EXPERT VIEW

Beyond the darkness: recent lessons from etiolation and de-etiolation studies

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Received 28 May 2019; Editorial decision 29 October 2019; Accepted 29 November 2019

Editor: Christine Raines, University of Essex, UK

Abstract

The state of etiolation is generally defined by the presence of non-green plastids (etioplasts) in plant tissues that would normally contain chloroplasts. In the commonly used dark-grown seedling system, etiolation is coupled with a type of growth called skotomorphogenesis. Upon illumination, de-etiolation occurs, marked by the transition from etioplast to chloroplast, and, at the seedling level, a switch to photomorphogenic growth. Etiolation and de-etiolation systems are therefore important for understanding both the acquisition of photosynthetic capacity during chloroplast biogenesis and plant responses to light—the most relevant signal in the life and growth of the organism. In this review, we discuss recent discoveries (within the past 2–3 years) in the field of etiolation and de-etiolation, with a particular focus on post-transcriptional processes and ultrastructural changes. We further discuss ambiguities in definitions of the term ‘etiolation’, and benefits and biases of common etiolation/de-etiolation systems. Finally, we raise several open questions and future research possibilities.

Keywords: chloroplast biogenesis, de-etiolation, etiolation, etioplast, prolamellar body, skotomorphogenesis.

Introduction: defining etiolation

Etiolation involves prolonged growth in the absence of light that results in the development of etioplasts in tissue that would have chloroplasts if subjected to light. Etioplasts do not contain chlorophyll or stacked thylakoid membranes, but rather have a paracrystalline lipid–pigment–protein structure known as the prolamellar body (PLB). The PLB consists largely of the plastid lipids monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG), and an association of the chlorophyll precursor protochlorophyllide (Pchlide), the light-dependent protochlorophyllide oxidoreductase (LPOR) that is responsible for its conversion, and the cofactor NADPH (Fig. 1; etioplast composition and structure reviewed, for example, in Kowalewska et al. (2019) and Pribil et al. (2014)).

As most scientifically observed etiolation systems involve (aseptic) germination and growth of seedlings in complete darkness, the term ‘etiolated’ is commonly defined additionally by the presence of a skotomorphogenic phenotype of elongated hypocotyls, shortened roots, and small, closed cotyledons (Fig. 1; reviewed in Josse and Halliday, 2008). In these systems, the light–driven etioplast–to–chloroplast transition is coupled to a transition from skotomorphogenic to photomorphogenic growth. These morphogenic traits
are often portrayed in quantifiable and continuous terms, with variables of hypocotyl length, apical hook angle, and cotyledon angle considered. By these definitions, aberrant ‘photomorphogenic in darkness’ or ‘skotomorphogenic in light’ phenotypes have been utilized to identify multiple components involved in light sensing, signaling, or downstream responses. Many of these components have since been shown to have broad roles in non-etiolation-related light response.

The majority of the data discussed in this Expert View refer to work undertaken in such seedling-based etiolation/de-etiolation systems. The various limitation of these systems and possible alternative or complementary systems are also discussed (in the section ‘New systems required and new lessons learned’).

More broadly, the term ‘etiolated’, which has etymological roots in the French étiolier (i.e. straw), is still used as a descriptor for a range of pale or yellowing phenotypes. These include nitrogen-deficient rice (Oryza sativa; Sun et al., 2018a), graft-incompatible pomello (Citrus grandis; He et al., 2018), and heavy-metal-treated wheat (Triticum aestivum; Semenova et al., 2017). Similarly, a skotomorphogenic phenotype observed in infected light-grown creeping bentgrass (Agrostis stolonifera; Roberts et al., 2016) was recently termed ‘bacterial etiolation’. We consider these phenotypes to be largely outside our personal definition of etiolated tissues (i.e. having etioplasts), and will not discuss them within this work. Nonetheless, we note that in recent years, similar ‘etiolated’ phenotypes have been linked to pigment accumulation (Chen et al., 2018b) and light signaling defects (Peng et al., 2019). Furthermore, the pale barley (Hordeum vulgare L.) albostrians mutant (Muramoto et al., 1999), has been shown to contain structures in its albino sectors that are highly reminiscent of transforming PLBs (Li et al., 2019). As such, these ‘etiolated’ plants should be considered a potential source of new players in the regulation of chloroplast development, particularly in non-model species. Finally, this review will not discuss etiolation-like responses in non-angiosperm species.

