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ORIGINAL RESEARCH ARTICLE

Photomodulation of strigolactones in mediating sunflower seedling growth

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Abstract

Plants produce a large variety of non-proteinaceous biochemicals through primary and secondary metabolism. These compounds may act as signaling molecules, plant hormones, growth regulators (other than hormones), or protectants from parasitic infections. In various attempts by scientists world over, a number of novel plant growth regulators have been discovered in the recent past. Over the past decade interesting information has been obtained on the biosynthesis, photomodulation and physiological roles of strigolactones (SLs) which are derived from the carotenoid biosynthesis route. Adequate evidence is now available on their actions through transport to the target sites in the plant system. The regulatory roles of strigolactones have further been observed to be modulated by light in more than one ways. Present investigations report the photo modulation of strigolactones (SLs) in sunflower seedlings' growth at their early developmental stages (2d, 4d, 6d). These observations indicate the migration of a probable light-sensitized signaling molecule (yet to be identified) or a SL precursor from light-exposed aerial parts to the seedling roots maintained in dark. Thus, a photo modulation and migration of SL precursor/s is evident from the present work.

Keywords: Strigolactones; Signaling Mechanisms; Photomodulation; Lateral Roots.

Introduction

Strigolactones (SLs) are carotenoid-derivatives and plastidial in origin which were first identified as germination stimulants for the seeds of root parasitic weeds such as *Striga*, *Orobanche*, *Phelipanche* spp. (Xie *et al.*, 2010). Subsequently, SLs were observed acting as signaling molecules in the rhizosphere to detect host for arbuscular mycorrhiza. A variety of SLs differing in the side group associations on the four-ringed basic structure have been identified from a number of plants using sophisticated techniques, such as HPLC, LC-MS, FT-IR and NMR (Fig. 1). To date, more than 15 SLs have been characterized from various plant spp. (Table 1). Additionally, a number of synthetic analogs are also now commercially available. These include GR5, GR7 and GR24 (Xie *et al.*, 2010; Yoneyama *et al.*, 2011). Since their discovery, SLs have been reported to control various developmental processes in plants. These include modulation of shoot architecture, primary root elongation, lateral root development, initiation of adventitious root, root hair growth and mycorrhizal colonization. In order to exert their influence on the above-stated processes, SLs may either act directly or through interaction with auxins, cytokinins, abscisic acid and/or ethylene. More than two plant hormones, ethylene and auxin may also interact with SLs to control a developmental response.

Light promotes SL production in sorghum roots (Weerasuriya *et al.*, 1993). Several lines of evidence have now established a connection between SL signaling pathways and light (Waldie *et al.*, 2010). SLs act as positive regulators of various photo-modulated processes. Exposure to a synthetic analogue of SL (GR24) induces several light signaling-related genes in *Arabidopsis* seedlings (Mashiguchi *et al.*, 2009). Photomodulation of GR24-induced genes has also been demonstrated in the leaves of plants exposed to different light regimes (Guo *et al.*, 2008). Analysis of *sl-ort1*, a tomato mutant deficient in strigolactone biosynthesis, has shown

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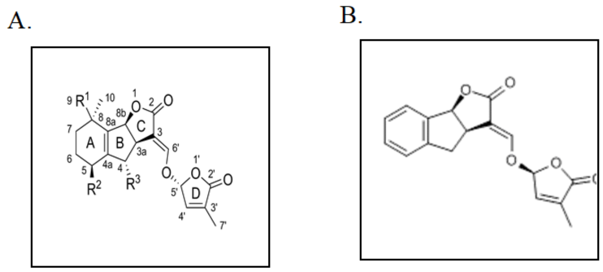

Fig. 1: A. Basic structure of SL (5-Deoxystrigol); and B. GR24 - a synthetic strigolactone.

