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Full Length Article

Capsicum Heterotrimeric G proteins are Up-regulated under UV-B Radiation Stress

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Abstract

Heterotrimeric G-proteins (G proteins) constitute a classical signal transduction system which can operate together with G-protein coupled receptors (GPCRs) and regulators of G-protein signaling (RGS) in environmental stress-related pathways. Among several environmental factors that can cause stress in plants, ultraviolet B (UV-B) radiation affects many aspects of plant physiology and activating diverse signaling pathways. Signaling response of *Capsicum* plants to UV-B radiation has not been studied well. In this study, we studied the expression profile of G proteins, GPCR and RGS genes from stems and roots of *Capsicum* plants subjected to stress with 1, 2, 3, 6, 12, 18, 25 and 30 h of UV-B radiation. *CaGα1* and *CaGβ1* genes exhibited an increased expression after 18 h of UV-B radiation treatment in stems, while *CaGγ1*, *CaGγ2*, *CaRGS1* and *CaGPCR* genes showed no significant changes in expression. In roots, *CaGα1* and *CaRGS1* genes showed an increasing expression profile after 3, 18 and 25 h after UV-B radiation but its expresion was not statistically significant. Signaling response to UV-B-radiation in *Capsicum* was mediated by G proteins in a specific-tissue manner where *CaGα1* and *CaGβ1* have an active role in stems. The expresion profiles found in this study were associated with UV-B induced responses in plants, however, the specific roles of G protein members induced by UV-B radiation in *Capsicum* remains to be elucidated. These results provide evidence of possible role of G protein signaling system in response to UV-B radiation in *Capsicum*, open for new insights about the search of new genes to be used as molecular markers for manipulation to enhance UV-B radiation stress tolerance in crop plants. © 2018 Friends Science Publishers

Keywords: *Capsicum*; UV-B radiation; Heterotrimeric G proteins; G-protein coupled receptor; regulator of G-protein signaling protein; qPCR

Introduction

Heterotrimeric G proteins (G proteins) are composed of Gα, Gβ and Gγ subunits and constitute a membrane signal transduction mechanism, regulating various fundamental processes in animals and plants (Stateczny *et al*., 2016). G proteins can couple external signals through cell surface receptors to appropriate intracellular molecules that mediate cell responses (Xu *et al*., 2016). A G-protein coupled receptor (GPCR) perceives external stimuli and facilitates the GDP→GTP bound on Gα. This allows dissociation of the heterotrimer into Gα-GTP and Gβγ. Gα-GTP and Gβγ can independently initiate specific signaling pathways. Intrinsic GTPase activity of Gα hydrolyzes GTP and returns the heterotrimer to its inactive state (Subramaniam *et al*., 2016). But in some cases, GTPase activating proteins (GAPs) can accelerate GTP hydrolysis to regulate G protein activation-deactivation cycle (Stateczny *et al*., 2016). Some GPCR-like proteins have been reported in plants, but the GTP exchange factor (GEF) activity has not been proven (Roy Choudhury and Pandey, 2016). Moreover, in *Arabidopsis*, G proteins can self-activate, because the Gα subunit (AtGPA1) can be joined to GTP the most of the time, this suggests that signaling in plants is mostly performed by a GAP like the regulator of G protein signaling (RGS) proteins, speeding up the deactivation (Urano and Jones, 2014).

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Compared with human genome that possesses 23Gα, 5 Gβ y 12 Gγ (Temple and Jones, 2007), *Arabidopsis* genome has only one Gα, one Gβ and three Gγ genes (Ma *et al*., 2015). Despite few members integrate *Arabidopsis* genome, plant G proteins and some other components of this signaling system have been implicated in cell division (Chen *et al*., 2006), morphological development (Lease *et al*., 2001; Anderson and Botella, 2007; Izawa *et al*., 2010; Romero-Castillo *et al*., 2015), response to light stimuli (Warpeha *et al*., 2006), salinity (Misra *et al*., 2007), temperature (Yadav and Tuteja, 2011; Yadav *et al*., 2012; Yadav *et al*., 2013; Yadav *et al*., 2014) and UV-B radiation (Warpeha *et al*., 2008). Ultraviolet radiation B (UV-B, 280-320 nm) is a natural stressful factor for plants. UV-B can drive to severe damage on plants and crops, usually with anato-morphological, metabolic and molecular effects (Carrasco-Ríos, 2009; Fina *et al*., 2017; Khudyakova *et al*., 2017). Growth inhibition is one of the mainly responses of plants to UV-B exposure, affecting leaf growth in many of plants species (Fina *et al*., 2017). Reactive oxygen species (ROS), such as hydrogen peroxide, singlet oxygen, hydroxyl radical and superoxide radical are generated by photosynthesis in response to some types of biotic and abiotic stresses, including UV-B radiation (Fina, 2017; Hussain *et al*., 2018a, b). Being sessile organisms, plants respond and adapt to UV-B radiation effects through mechanisms such as the oxidation of phytohormones that induct cell size, synthesis of secondary metabolites, DNA repairs and transcription of genes related to photosynthesis, oxidative stress and phenylpropanoids (Carrasco-Ríos, 2009).