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**Fig. 1.** Etiolated phenotypes in plants (exemplified in Arabidopsis). (A) Plants grown in extended darkness develop etioplasts (upper panels). These plastids are physically defined by the presence of a paracrystalline membrane structure called prolamellar body (PLB), as well as prothylakoids (PT, indicated by white arrowheads). In the light, photosynthetic tissue develops chloroplasts (lower panels), which are defined structurally by thylakoid membranes that contain grana stacks (G, white asterisks) and stroma lamellae called stroma thylakoids (ST, white arrowheads). Images are from 6-day-old dark-grown Arabidopsis plant (upper panel), and a light-grown Arabidopsis plant at the rosette stage (lower panel). (B) Etiolation and de-etiolation studies generally involve germination and growth of seedlings in darkness, resulting in skotomorphogenic growth (left). This is defined by the presence of an apical hook (AH), closed and pale cotyledons, and an elongated hypocotyl. By contrast, plants grown the light (photomorphogenic conditions; right) have shorter hypocotyls, and open, green cotyledons. C, cotyledon; H, hypocotyls. Images taken from a 7-day-old dark-grown and a 9-day-old light-grown Arabidopsis seedling. (C) De-etiolation of dark-grown (etiolated) seedlings involves straightening of the apical hook, opening and greening of the cotyledons, as well as the transition from etioplast to chloroplasts (refer to Fig. 3). The etiolated seedlings were exposed to continuous white light (95 µmol photons m⁻² s⁻¹) for 6, 12, and 48 h.
species, a still under-represented and debated research field (reviewed in Mathews, 2006).

Recent developments in understanding etiolation and the etioplast-to-chloroplast transition

The response to light was one of the earliest phenomena observed in plants by naturalists, and much progress has been made in understanding both the perception of light by various photoreceptors, and the resultant signaling cascades that lead to transcriptional activation or repression of genes involved in de-etiolation. We will not discuss these processes, which have been recently reviewed (Casal et al., 2014; Huang et al., 2014; Casal and Qüesta, 2018; Pham et al., 2018; Podolec and Ulm, 2018), but rather focus here on breakthroughs in post-transcriptional regulation and ultrastructural changes during etiolation and de-etiolation (summarized in Box 1; Fig. 2).

Small RNAs fine-tune temporal and spatial expression of genes during de-etiolation

Small regulatory RNAs (sRNAs) are 20–24 nt-long molecules that regulate gene expression via RNA-dependent DNA methylation, translation inhibition, or mRNA cleavage (reviewed in Borges and Martienssen, 2015; Singh et al., 2018). Several important studies have highlighted the control of canonical light reception and response pathway factors by sRNAs, and the reciprocal light-based regulation not just of certain sRNA, but of the sRNA biogenesis process itself via these factors (Sorin et al., 2005; Zhang et al., 2011; Cho et al., 2014; Tsai et al., 2014; Achkar et al., 2018; Sun et al., 2018b). We refer the reader to two recent reviews (Sánchez-Retuerta et al., 2018; Manavella et al., 2019) for more details.

Recently, sRNAs were implicated in defining seedling tissue- or position-dependent greening responses: differential accumulation of certain sRNAs, and certain groups of sRNAs, was observed in different tissue types (Li et al., 2014). Most recently, two large-scale studies were undertaken: Lin et al. (2017) profiled sRNAs during Arabidopsis de-etiolation, while Xu and colleagues (2017) undertook comparative miRNA profiling in rice and maize (Zea mays) to understand the establishment of photosynthesis in C3 versus C4 species. These studies, which defined several specific sRNA roles, such as the repression of photomorphogenic growth by miR396 via members of the Growth Regulating Factors family (Lin et al., 2017), provide

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**Box 1. Key developments in understanding de-etiolation**

- **Small regulatory RNAs are highly dynamic during greening**
  Recent large-scale studies of small regulatory RNA (sRNA) changes during greening in Arabidopsis (Lin et al., 2017), rice, and maize (Xu et al., 2017) provide pioneer datasets, suggest new roles for several sRNAs, and demonstrate the power of de-etiolation systems in investigating pairwise relationships.