reduced level of chlorophyll in the leaves, indicating that SL production is induced by light (Dor *et al.*, 2010; Koltai *et al.*, 2010). Mayzlish-Gati *et al.* (2010) have recently demonstrated that GR24 induces genes for Rubisco and chlorophyll alb-binding protein precursors. Their expression is reduced in *sl-ort1* mutant of tomato in comparison with the wild strain. Thus, reduced chlorophyll level correlates with SL perception or synthesis disruption. Since SLs are derived from the carotenoid biosynthetic pathway, a crosstalk between SLs and photo modulated pathways seems necessary for coordinated plant growth and development. SLs regulate nuclar localization of the ubiquitin ligase-COP1, which partially controls the level of HY5, a transcription factor (Tuschiya *et al.*, 2010). Koltai (2010) undertook extensive investigations and showed that above certain threshold level, light intensity positively regulates the transcription of *Sl-CCD7* in tomatoes whereby *CCD7* transcription increased twenty-three-fold under full light in comparison with those under sixty percent shading. Auxin is believed to be one of the factors which can affect SL biosynthesis in plants via the AXR1/TIR1 and IAA12 signal transduction pathway (Hayward *et al.*, 2009). Thus, light likely enhances auxin transport to the roots, which may be responsible in part for increase of CCD7 expression, leading to elevation of SLs levels.

Novel feature of the present work is with reference to the photomodulation of SL biosynthesis during seed germination. Present findings, thus, provide significant indication of photo modulation of SLs in mediating sunflower seedling growth at early stages of development.

Materials and Methods

Plant material Sunflower (*Helianthus annuus* L. cv. KBSH-53) seeds were procured from the University of Agricultural Sciences, Bangalore, India. They were thoroughly washed and surface sterilized with 0.005% $HgCl_2$ for 2 min, followed by extensive washing in distilled water. Seeds were then imbibed for 2 h in double distilled water and germinated on moist germination sheets at 25±3 °C. Seedlings were raised either in light or dark and irrigated with distilled water. Roots of seedlings were wrapped in germination paper to maintain their growth in dark. Light-grown seedlings were maintained in a photoperiod cycle of 16 h light/8 h dark diurnally at a fluence of 4.3 W.m-2. Seedlings at different developmental stages exhibiting uniform growth were selected for photo modulated analysis. Seedlings raised in presence of GR24 (3μM) in light and dark at their different developmental stages were also selected for analysis.

Table 1: Some major SLs identified and characterized in plants

Plants	*Major SLs Identified*	*References*
Cotton	Strigol and strigyl acetate	Sato *et al.* 2005
Lotus	5-Deoxystrigol	Akiyama *et al.* 2006
Tomato	Solanacol and didehydro orobanchol	López-Ráez *et al.* 2008
Pea	Peagol and peagoldione	Evidente *et al.* 2009
Arabidopsis	Orobanchol, orobanchyl acetate, 5-Deoxystrigol	Kohlen *et al.* 2011
Sunflower and safflower	Orobanchol, orobanchyl acetate, 5-Deoxystrigol, 7-oxoorobanchyl acetate	Yoneyama *et al.* 2011
Sorghum, maize and millet	Sorgomol, sorgolactone, 5-Deoxystrigol	Yoneyama *et al.* 2011
Petunia	7-hydroxyorobanchyl acetate, orobanchyl acetate, 7-oxoorobanchyl acetate	Yoneyama *et al.* 2011
Rice	Orobanchol, orobanchyl acetate, ent 2' epi-5-Deoxystrigol	Xie *et al.* 2013
Tobacco	Solanacol, solanacyl acetate, orobanchol, 5-Deoxystrigol, orobanchyl acetate	Xie *et al.* 2013

Results

Following imbibition for 2 h, sunflower seeds were wrapped in moist germination paper and allowed to germinate at 25 ± 2 °C in dark or light (16/8 h photoperiod provided diurnally) for 6 days. Sunflower seedlings show faster hypocotyl elongation right from 2 day stage in dark in contrast with slower extension growth in light at all the three stages of seedling development examined (Fig. 2). Detailed evaluation of the pattern of seedling growth undertaken showed marked differences in root growth and architecture as well. Thus, the extension growth of primary root was observed to be faster in dark-grown seedlings than those grown in light. After 6 days, it was more in light. In addition to primary root growth, significant differences were observed in the extent of lateral root formation in dark or light-grown seedlings. These differences were most noteworthy in 9 day old seedlings, where profuse lateral root initiation was evident along the length of primary root in response to light. Under similar conditions in dark, lateral root formation was evident at a much-reduced level. Aerial parts of seedlings also showed noteworthy differences in the growth pattern whereby apical hook was found to be persistent both in light and dark at 2 day stage but the hook vanished at 4 day stage in light. The straightening of cotyledons was a much slower process in dark-grown seedlings. In contrast to the extended growth of hypocotyl in dark, the extension growth of hypocotyl was much reduced in light and this accompanied the greening of seedling cotyledons due to chlorophyll biosynthesis.

