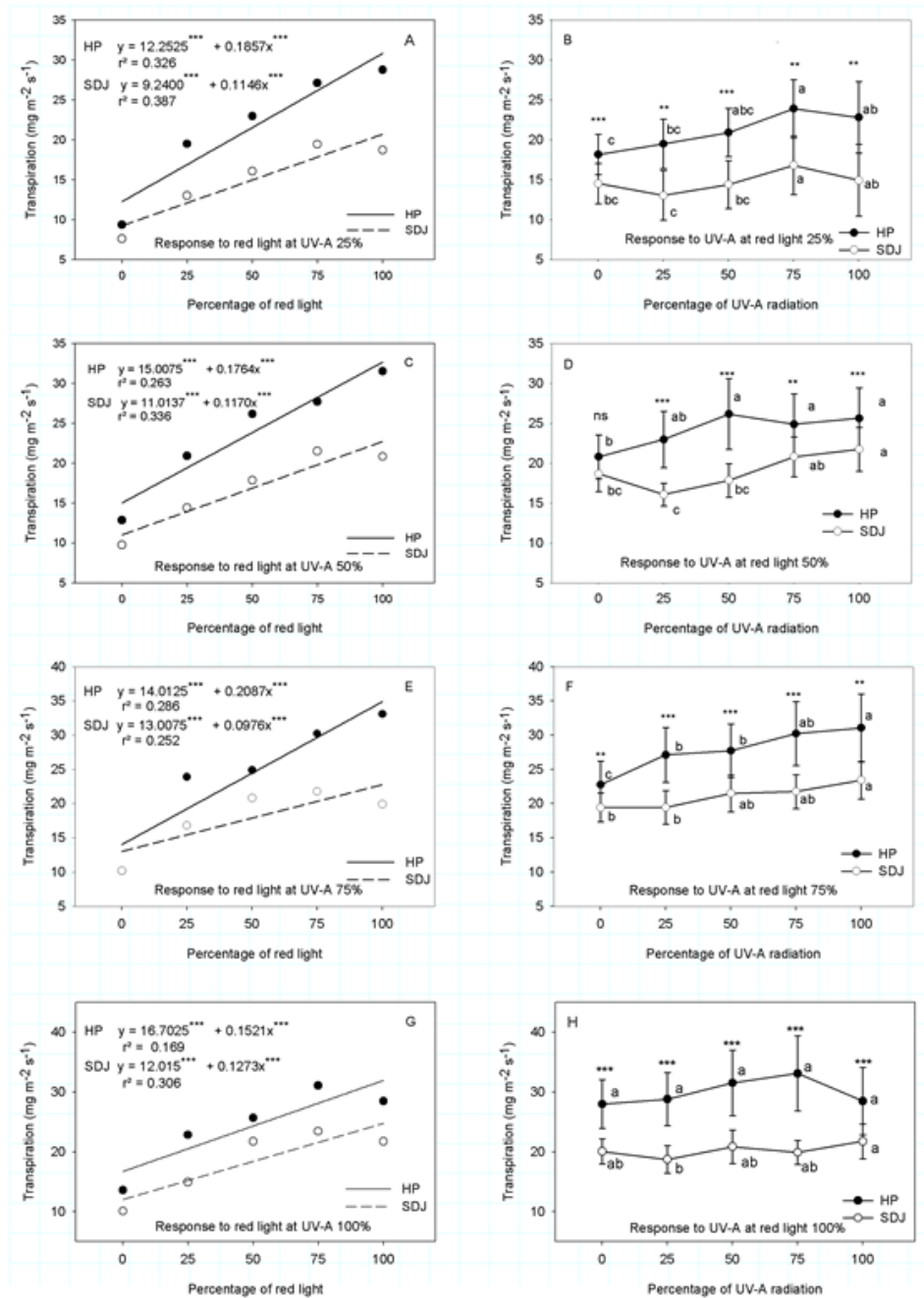


Fig 5. Response in transpiration rate to red light and ultraviolet (UV)-A by two rice cultivars (The t-value was used to compare the regression coefficients (β_1) between the two equations. On the right panels, letters are used for the mean comparison within each cultivar. Different letters indicate significant difference within each line at $\alpha = 0.05$ level by Duncan's multiple range test. Asterisks show significant differences in the means between cultivars; ns, nonsignificant, * significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$).

photosynthesis and transpiration rate increases with increasing PPFD (Alexander et al., 1995). Moreover, higher photosynthesis at high PPFDs is the result of higher photosynthetic electron transfer rate (ETR), resulting from physiological and morphological changes in response to the high R:FR light (Shibuya et al., 2010). Because photosynthesis requires light in the vicinity of the chlorophyll *a* and *b* absorption peaks (at 662 nm and 642 nm, respectively) (Tamulaitis et al., 2005), and low R:FR reduces photosynthesis, chlorophyll, and the chlorophyll *a/b* ratio (Pons and Berkel, 2004), higher photosynthetic rates and higher ETR at high R:FR is the result of higher relative chlorophyll content per leaf area (Shibuya et al., 2010).

