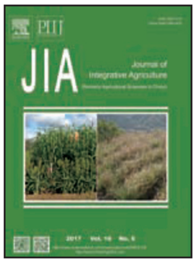
Journal of Integrative Agriculture 2017, 16(6): 1244–1255

Available online at www.sciencedirect.com

ScienceDirect



REVIEW

The molecular mechanism of shade avoidance in crops — How data from *Arabidopsis* can help to identify targets for increasing yield and biomass production

TANG Yun-jia[1], **Johannes Liesche**[1, 2]

[1] College of Life Sciences, Northwest A&F University, Yangling 712100, P.R.China
[2] Biomass Energy Center for Arid and Semi-arid lands, Northwest A&F University, Yangling 712100, P.R.China

Abstract

In order to prevent or counteract shading, plants enact a complex set of growth and developmental adaptations when they sense a change in light quality caused by other plants in their vicinity. This shade avoidance response (SAR) typically includes increased stem elongation at the expense of plant fitness and yield, making it an undesirable trait in an agricultural context. Manipulating the molecular factors involved in SAR can potentially improve productivity by increasing tolerance to higher planting density. However, most of the investigations of the molecular mechanism of SAR have been carried out in *Arabidopsis thaliana*, and it is presently unclear in how far results of these investigations apply to crop plants. In this review, current data on SAR in crop plants, especially from members of the Solanaceae and Poaceae families, are integrated with data from *Arabidopsis*, in order to identify the most promising targets for biotechnological approaches. Phytochromes, which detect the change in light caused by neighboring plants, and early signaling components can be targeted to increase plant productivity. However, they control various photomorphogenic processes not necessarily related to shade avoidance. Transcription factors involved in SAR signaling could be better targets to specifically enhance or suppress SAR. Knowledge integration from *Arabidopsis* and crop plants also indicates factors that could facilitate the control of specific aspects of SAR. Candidates are provided for the regulation of plant architecture, flowering induction and carbohydrate allocation. Yet to-be-elucidated factors that control SAR-dependent changes in biotic resistance and cell wall composition are pointed out. This review also includes an analysis of publicly available gene expression data for maize to augment the sparse molecular data available for this important species.

Keywords: shade avoidance response, phytochrome B, *Zea mays*, *Solanum lycopersicum*, biomass, carbon allocation

1. Introduction

In many environments, plants compete with neighboring plants for access to their main energy source, the sunlight. They sense the differences in the light's wavelength composition caused by other plants in their vicinity and launch a complex response in order to avoid shading. The most visible change is increased vegetative growth at the expense of reproductive development. For many crop plants, this

---

Received 22 March, 2016 Accepted 22 June, 2016
TANG Yun-jia, E-mail: yunjiatang@hotmail.com; Correspondence Johannes Liesche, Mobile: +86-17789133531, E-mail: liesche@nwsuaf.edu.cn

doi: 10.1016/S2095-3119(16)61434-X

shade avoidance response (SAR) is the main parameter for setting the maximum planting density (Smith 1982; Clay *et al.* 2009). Finding ways to control the plant's response to competition could lead to higher planting densities and, thereby, increase yield per area. This requires a detailed understanding of SAR on a molecular level.

So far, the molecular mechanism of SAR has been investigated mainly in *Arabidopsis*, where numerous studies have led to a detailed understanding of the triggers, signaling cascades and effectors. Here, current knowledge of the mechanism of shade avoidance in *Arabidopsis* is briefly summarized, followed by a detailed evaluation of how data from *Arabidopsis* can inform breeding efforts in crop species.

The analysis mainly focuses on members of the Solanaceae and Poaceae families. The Solanaceae contain several important crop plants, especially potato (*Solanum tuberosum*) and tomato (*Solanum lycopersicum*), which are the 5th and 9th most produced plant commodities worldwide (Faostat 2013). Potato and tomato are two crop plants in which the characterization of SAR has progressed relatively far. In contrast, only limited data are available for grasses, the Poaceae. Investigating SAR in grasses has special relevance now, as food grasses, such as maize (*Zea mays*), rice (*Oryza sativa*) and wheat (*Tritium aestivum*), provide the majority of calories that humans consume every day, and non-food grasses, such as *Miscanthus* and switchgrass (*Panicum virgatum*), are increasingly grown as feedstocks for lignocellulosic biofuels. Detailed knowledge of SAR, at molecular and systems levels, could accelerate the identification of biotechnological targets for improving biomass production of energy crops by increased vegetative growth (Warnasooriya and Brutnell 2014).