Seedling growth in the presence of 3 μM GR24 - a synthetic SL, brought about noteworthy differences in lateral root formation in dark-grown seedlings (Fig. 3). No significant differences were observed in primary root length and hypocotyl extension in dark-grown seedlings in response to GR24. Similar observations were recorded on the impact of GR24 on hypocotyl growth, primary root extension and lateral root formation in all stages of light-grown seedlings (Fig. 4).

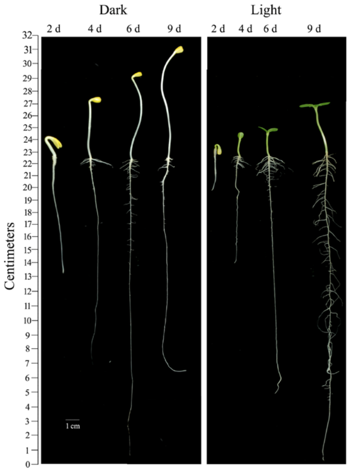

Fig. 2: Differences in sunflower seedling growth and root development in response to light (16/8 h light/dark cycles diurnally; 4.3 W.m-2) and dark. d refers to days of seedling growth

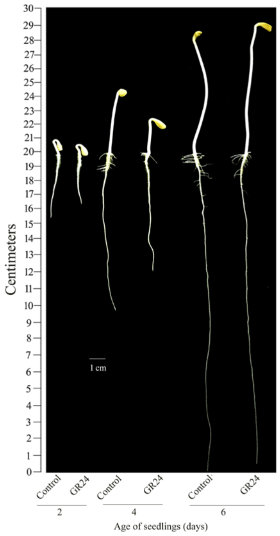

Fig. 3: Effect of GR 24 (3μM) on seedling growth and lateral root development in dark

Discussion

Light is one of the most important environmental factors that regulates plant growth and developmental pattern. Seedling development follows two contrasting patterns in response to light or dark i.e. photomorphogenesis or skotomorphogenesis (etiolation). Dark-grown seedlings are characterized by elongated hypocotyls and closed cotyledons rested on an apical hook (Abbas *et al.*, 2013; Mazzella *et al.*, 2014). This allows seedlings to emerge from the soil as rapidly as possible. Light-grown seedlings exhibit shorter hypocotyls and expanded green cotyledons, thus minimizing the longitudinal extension growth (McNellis *et al.*, 1994). Similar pattern of photomodulated sunflower seedling growth is observed in present work. Light-induced morphogenic development has been shown to be regulated through multiple photoreceptor-mediated signaling pathways, including blue light photoreceptor-cryptochrome, and red/far-red light photoreceptor-phytochrome (Lian *et al.*, 2011; Liu *et al.*, 2011; Shen *et al.*, 2005; Al-Sady *et al.*, 2006). Recent investigations have shown the convergence of light and phytohormone signaling pathways through various transcription factors, such as HY5 and phytochrome interacting factors (PIFs). HY5 has been shown to be involved in mediating auxin, GA and ABA signaling (Chen *et al.*, 2008; Cluis *et al.*, 2004; Weller *et al.*, 2009). Phytochrome interacting factors (PIFs) 1, 3, 4 and 5 play an important roles in seedling morphogenesis, seed germination, chloroplast development, response to high temperature and shade avoidance (Oh *et al.*, 2004; Lorrain *et al.*, 2008; Koini *et al.*, 2009; Stephenson *et al.*, 2009). In plants, differential subcellular localization of several key regulators seems to play an important role in the control of light-dependent development. For example, light signals initiate the nuclear import of phytochrome B and specific transcription factors (Harter *et al.*, 1993;

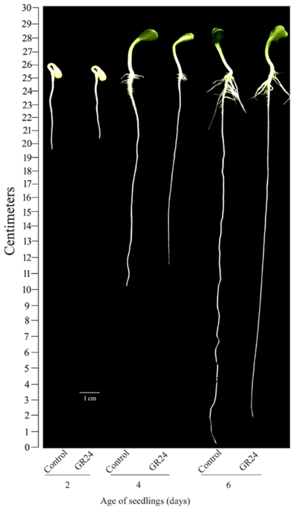

Fig. 4: Effect of GR 24 (3μM) on seedling growth and lateral root development in light (16/8 h light/dark diurnally; 4.3 W.m^{-2})