- **TOR connects light and nutrient signaling**
  The indirect activator of translation, target of rapamycin (TOR), acts downstream of the COP1–auxin cascade during de-etiolation (Chen et al., 2018a), but is also involved in light-independent developmental regulation in response to sugars (Mohammed et al., 2018). The complex demand/supply of resources associated with establishing photosynthesis has implications for the regulation and kinetics of chloroplast development, and for currently used etiolation systems.

- **Availability, not just abundance, counts for transcripts and proteins**
  Thousands of mRNA species are present yet translationally repressed by sequestration to processing bodies (P-bodies) in the dark (Jang et al., 2019). For plastid-encoded thylakoid membrane proteins, association of respective mRNA to ribosomes localizes them to membranes, but the membrane to soluble mRNA fraction changes little during greening (Legen and Schmitz-Linneweber, 2017). Soluble versus membrane localization of glutamyl-tRNA reductase (GluTR) does change with lighting, and the soluble (active) fraction shows early correlation with chlorophyll content (Schmied et al., 2018).

- **Singlet oxygen causes PSII damage and acts as a retrograde signal during de-etiolation**
  The early assembly of the PSII oxygen evolving complex results in the (damaging) formation of singlet oxygen (1O2; Shevela et al., 2019). 1O2 retrograde signaling mediates de-etiolation via the EXECUTER1 pathway (Chen et al., 2015; Carmody et al., 2016). A de-etiolation system was recently used to assign function to the elusive integrator of retrograde signalling, GUN1 (Wu et al., 2018).

- **Finally looking at membrane lipids (and how they get there)**
  Three recent studies investigated the effect of decreased MGDG (Fujii et al., 2017) and DGDG (Fujii et al., 2018) content on etioplast formation and greening (Fujii et al., 2019). They emphasize the role of DGDG in the dynamics of tubular-lamellar transformation occurring during PLB-thylakoid membrane transition as well as the crucial role of both neutral galactolipids in the membrane-associated steps of Chl biosynthesis. Future studies, using diverse systems and 3D imaging techniques, are suggested to further this developing field.
important pioneer work that defines global sRNA responses to greening (Fig. 2B). Furthermore, they demonstrate the use of de-etiolating systems—in which large scale yet highly temporally controlled changes occur—as a powerful tool for investigating pairwise relationships, for example, between regulators and their targets (Xu et al., 2016; Page et al., 2017; Xu et al., 2017).

TOR connects light and nutrient signaling to activate translation

Target of rapamycin (TOR) is an evolutionarily conserved protein kinase that acts as a central hub to control cellular- and organism-level development (reviewed in Caldana et al., 2019; Xiong and Sheen, 2014). Disruption of TOR results in plants with reduced chloroplast size and number, poorly developed thylakoid membranes, and decreased expression of key photosynthesis-related proteins (Xiong et al., 2017). Furthermore, TOR (i) is required for proper regulation of photomorphogenic growth via regulation of translation and brassinosteroid signaling (Xiong et al., 2017), (ii) acts as an indirect positive regulator of chlorophyll biosynthesis and photosynthesis-related genes (Li et al., 2015), and (iii) is involved in the accumulation of the MGDG and DGDG synthases (Sun et al., 2016). Thus, TOR positively contributes to plastid development. Nonetheless, seedlings with repressed TOR activity were recently reported to undergo more rapid accumulation of chlorophyll, PS-related transcripts, and plastid
membrane lipids during de-etiolation—surprising results that the authors attributed to altered nutrient content of TOR-repressed seeds (Zhang et al., 2018). Indeed, recent research underlines the essential role of TOR in sugar-status response during early development. This includes (indirect) positive control of cell elongation in dark-grown seedlings (Zhang et al., 2016), and de-repression of shoot apical meristem growth in the dark via sugar-induced TOR activity (Li et al., 2017b; Mohammed et al., 2018). In light of a recently clarified position for TOR in the constitutively photomorphogenic 1 (COP1)–auxin cascade (Chen et al., 2018a), these findings suggest that TOR balances light and sugar signaling to control plant and plastid development both at near-instantaneous and at more gradual time scales (Fig. 2C).