2. The shade avoidance response in *Arabidopsis*

Since the original description of SAR, it was clear that it is a process of incredible complexity, including numerous signaling cascades, the interplay of different phytohormones and multiple levels of growth responses (Smith 1982; Kutschera and Briggs 2013). It is therefore no surprise that most of the research on the mechanism of SAR has been performed on the model plant *Arabidopsis*. The wealth of genetic tools, bioinformatics resources and a simple experimental system have facilitated a detailed investigation. A brief summary of the current knowledge of SAR in *Arabidopsis* is provided here as reference for the following discussion of SAR in crop plants. The reader may be referred to excellent review articles for an in-depth description of different aspects of SAR in *Arabidopsis*, such as signaling (Ruberti *et al.* 2012; Wang and Wang 2015) or the role of different hormones (Stamm and Kumar 2010).

Under full sunlight, plants are exposed to relatively equal fluxes of 600–700 nm red (R) and 700–800 nm far-red (FR) light (Holmes and Smith 1975). While R light is absorbed by the green tissues, FR light is largely reflected or transmitted (Cumming 1963). The decrease in R:FR ratio caused by neighboring plants was found to be the trigger for SAR. The dependence on a certain wavelength ratio means that the process is unrelated to general shading, which equals a decrease in light levels of all wavelengths. Phytochrome B (PHYB) was identified as the primary photoreceptor to sense changes in R:FR ratio and activator of the SAR signaling cascade (Morgan and Smith 1976; Halliday *et al.* 1994). Other photoreceptors involved are phytochrome A (PHYA), which can antagonize PHYB action (Mazzella *et al.* 1997), and phototropins and UV RESISTANCE LOCUS 8 (UVR8), which are involved in the regulation and attenuation of SAR (Casal 2013; Fraser *et al.* 2016). Of importance is also the blue-light receptor cryptochrome 1 (CRY1), which can induce SAR independently of PHYB (Keller *et al.* 2011).

Gene expression profiling of plants grown under low and high R:FR light environments and extensive mutant plant analysis led to the identification of components of SAR. Phytochromes exist either in the activated FR-light absorbing state or the inactive R-light absorbing state. Only activated phytochromes interact with phytochrome interacting factors (PIFs), which act as the master regulators for the different downstream signaling cascades (Leivar and Quail 2011). The interaction with PHYB leads to the degradation of PIFs, which has direct effects on the expression of downstream transcription factors (Lorrain *et al.* 2008; Ciolfi *et al.* 2013). These transcription factors that act as positive and negative regulators influence the biosynthesis and action of phytohormones in an organ-specific manner which then results in the observed growth responses (Stamm and Kumar 2010). Recently, also cryptoptochromes were shown to directly interact with PIFs to control plant growth (Ma *et al.* 2015; Pedmale *et al.* 2016).

In *Arabidopsis* seedlings, auxin, gibberellic acid (GA) and brassinosteroids (BR) are involved in hypocotyl elongation (de Wit *et al.* 2014; Nozue *et al.* 2015), while ethylene was implicated as well (Pierik *et al.* 2009). Petiole elongation seems to be controlled by GA and jasmonic acid (Nozue *et al.* 2015), while auxiliary bud growth under shading is controlled by abscisic acid (Reddy *et al.* 2013). Root growth might be restricted through changes in auxin and ethylene levels (Ruzicka *et al.* 2007; Stepanova *et al.* 2007). Leaf development is inhibited during shade avoidance through an increase of the auxin-to-cytokinin ratio in the leaf meristem (Carabelli *et al.* 2007). Other important components of SAR are changes to the circadian clock and early flowering