G proteins have been implicated in the plant response to damage caused by UV-B radiation. In *Arabidopsis*, GPA1 (Gα subunit) activation is UV-B induced and promotes stomatal movement through H_2O_2 and NO production (He *et al*., 2013). The production of UV-B absorbing compounds, such as phenolic compounds and flavonoids, is another, and well studied UV-B radiation protective mechanism in plants (Zlatev *et al*., 2012). Warpeha *et al*. (2008) found that in *Arabidopsis*, GCR1 (G protein coupled receptor) and GPA1 initiates a signaling pathway that confer UV radiation protection to the plant, activating prephenate dehydratase1 (PD1), a precursor of a wide variety of secondary metabolites produced by the penylpropanoid pathway.

Bell pepper (*Capsicum annuum* L.) is a crop of agricultural importance of the Solanaceae family, the needs of its production and market for human food, bell peppers rank fifth among the top 20 products that Mexico markets internationally, and a third place in export preceded only by the sale of tomato and avocado (SAGARPA, 2017). Recently, Romero-Castillo *et al.* (2015) identified the G protein complex and their RGS genes in bell pepper plants. They found in the promoter region of *Capsicum* G protein and RGS genes, the presence of elements related to stress response and development.

In *Capsicum*, UV-B radiation induces an increase in content of flavonoids for protection (León-Chan *et al*., 2017). However, the signal transduction systems that initiate this defense response in *Capsicum* plant tissues are little explored. Studies about characterization of some components of G proteins signaling have been initiated in *Capsicum* such as Romero-Castillo *et al*. (2015). We showed that some genes of this signaling system respond to UV-B radiation in a specific-tissue manner. In this study, this hypothesis was tested by qPCR analysis of genes in stems and roots of *Capsicum* plants UV-B irradiated.

Material and Methods

Plant Material and Stress Treatment

In order to obtain the experimental material to evaluate G proteins genes expression under UV-B conditions, the bell pepper (*Capsicum annuum* L.) cv. Cannon plants were produced as described by León-Chan *et al*. (2017). Twenty-eight DAS (days after sowing), we used a completely randomized block factor design, where bell pepper plants were put in a plant growth chamber (GC-300TLH, JEIO TECH; South Korea) for three days under the following conditions: 12 h photoperiod (from 6:00 to 18:00 h) of PAR (photosynthetically active radiation) (972 $\mu mol \bullet m^{-2} \bullet s^{-1}$), 25/20°C (day/night) temperature and relative humidity of 65%. After that, treatments of UV-B radiation (UV-B) were applied; briefly, plants were irradiated for 6 h with PAR (from 06:00 to 10:00 and 16:00 to 18:00 h) and for 6 h of UV-B irradiation (72 $kJ \bullet m^2$, from 10:00 to 16:00 h). The UV-B radiation was applied using three Phillips TL 100W/01 lamps (Germany) with a narrow waveband between 305 to 315 nm and peaks at 311 nm; the distance between plant leaves and UV-B lamps was 50 cm, and the UV-B irradiance was measured by a UV A/B light meter (SPER SCIENTIFIC, model 850009; Scottsdale, AZ, USA). The UV-B radiation treatment was initiated at day 31 and sampling started at 10:00 h just before turn the radiation UV-B lamps on; therefore, 10:00 h at day 31 was considered as time 0 h. Then, the next samples were collected after 1, 2, 3, 6, 12, 18, 25 and 30 h of exposure. Samples (10 seedlings per treatment) were frozen in liquid nitrogen and stored at -80 °C in an ultra-low temperature freezer (Revco UxF40086A, Thermo Scientific; USA) until analysis.