Sakamoto & Nagatani, 1996; Terzaghi *et al.*, 1997). Light also leads to reduction in the nuclear abundance of COP1, which is a repressor of photomorphogenetic development, as is evident from the GUS-COP1 localization pattern in *Arabidopsis* (von Arnim & Deng, 1996). Differential growth pattern of sunflower seedlings is also evident in terms of elongated hypocotyls, closed cotyledons and apical hook formation in response to dark (Yadav, 2010). Fatty acids mobilization, both in whole cotyledons (including oil bodies), has also been shown to be modulated by light during seed germination (Yadav & Bhatla, 2015). Oil bodies exhibit Enhanced free fatty acid accumulation during light-stimulated lipid mobilization in sunflower seedlings (Yadav & Bhatla, 2015). These observations highlight the adaptive features of sunflower seedlings in response to light or dark. Thus, present observations on the effect of light on sunflower seedling growth are in congruence with earlier report (Yadav, 2010). Earlier investigations have also shown that light prevents the asymmetric distribution of auxin and other growth hormones in the apical hook region (Mazzella *et al.*, 2014). This indicates a possible correlation between hook formation (present work) and the asymmetric distribution of auxin and other growth hormones in the apical region in seedlings growing in dark. Recent investigations have also revealed ERF VII (group seven ethylene response factors) - induced accumulation and stabilization of the apical hook in the absence of oxygen or in dark (Potuschak & Bachmair, 2015; Abbas *et al.*, 2013). The light-induced proliferation of lateral roots (present work) is in agreement with recent investigations that light plays an important role in lateral root formation by modulating shoot-derived auxin in tomato seedlings (Thomas *et al.*, 2014). Several other reports suggest the role of auxin as a central player in lateral root development (Benková *et al.*, 2003; de Smet *et al.*, 2007; Laplaze *et al.*, 2005; Negi *et al.*, 2008; Péret *et al.*, 2009). Several plant species have shown white light-induced inhibition of primary root growth (Kurata & Yamamoto, 1997; McKendree & Smith, 1990; Fereidouni *et al.*, 2012; Hisayo *et al.*, 2009). Investigations into light-induced inhibition of root elongation of *Zea mays* primary roots have shown the production of some growth-inhibiting factor(s) by root cap and their movement into the elongation zone of primary roots to elicit their effect (Wilkins & Wain, 1975). Current work has also reported the light-induced inhibition of primary root growth at all stages of their development.

Among higher plants, SLs regulate plant architecture through modulation of shoot branching and root growth and development (Rasmussen *et al.*, 2013). SLs are known to be synthesized both in root and stem and are transported across xylem (Kohlen *et al.*, 2011). Since auxin transport and its consequent accumulation play crucial roles in root development, SLs are expected to regulate auxin fluxes. SLs may change the localized auxin level by altering auxin biosynthesis or its polar transport (Rasmussen *et al.*, 2013). Role of SLs in reducing polar auxin transport has also been made evident through its effect on PIN distribution. In Petunia, ATP binding cassette (ABC transporter) PDR1 has been reported to be critical for SL transport (Kretzchmar *et al.*, 2012). Recently, a depletion of PIN1 from the xylem parenchyma cells was observed in response to SL (Shinohara *et al.*, 2013). GR24 application suppresses LR primordia development (Ruyter-Spira *et al.*, 2011). GR24 induced inhibition of lateral root formation at all stages of seedling development in response to light or dark has been made in the present work. These results suggest that SLs modulate localized auxin concentration and SL action is dependent on the auxin status of the plant. A negative influence of SL on LR formation has also recently been reported in *Arabidopsis* based on analysis of mutants flawed in SL biosynthesis or signaling and the treatment of seedlings with GR24 (Kapulnik *et al.*, 2011; Ruyter-Spira *et al.*, 2011). Thus, present investigations confirm the involvement of SL on lateral root formation. Several unanswered questions, however, still need to be investigated at biochemical and genetic levels to understand the mechanism of SL perception and signaling.

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