

REVIEW

Phototropism: Growing towards an Understanding of Plant Movement^{OPEN}

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Phototropism, or the differential cell elongation exhibited by a plant organ in response to directional blue light, provides the plant with a means to optimize photosynthetic light capture in the aerial portion and water and nutrient acquisition in the roots. Tremendous advances have been made in our understanding of the molecular, biochemical, and cellular bases of phototropism in recent years. Six photoreceptors and their associated signaling pathways have been linked to phototropic responses under various conditions. Primary detection of directional light occurs at the plasma membrane, whereas secondary modulatory photoreception occurs in the cytoplasm and nucleus. Intracellular responses to light cues are processed to regulate cell-to-cell movement of auxin to allow establishment of a trans-organ gradient of the hormone. Photosignaling also impinges on the transcriptional regulation response established as a result of changes in local auxin concentrations. Three additional phytohormone signaling pathways have also been shown to influence phototropic responsiveness, and these pathways are influenced by the photoreceptor signaling as well. Here, we will discuss this complex dance of intra- and intercellular responses that are regulated by these many systems to give rise to a rapid and robust adaptation response observed as organ bending.

INTRODUCTION

Plants have evolved a variety of responses to maintain optimal growth and development under ever changing environmental conditions. Photoreceptors and their associated signaling pathways are one way plants cope with changes in their environment, integrating signals of light quality and quantity, to adaptively modify overall growth characteristics from seed germination to reproduction (Kami et al., 2010; Pedmale et al., 2010; Chen and Chory, 2011). Although many photoreceptors, signaling pathways, and processes they regulate have been identified, this review will focus specifically on the components associated with the induction, modulation, and establishment of phototropic responses in higher plants.

Phototropic responses, or a plant's ability to reorient organ growth toward (positive phototropism) or away (negative phototropism) from a directional light source, has fascinated researchers for well over a century (Holland et al., 2008). Among the historical references to plant phototropism, Darwin's *The Power of Movement of Plants* (1880) is arguably the most well known. Therein, Darwin describes a mysterious substance that is transduced from the tip of the seedling, where the light signal is perceived, to lower portions of the seedling, where the signal response can be observed in the form of directional growth changes (Darwin, 1880). It was not until the 1920s that a significant breakthrough occurred when Fritz Went (Went, 1926), working on phototropism in the oat (*Avena sativa*) coleoptile, isolated and identified Darwin's mysterious substance as the plant hormone auxin. Together with work by Nicolai

Cholodny (Cholodny, 1927) on oat root gravitropism (bending response to change in the direction of the gravity vector), these findings formed the basis for the Cholodny-Went hypothesis (Went and Thimann, 1937), which proposes that tropisms result from the lateral redistribution of auxin in response to tropic stimuli. In the case of coleoptile (and stem) phototropism, auxin is redistributed from the lit flank (side closest to the incident light) to the shaded flank (side farthest from the light source) leading to differential auxin-stimulated cell elongation in the shaded versus lit portion of the organ and, thus, curvature toward the light source (Went and Thimann, 1937; Eamon et al., 2006; Holland et al., 2008) (Figure 1). Yet, despite over 100 years of intensive study, the photoreceptor(s) responsible for sensing directional light remained elusive until the 1990s when work in Winslow Briggs' laboratory at the Carnegie Institution of Washington (Stanford, CA) led to the identification of the phototropins (Short and Briggs, 1990; Raymond et al., 1992; Liscum and Briggs, 1995; Huala et al., 1997; Christie et al., 1998). Much like the work of Cholodny and Went, the findings of Briggs and colleagues represented a seminal step in our understanding of plant biology. In the following section, we will review our current understanding of phototropin structure and function in phototropic signaling.

PHOTOTROPINS

Primary Photoreceptors Modulating Blue Light-Induced Phototropism and Other Responses That Optimize Photosynthetic Capacity

In higher plants, there are two phototropins (photo): phot1 and phot2 (Huala et al., 1997; Jarillo et al., 2001; Suetsugu and Wada,

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