Primer Design

For the bell pepper G-protein coupled receptor identification, the known sequence of Rice GPCR gene (*OsGPCR*) (accession number HQ676132.1) was aligned with the BLAST (Basic Local Alignment Search Tool) programm. The predicted sequence for a *Capsicum annuum* GPCR with 70% identity with *OsGPCR*, was used to design primers. cDNA for *OsGPCR* amplification was synthesized

using SuperScript® III First-Strand (Invitrogen Life Technologies, USA) and its yield and purity was examined with a Nanodrop 2000c (Thermo Fisher Scientific, USA). The primers used in PCR reactions were desing using the Geneious software. A *Capsicum annuum* G-protein coupled receptor (*CaGPCR*) DNA fragment of 491 pb was amplified by PCR using forward primer (5´-GGTCATGTAGGGATCCTTCC-3´) and reverse primer (5´-TTGCCTTTCCTGTGTGTC-3´) and first strand cDNA from bell pepper cv Cannon as a template. The PCR amplicon was sequenced by the Sanger method with AB3730 DNA Analyzer (Applied Biosystems, Japan). The sequence was aligned with BLAST in the GenBank database and the analysis showed about 98% identity with predicted *Capsicum annuum* GPCR. The *CaGPCR* sequence from bell pepper cv Cannon was used for the qPCR primer design of forward primer (5´-GGCTCCAAATCCTCTACATCAG-3´) and reverse primer (5´- GGTTCTTCTGTTATGCTCAGGG-3´). Specific primers for G proteins and RGS genes of *Capsicum* were reported by Romero-Castillo *et al*. (2015).

Isolation and cDNA Synthesis

To obtain the cDNA for qPCR amplifications, the total RNA was isolated from 100 mg of stress treated and non-treated stems and roots of plants, using TRIzol® reagent (Invitrogen Life Technologies, USA). Genomic DNA contamination was removed by DNase treatment with TURBO DNA-free™ Kit (Thermo Fisher Scientific, USA). The total RNA obtained was used as template for cDNA synthesis. The first strand cDNA was synthesized from 2 µg of total RNA using SuperScript® III First-Strand (Invitrogen Life Technologies, USA) using oligo (dT) 20 according to the manufacture´s instructions.

Quantitative Real-time PCR (qPCR)

To carry out the the transcript profiles of *CaGα1*, *CaGβ1*, *CaGγ1*, *CaGγ2*, *CaRGS1* and *CaGPCR1* by qPCR we used the cDNA of stems and roots of plants treated with UV-B radiation. Before qPCR reactions, we carry out validation assays, which include a specificity analysis through melt curves, amplicon size analysis and sequencing. An efficiency analysis was perfomed using standard curves across multiple $\log_{10}$ units. Finally, we evaluated the efficiency of PCR looking for a theoretical maximum of 100%. qPCR reactions were performed on CFX96 Touch™ Real-Time PCR Detection System (Biorad, USA) using Rotor-Gene SYBR Green PCR Master Mix (Qiagen, Germany). For qPCR reactions, we used a "no RT control" to identify signal due to genomic DNA contamination and qPCR reactions were perfomed using specific primers for G proteins and *RGS* genes of *Capsicum* previously reported by Romero-Castillo *et al*. (2015). *Capsicum* ubiquitin-conjugating protein (UBI-3) (AY486137.1) was used as a normalization control. The qPCR experiment was repeated twice independently and each experiment included three technical replicates for each sampling time. Relative gene expression was calculated using $2^{-(\Delta\Delta Cq)}$ according with Livak´s method (Livak and Schmittgen, 2001). To calculate the relative expression level of genes, the 0 h time point was considered as the calibrator condition. Statistical analysis was performed using analysis of variance (ANOVA) with Fisher´s pairwise comparison test using Minitab 17 statistical software.

Results

Gene Expression of G proteins, *RGS* and *GPCR* in Stems and Roots of *Capsicum* Plants

In *Capsicum* stems, *CaGα1* gene showed a significant increase in transcript levels by 5.4 fold at 18 h after UV-B radiation was started and subsequently the transcript levels dropped (Fig. 1A), while UV-B radiation induced significantly the *CaGβ1* transcript by 3.9 fold at 18 h of exposure (Fig. 1D). On the other hand, *CaRGS1*, *CaGPCR*1, *CaGγ1* and *CaGγ2* did not show statistically significant differences in their expression by UV-B radiation exposure (Fig. 1B, C, D and F). Despite, UV-B treatment caused a weak increased of *CaRGS1* and *CaGPCR*1 of 2.3 fold at 12 h after exposure (Fig. 1B and C). In the gene expression analysis of *CaGα1*, *CaGβ1*, *CaGγ1*, *CaGγ2*, *CaRGS1* and *CaGPCR1* in roots, no statistical differences were found in the relative expression of the evaluated genes according to Fisher´s pairwise comparison test. Despite no significant differences in gene expression were found, *CaGα1* and *CaRGS1* expression profiles seem to show certain similarity, particularly in the increase of expression up to 5.8 and 2.5 fold at 3 h, respectively. After 3 h of exposure its transcript levels dropped and then raised again up to 4.9 and 1.7 fold at 18 h mantaining its transcript levels at 25 h (Fig. 2A and B).

