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Article Addendum

Opposite Ends of the Spectrum

Plant and Animal G-Protein Signaling

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Addendum to:

The GCR1, GPA1, PRN1, NF-Y Signal Chain Mediates Both Blue Light and ABA Responses in Arabidopsis

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ABSTRACT

Different classes of biotic (e.g., plant hormones) and abiotic (e.g., different wavelengths of light) signals act through specific signal transduction mechanisms to coordinate all aspects of plant development. Full signal transduction chains have not yet been described for most light or hormonal-mediated events despite the wide range of events early in development which are dependent upon hormonal and light signals. We recently reported a single signal transduction chain which can be initiated by both blue light (BL) and ABA, and which leads to the expression of specific members of the *Lhcb* gene family in the apical bud of etiolated Arabidopsis seedlings. The signal transduction chain consists of GCR1 (one of two Arabidopsis proteins coding for a potential G-protein coupled receptor), GPA1 (the sole Arabidopsis Gα subunit), PRN1 (Pirin1, one of four members of an iron-containing subgroup of the cupin superfamily), and a Nuclear Factor -Y (NF-Y) heterotrimer comprised of A5, B9 and possibly C9. The same signaling proteins control ABA-mediated delay of germination.

PLANT VERSUS ANIMAL SIGNALING SYSTEMS

Heterotrimeric G-protein mediated cell signaling is one of the most highly conserved signaling mechanisms among eukaryotes.[1] In terms of signaling components, animals and higher plants have very different genomic situations. Higher plants have one or two copies of G-protein coupled receptors and G protein components, whereas the number present in animal genomes can number in the hundreds.[2,3] In Arabidopsis, a GCR1 homolog called GCR2 has recently been reported and characterized as involved in the delay in germination, potentially antagonistic to the role of GCR1.[4] The situation is reversed for transcription factors, where plants have numerous types and many copies in a given gene family and animals may have single copy. A good example are the NF-Y factors where the A, B and C subunits in Arabidopsis number ten, ten and nine, respectively,[5,6] but in humans there is only one copy of each subunit. This suggests that signaling specificity for plant signal transduction mechanisms may reside at the level of effectors, modifications of signaling components, and/or gene expression itself rather than in the receptors or G-protein sub-types.

The hypothesis presented above is supported by our recent findings that several different effectors are able to relay abiotic or biotic information received from the sole Arabidopsis Gα, in different tissues and at different developmental stages.[7] It is also supported by the increasing number of different effector proteins that interact with the Arabidopsis Gα subunit including PRN1,[8] Phospholipase C,[9] Phospholipase Eα1,[10] PD1[11] and THF1.[12]

MULTIPLE PLANT-RELATED SIGNALS SHARE THE GCR1-GPA1 SYSTEM BUT NOT THE SAME EFFECTORS OR EVEN FURTHER DOWNSTREAM COMPONENTS SUCH AS TRANSCRIPTION FACTORS

The possibility of abiotic and biotic signals stimulating the same pathway is not a new concept in plant biology.[11,13-15] Both BL (biotic) and ABA (abiotic) are reported to be able to regulate the same pathway(s) as confirmed by various methodologies.[11,16-17] We recently demonstrated using both genetic and photobiological methods, that GCR1 and GPA1, as signal transduction components, are both critical to the ability of BL and ABA to mediate *Lhcb* expression in etiolated seedlings.[7] We also demonstrated that both BL