However, minimal differences in photosynthesis have been observed between rice leaves grown under 350 compared with 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Makino et al., 1997). Several studies have compared photosynthetic rates among 32 cultivars of japonica rice (Sasaki and Ishii, 1992), and among varieties including indica and japonica and other species of *Oryza* such as Asian, African, and wild species (Cook and Evans, 1983a; Masumoto et al., 2004; Sasaki and Ishii, 1992; Takano and Tsunoda, 1971; Xu et al., 1997; Yeo et al., 1994). These studies showed that photosynthesis differs significantly among genotypes (Ohsumi et al., 2007), and large genotypic variations exist in photosynthesis of rice and its relatives (Cook and Evans, 1983b; Yeo et al., 1994). These results

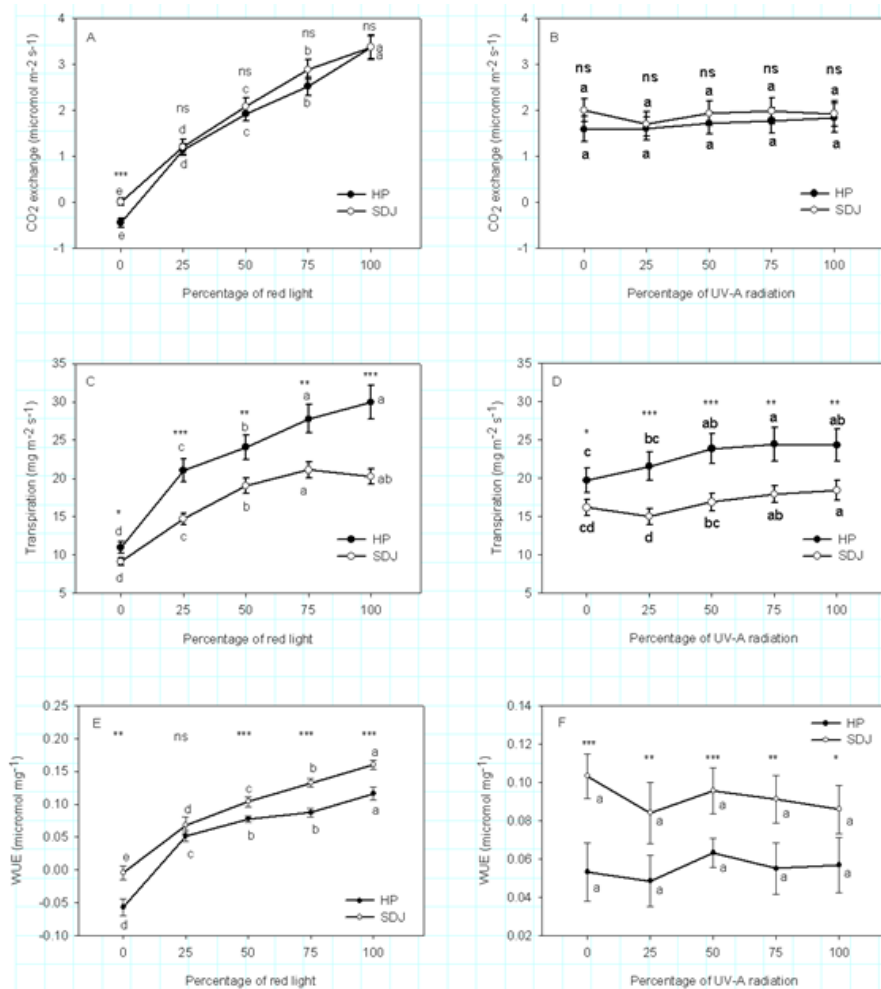


Fig 6. The overall response of CO₂ exchange rate, transpiration rate and WUE to red light and ultraviolet (UV)-A (Left panels represent the average of all UV-A at each red light level, whereas the right panels show the average of all red light at each UV-A level. Each point represents the average of 40 observations). Asterisk show significant differences in the means between cultivars; ns, nonsignificant, * significant at P < 0.05, ** significant at P < 0.01, *** significant at P < 0.001).

were consistent with the present finding that SDJ ($1.91\mu\text{mol m}^{-2} \text{s}^{-1}$) showed a higher overall CO₂ exchange rate than that of HP ($1.71\mu\text{mol m}^{-2} \text{s}^{-1}$), even though they were not significantly different at each red light and UV-A level. Transpiration differs by varieties (Hartmann, 2010); transpiration of HP was significantly higher than that of SDJ, both in overall average and at each level of red light and UV-A. Therefore, the reduction in transpiration rate would not necessary to reduce photosynthetic rate (Zhanga et al., 2008). In the present experiment, WUE of SDJ was higher than that of HP as a consequence of higher CO₂ exchange rate together with lower transpiration in SDJ. WUE varies substantially among species and genotypes within a species (Yoo et al., 2009). Higher WUE derived from higher intrinsic leaf photosynthetic capacity is generally considered beneficial. Even though increased WUE does not guarantee improved yields unless the additional assimilates are allocated appropriately to reproductive sinks (Fish and Earl, 2009), it is feasible that WUE could be improved by decreasing transpiration without a reduction in CO₂ uptake (Yoo et al., 2009). Therefore, higher CO₂ exchange rates, higher WUE together with lower transpiration in SDJ indicated that SDJ used water more efficiently than that of HP, and that SDJ could be used to improve drought tolerance.