Discussion

The stems, in particular, its vascular tissue, is involved in the movement of resources to different plant organs, it also provide mechanical support, and function as a long-distance communication system of abiotic and biotic environmental conditions (Lucas *et al*., 2013). Signaling pathways through G proteins are key in physiological processes in stems of some species (Anderson and Botella, 2007). In *Capsicum*, UV-B radiation exposure of stems induced a significant increase in transcript levels of *CaGα1* and *CaGβ1* genes. Although it is not possible to indicate the function that CaGα1 y CaGβ1 are fulfilling in the stems of *Capsicum* under these conditions, it is known that UV-B can cause direct and indirect effects on plants. Direct effects are related to growth, photosynthetic assimilation, cell division and development, whereas indirect effects manifest with synthesis of secondary metabolites (Prado *et al*., 2016).

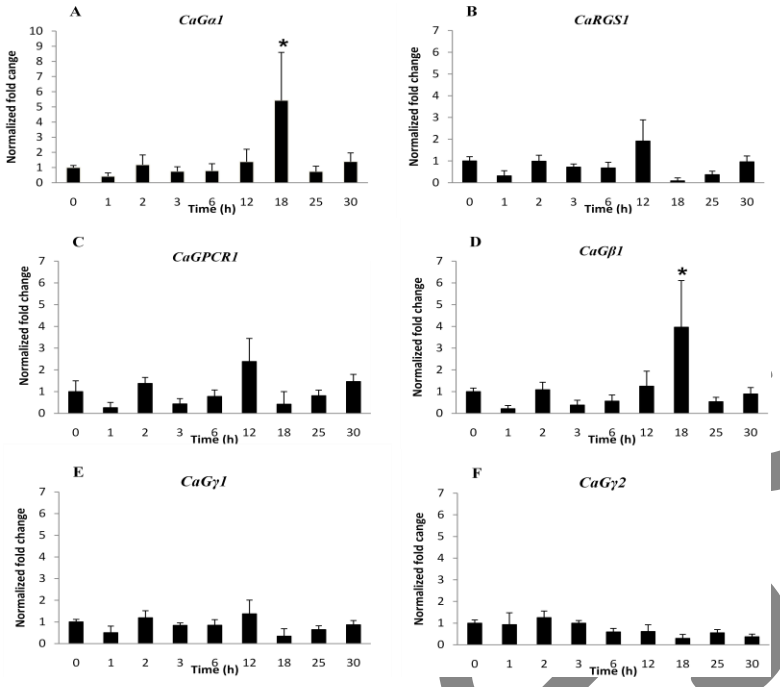

Fig. 1: Expression profile of G-protein genes of *Capsicum annuum* determined by qPCR. Total RNA was isolated from 30 days-old plant stem samples collected at different time intervals after UV-B treatment. Relative gene expression levels of *CaGα1*, *CaRGS1*, *CaGPCR1*, *CaGβ1*, *CaGγ1* and *CaGγ2* (A-F) were normalized against UBI-3 gene expression and with respect to control (0 h). Error bars represent the standard error of the mean of two independent experiments, each experiment consisting of three technical replicates. *Indicate values statistically different at $P < 0.05$ according to Fisher´s pairwise comparison test