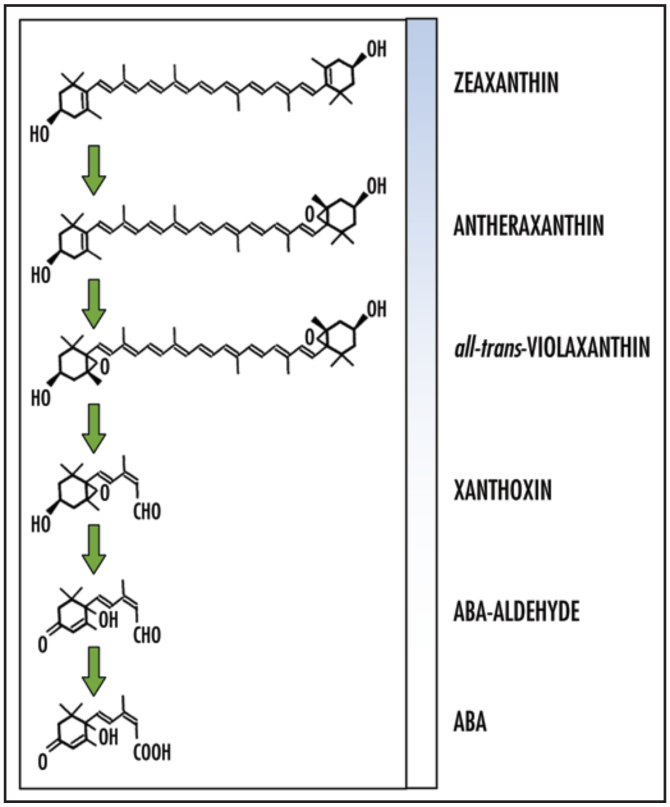

Figure 1. ABA synthesis pathway: from BL-absorbing zeaxanthin, to the hormone ABA.

and ABA act through the same signaling chain comprised in part of GCR1 and GPA1, suggesting the possibility that GCR1 can act as a receptor for both BL and for ABA. BL or ABA treatments also result in increased phenylpropanoid production in etiolated seedlings, acting once again via the GCR-GPA1 pathway.[11] This is yet further confirmation that the G-protein mediated pathway is core to many signaling pathways and that these pathways diverge at the effector level.

Even beyond the effector level (as outlined previously), in this case PRN1, there is divergence of the pathways depending on tissue type or developmental state of the tissue in which the signaling mechanism is present. NF-Y-B9 (also known as LEC1) is the only "B" subunit with responsible for the BL regulation of *Lhcb* expression in etiolated Arabidopsis seedlings. However, B9 and B6 (also known as LEC-1-Like) have a role in the mechanism that inhibits the ABA-mediated delay in germination.[7,8]

Similarly NF-Y-B9 is known to have a solo and critical role in the development of the embryo and events in late embryogenesis, responding to both biotic and abiotic stimuli.[18-20] NF-Y-B9 and NF-Y-B6 are both known to interact with proteins found in tissues other than the developing embryo, such as FUS3, itself involved in vegetative processes,[21] and ABI3, active in the shoot apex.[22-24]

THE CASE FOR MULTIFUNCTIONAL RECEPTORS

It is unclear how, but clear that, both BL and ABA require GCR1 and use the same proteins of GCR1 and GPA1 in the cotyledons of etiolated seedlings. Light and hormone signals have a different physical nature, so it is reasonable to assume the existence of two separate receptors that might in some way feed into the GCR1-GPA1 system. However, because of the relationship between ABA and BL absorbing carotenoids, we also can propose a "combined" receptor that can respond to both the biotic ABA signal and abiotic BL stimuli. ABA is derived from an asymmetric cleavage of BL-absorbing carotenoids (i.e., zeaxanthin, antheraxanthin, violaxanthin) as shown in Figure 1. Due to the structural relationship between the heterocyclic head group on ABA, and the carotenoid from which it originally derives, it is possible that a single receptor could bind, either ABA or a blue light-absorbing carotenoid.

Blue light-absorbing carotenoids are proposed as receptors for some phenomena in plants,[25-26] and a carotenoid-based chemical structure is the photoreceptor for rhodopsin, the rod-based photoreceptor which interacts with transducin, a G-protein involved in vision.[1] It may be in some systems where there are a paucity of receptors and G-proteins, that over time one receptor has become adopted for use with several signals.

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