Materials and methods

Plant materials

Two medium-late maturing Korean rice cultivars, Hopumbyeo (HP) and Shindongjinbyeo (SDJ), were used. Hopum is a new japonica cultivar developed in 2006 as an active tillering type (Ko et al., 2008), whereas SDJ was developed in 1999 and is a low-tillering heavy panicle type cultivar (Park et al., 2010). Concerning the agronomic characteristics of the two cultivars, the plant height (cm), number of panicles per hill, number of seeds per panicle and fill grain percentage were 68, 14, 106 and 89 for HP and 80, 12, 96 and 94 for SDJ (Kim et al., 2008).

Light source

Red (660 nm) and UV-A (365 nm) LEDs were used. The LED power supply was specially made to control light intensity independently at from 0 to 100% of maximum electric power. The rice was treated with combinations of five light intensity levels (0, 25, 50, 75, and 100% of maximum electric power) of red light (660 nm) and UV-A (365 nm) radiation. The photosynthetically active radiation (PAR) measured at a 10 cm distance from the center of the

red light source were 156, 195, 237, and 254 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at 25, 50, 75, and 100% of maximum power, respectively. Those of UV-A light were 0.174, 0.256, 0.390, and 0.437 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at 25, 50, 75, and 100 % of maximum power, respectively.

Photosynthesis and transpiration analysis

Rice plant samples were obtained from field grown rice at the experimental farm of Chonbuk National University. Two hills from each cultivar at the maximum tillering stage were moved into pots of 19.5 cm height with 16 cm diameters. To use the same soil and water conditions between the pots and the field, the plants were dug up and moved together with the soil ball that filled up to a 17 cm height of the pot. As soon as the plants were in the pots, the pots were filled with water to 2 cm above the soil surface in the pot, and kept in the dark in the laboratory before measuring photosynthesis.

CO_2 exchange and transpiration rates were measured using a photosynthesis monitor (PTM-48M, Daletown Co. Ltd., Nicosia, Cyprus). The monitor was a four-channel automated system for monitoring CO_2 exchange and transpiration of plant leaves. The system was equipped with a set of four original self-clamping leaf chambers that operate one-by-one in such a manner that one of the leaf chambers is closed while all others remain open. In the present experiment, the photosynthetic monitor was set up for a 15 minute measurement time interval. Fully expanded, tallest leaves were, first, placed inside the clamps of leaf chambers. Then, the whole plant was provided each combination of light for 30 minutes; therefore, two subsamples of data were recorded automatically for each treatment. The LED light was placed about 1 cm directly above the top of the plant canopy. Four leaf chambers were installed about 10 cm below the LED light source. The RTH-48 meter was also placed at the center of the four leaf chambers to measure PAR. The conditions in the plant chamber were measured by the sensor in the RTH-48 meter linked to a photosynthesis monitor. The conditions were 429 ± 0.89 ppm CO_2 , $27.99 \pm 0.069^\circ\text{C}$ air temperature, 68.5 ± 0.14 % relative humidity, and 1.19 ± 0.006 kPa vapor pressure deficit at the time of the experiment. When photosynthesis and transpiration rates were obtained, the WUE was calculated as the ratio of photosynthesis to transpiration (Fish and Earl, 2009) in order to determine the differences in WUE between the two cultivars.

Statistical analysis

As the experiment was designed to study the effect of increasing levels of red light and UV-A radiation, the statistical analysis evaluated the response trends. A quadratic polynomial response curve was fit for the five levels of red light and UV-A. Therefore, an analysis of variance, a trend analysis, and an analysis of covariance (ANCOVA) were carried out using SAS software (SAS Institute, Cary, NC, USA). Treatments that showed a significant response in the trend analysis were subjected to a regression analysis and a lack of fit test for the regression model to determine if higher order polynomial models or multiple regression models were necessary (Wildman-Pepe and Schott, 1991). Only when there were no significant lack of fit results for both cultivars, i.e., the linear regression model was suited for estimation, the regression coefficients were compared among each light treatment within cultivars and between cultivars within each light treatment. Treatments that did not show significant responses in the trend analysis were subjected to mean comparison using Duncan's Multiple Range Test at $\alpha=0.05$.

Conclusion

Effect of different light quality (red light and UV-A) on CO_2 exchange, transpiration rates and WUE were studied in two rice cultivars. SDJ showed a higher CO_2 exchange rate than that of HP under the off-light condition and on average with UV-A alone, but they were not different on under red light alone. HP revealed a higher transpiration rate than that of SDJ under UV-A alone and red light alone ; however they were not different when the lights were off. Both CO_2 exchange and transpiration rates of the two rice cultivars responded linearly to increasing red light percentage with the same increase rates (β_1), and the response was constant regardless of the presence of UV-A radiation.

Acknowledgments

This work was supported by the Industrial Technology Research Infrastructure Program (N0000004) funded by the Ministry of Knowledge Economy (MKE, Korea).

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