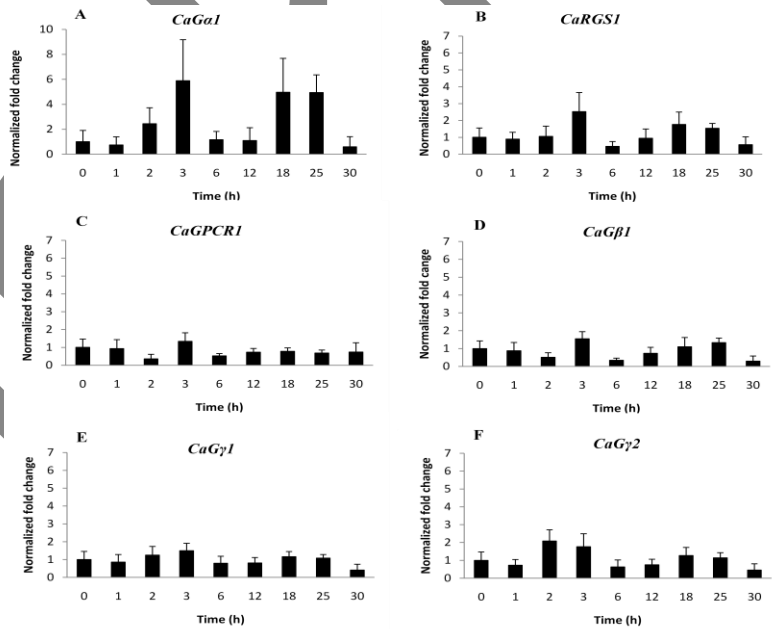

Fig. 2. Expression profile of G-protein genes of *Capsicum annuum* determined by qPCR. Total RNA was isolated from 30 days-old plant root samples collected at different time intervals after UV-B treatment. Relative gene expression levels of *CaGα1*, *CaRGS1*, *CaGPCR1*, *CaGβ1*, *CaGγ1* and *CaGγ2* (A-F) were normalized against UBI-3 gene expression and with respect to control (0 h). Error bars represent the standard error of the mean of two independent experiments, each experiment consisting of three technical replicates. *Indicate values statistically different at $P < 0.05$ according to Fisher´s pairwise comparison test

In this sense, Singh *et al*. (2014) indicated that growth and developmental processes were the most sensitive to UV-B radiation in maize. Whereas, in tobacco it was observed that antisense-*Gβ* plants exhibited stems reduced in length, which were unable to grow without support (Peskan-Berghofer *et al*., 2005). In this study, up-regulation of *CaGβ1* gene was UV-B-induced, suggesting a specific role of CaGβ1 in these stress signaling pathways. On the other hand, it is known that *Arabidopsis* Ga subunit (GPA1) is a positive regulator of UV-B radiation initiating the synthesis of phenylalanine, a precursor of a large number of secondary metabolites of protection (Warpeha *et al*., 2008), which is one of the most basic and studied plant strategy for attenuation of UV-B radiation (Solovchenko and Schmitz-Eiberger, 2003). Plants increase transcription of genes required to reduce UV-B radiation impact, some genes that encode enzymes for pigments synthesis which reduce penetration of UV-B radiation, such as flavonoides and other secondary metabolites (Fina, 2017). Herein, gene expression analysis demostrated that *CaGα1* gene was up-regulated by UV-B radiation maybe as a stress-induced plant response to cope with radiation. In classical G protein signaling, Gα and Gβ subunits act as two functional modules (Xu *et al*., 2016). In *Capsicum*, both *CaGα1* and *CaGβ1* genes were strongly UV-B-induced and probably have different roles in signaling response to UV-B. These results suggest that G proteins are involved in early signaling of physiological processes stress-related in *Capsicum*.

On the other hand, root is the underground organ in terrestial plants that do not grow in a total darkness environment due to the fact that sunlight can penetrate the soil surface affecting root growth. In addition, light perceived by shoots, especially UV-B radiation, can also affects root architecture (Mo *et al*., 2015). Root growth and architecture depend on cell division of root apical meristems and subsequent cell elongation (Perfus-Barbeoch *et al*., 2004). Null mutant of AtRGS (*AtRGS1*) in *Arabidopsis* increased cell production in primary roots due to lack of GAP activity and subsequent steady-state pool of activated Gα, which modulate cell division in apical meristems (Chen *et al*., 2003). Moreover, null mutants of AGB1 and GPA1 (*agb1* and *gpa1*) in *Arabidopsis* showed more and fewer lateral roots, respectively. Whereas Gα is a positive modulator of cell division in apical meristems, Gβ plays an opposite role attenuating cell division (Chen *et al*., 2006). In this study, we evaluated if *Capsicum* plants responded to UV-B radiation through G protein signaling system in a tissue-specific way, since G protein expression was observed induced in stem. Despite no statistical differences were found in the relative expression of the evaluated genes in roots, *CaGα1* and *CaRGS1* expression profiles seem to show similarity under UV-B radiation treatment of roots. Statistical confirmation of these observations in later experiments would suggest that CaGα1 participates in the response to UV-B radiation in roots, which could be probably being regulated by CaRGS1. According with Choudhury *et al*. (2012), Gα and RGS can display similar expression profiles because these proteins work together in G protein signaling regulation. It is probably that UV-B radiation after 3 h of exposition of *Capsicum* plants could affects roots, where these components of G protein signaling could play a specific role.

Conclusion

Results of this study indicate that UV-B radiation up-regulates *CaGα1* and *CaGβ1* genes in stems of *Capsicum* plants, while *CaGα1* and *CaRGS1* genes exhibited a similar expression profile in roots of *Capsicum* plants, although no statistically significant. G proteins response to UV-B-radiation in *Capsicum* occurs in a specific-tissue manner where *CaGα1* and *CaGβ1* have an active role in stems.

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