Recent studies have suggested that chloroplast protein production represents ~70% of the ATP cost of total cellular protein synthesis (Li et al., 2017a), and two-thirds of the cellular nitrogen budget (Evans and Clarke, 2019). The need for greening seedlings to balance the cost of photosynthesis with its ultimate reward may therefore define (i) the control of gene expression that exerts control primarily at the (costly) translational stage (Shen et al., 2009; Ning et al., 2016); and (ii) the recently observed multi-phase accumulation of photosynthesis-related products and activities (Dubreuil et al., 2018; Armarego-Marriott et al., 2019). We note that, in addition to defining greening, the availability of resources like carbon (Kósa et al., 2015) and nitrogen (Vitányi et al., 2013) influences etioplast formation. Therefore, these recent works highlight the importance of considering resource availability in studying all aspects of etiolation and de-etiolation. Given that these resources arise from both (exhaustible) seed storage tissues and medium supplementation, it is clear that the choice of experimental system can largely influence observations.

Control by location: where is as important as when

As well as massive transcriptional changes (Ma et al., 2001), greening can result in a global 2-fold increase in translational activity, and altered translation of ~1/3 of all transcripts (Liu et al., 2012). Translation of cytosolic mRNAs can increase due to changes in the number of ribosomes on individual transcripts (ribosome density) or changes in the proportion of transcripts occupied by ribosomes (ribosome occupancy) (Liu et al., 2013). In the plastid, transcripts are sequestered to membrane fractions in a ribosome-dependent manner, but membrane association of transcripts changes only minimally during maize leaf greening, suggesting that ribosome density, and not occupancy, drives greening-induced translation (Legen and Schmitz-Linneweber, 2017) (Fig. 2D). Within the cytosol, light-stimulated translation has been linked to processing bodies (P-bodies): RNA–protein
complexes that are conserved in eukaryotes and regulate gene expression by degradation or translational arrest of mRNA (reviewed in Xu and Chua, 2011; Maldonado-Bonilla, 2014). Dark-grown seedlings of a P-body defective mutant (Xu and Chua, 2009) displayed prematurely opened apical hooks and augmented translation of thousands of transcripts, including those involved in the chlorophyll biosynthesis pathway (Jang et al., 2019). Despite previous links between sRNA-mediated mRNA cleavage and P-bodies (Pomeranz et al., 2010), Jang et al. (2019) noted limited overlap between mRNA cleavage and sequestration-induced translational ‘pausing’ (Fig. 2D2). Recently, physical sequestration has also been implicated in post-translational regulation. Localization of glutamyl-tRNA reductase (GluTR) to the chloroplast stroma, but not to the membrane, was associated with its enzymatic activity; and was shown to correlate with accumulation of chlorophyll during the early hours of greening (Schmied et al., 2018). Interestingly, GluTR partitioning also changes following dark exposure of light-grown plants, suggesting that this regulation has relevance beyond the etioplast-to-chloroplast transition (Schmied et al., 2018) (Fig. 2D3). Together, these recent studies underline that, in addition to cellular abundance of proteins and mRNAs, subcellular localization also needs to be taken into consideration.

Retrograde signaling: coupling the import and assembly of photosystems

Communication from the chloroplast to the nucleus, known as retrograde signaling, is a critical step during chloroplast biogenesis and maintenance (reviewed in Hernández-Verdeja and Strand, 2018; Rochaix and Ramundo, 2018; Leister, 2019; Pesaresi and Kim, 2019). Of six early identified Genomes uncoupled (gun) mutants defective in plastid-to-nucleus retrograde signaling (Susek et al., 1993), five (gun2–6) have defects in genes for enzymes involved in tetrapyrrole biosynthesis. More recently, a role for the enigmatic GUN1 in regulating protein import via the cytosolic heat shock protein 90 (HSP90) chaperone was clarified using a de-etiolation system (Wu et al., 2019). This followed observations that the GUN1 protein accumulates primarily during early chloroplast development (Wu et al., 2018) and that gun1 mutants showed retarded de-etiolation (Mochizuki et al., 1996). The early flowering phenotype observed in GUN1 overexpressing plants has led to the proposal that the protein may play a role in developmental phase transitions beyond chloroplast biogenesis (Wu et al., 2018).

Singlet oxygen (¹O₂) is produced early during greening as a by-product of tetrapyrrole biosynthesis (Zhang et al., 2015; Wang and Apel, 2019) and via early photosystem II (PSII) oxygen evolving complex activity (Zavafer et al., 2015). In addition to potentially causing significant harm to the developing chloroplast, including damage to emerging PSI complexes prior to their protective incorporation into grana stacks (Shevela et al., 2019), singlet oxygen may act in retrograde signaling via the Filamentation temperature sensitive H (FtsH; a membrane metalloprotease)-activated EXECUTER 1 (EX1) pathway (Dogra et al., 2017). Previous research suggests that the ¹O₂-mediated EXECUTER pathway primes etioplasts to develop into chloroplasts (Kim et al., 2009), and also mediates high-light responses in the chloroplast, by regulation of multiple nucleus-encoded stress related transcripts (Carmody et al., 2016). Localization of EXECUTER proteins to grana margins (Wang et al., 2016b) further supports a potential role during PSII repair. Recently, Dogra et al. (2019) showed that the oxidation of a specific tryptophan residue (Trp643) in the singlet oxygen sensor domain contained in EX1 is essential for membrane localization and protein stability, and is also required for FtsH2-mediated EX1 degradation and further, as yet undefined, signaling to the nucleus (Dogra et al., 2019). Interestingly, EX1 is also involved in carbon/nitrogen partitioning during light acclimation (Überegeru et al., 2015), supporting a strong link between nutrient regulation and controlled chloroplast development (Fig. 2E).

Structural and functional membrane dynamics: recent focus on lipids in the regulation of membrane rearrangements

Although thylakoid membranes and etioplast internal membranes are both primarily composed of the galactolipids MGDG and DGDG, the lipid to lipid ratios (MGDG:DGDG) and lipid to protein ratios change with greening (Selstam and Sandelius, 1984). The role of lipid composition and content in plastid membrane structure has been studied extensively for several decades, but has recently returned to the spotlight with the publication of several studies involving disruption of galactolipid synthesis enzymes. Studies with mutants having slight decreases in galactolipid content and showing disrupted membranes in fully developed chloroplasts (Mazur et al., 2019) display limited or no structural disruptions in etioplasts (Jarvis et al., 2000), an effect attributable to the lower absolute requirement for lipids in etioplasts (Fujii et al., 2014, 2017). In recent work, etiolated plants with severe MGDG and DGDG deficits were shown to accumulate less photoactive Pchlide, LPOR, and carotenoids compared with respective wild types (Fujii et al., 2017, 2018). The decrease in photoactive Pchlide levels in a MGDG–deficient mutant observed under sugar-supplemented growth conditions (Fujii et al., 2017) contrasts with previous Pchlide increases seen in soil-grown mutants (Aronsson et al., 2008), again underlining the role of resource availability on plastid development. The decrease in DGDG content also resulted in significant structural PLB lattice perturbations, strong reduction of prothylakoid number, and retarded PLB disassembly in the light (Fujii et al., 2019). Furthermore, while MGDG– and DGDG–deficient plants showed impairment in accumulation of Chl and the light-harvesting complex II protein LHCB1 during greening, changes in photosynthesis-related gene transcript accumulation were, relatively, delayed (Fujii et al., 2019), suggesting that lipid status is sensed indirectly (e.g. via disrupted protein insertion or function).

While these studies suggest differences in the roles of MGDG and DGDG during etiolation and de-etiolation, it is difficult to make concrete conclusions, due to the different reduction of galactolipid contents in each mutant and the inter-relationship between the lipids (DGDG is a downstream product of MGDG). These issues argue for alternative systems, such as the in vitro system recently used to show the requirement for
MGDG and charged lipids in regulating LPOR complex formation and activity (Gabruk et al., 2017), and support a need for further biophysical studies that investigate the detailed distribution of lipid phases inside membranes (Garab et al., 2017; Ugby et al., 2019). In vivo time-resolved 3D techniques (e.g., Kowalewska et al., 2016), may be used to answer several open questions in the field, including how the PLB is formed and how and from where membrane components are recruited during the formation of grana stacks. On the latter topic, inner membrane-localized MGDG synthase has been suggested to be both a point of contact between thylakoids and the inner envelope membrane, and a supplier of lipids during thylakoid biogenesis (Rocha et al., 2018). We note that the nature of contact point(s), as being either direct or involving vesicles or tubules, remains debated (reviewed in Lindquist et al., 2016; Lindquist and Aronsson, 2018; Mechela et al., 2019). Notably, a recent 3D analysis of the proplastid-to-chloroplast transition (Liang et al., 2018) visualized direct connection points, which were proposed to both act as lipid transfer points and align growing thylakoids. Given that factors associated with these connections have been implicated in both thylakoid biogenesis and maintenance (e.g., Gao et al., 2006; Patil et al., 2018), understanding such connections is likely to bear importance throughout the lifetime of the plastids (Fig. 2F).

Etiolation studies and the future

New systems required and new lessons learned

To date, etiolation and de-etiolation work focused on the study of molecular processes has commonly been undertaken with dark-grown seedlings. The benefits of this system include that it (i) requires limited growth time and space yet provides sufficient material compared with other experimental systems such as the shoot apical meristem, and (ii) is highly customizable by use of different timing and lighting regimes and introduction of different substances to the growth medium (López-Juez et al., 2008; Mohammed et al., 2018; Dóczi et al., 2019). Nonetheless, there are limitations to this system, which should not be overlooked. These include the difficulties in separating plastid development (i.e. etioplast-to-chloroplast transition) from general seedling development programs, as well as issues associated with observing chloroplast development only in cotyledons, which are programmed differently from true leaves (reviewed in Pogson et al., 2015). Some limitations of the present system may be overcome by using other species and systems, although we stress that both etioplast formation and light-induced de-etiolation may largely differ depending on the species, timing, and conditions used (Skupieff et al., 2017), making cross-system comparisons difficult. For example, both runner bean (Phaseolus vulgaris) and pea (Pisum sativum) (Kowalewska et al., 2016) show similar skotomorphogenic growth to Arabidopsis, yet develop true leaves in darkness (Fig. 3). PLBs have also been observed in non-seedling systems, both in young leaves of tobacco following extended dark treatment (Armarego-Marriott et al., 2019) and in the innermost leaf primordia of the closed and opening leaf buds of trees (Solymosi and Böddi, 2006; Solymosi et al., 2006, 2012). The problem of uneven lighting that arises from gradual cotyledon opening or seed-coat shading (e.g., Solymosi et al., 2007) was recently overcome by using duckweed (Lemnula punctata), a flat-leafed aquatic monocot (Monselise et al., 2015). More artificially, cell cultures (Dubreuil et al., 2018), and even a callus-based system (Schaub et al., 2018), have been used to investigate various aspects of plastid development, and may putatively be adapted for de-etiolation. Nonetheless, these experimental systems come with their own caveats, in particular multiple impacts of carbon supplementation on plastid development (Eckstein et al., 2012; Häusler et al., 2014). Such systems may help to address issues related to spatial diversity of plastid types, seen previously within the shoot apical meristem (Charuvi et al., 2012), in chloroplasts in different leaf regions (Gügel and Soll, 2017), and in etioplasts within different tissues (Kósa et al., 2017) or even single cells (Solymosi et al., 2012).

Curiously, while the etiolated state is largely defined by both the presence of a paracrystalline PLB and the absence of (stacked) thylakoid membranes, early studies in cucumber (Cucumis sativus; Ikeda, 1970) and avocado (Persea americana; Cran and Possingham, 1973), and more recent findings in bean (Phaseolus vulgaris) (Schoefs and Franck, 2008), various tree species (Solymosi et al., 2006), and tobacco (Nicotiana tabacum) (Armarego-Marriott et al., 2019), demonstrate that both structures can co-exist in a single plastid. Indeed, several studies indicate that PLB reformation may occur in young chloroplasts during extended darkness, or even during normal night periods during de-etiolation (see Fig. 3; Rudowska et al., 2012; Skupieff et al., 2017; reviewed in Solymosi and Aronsson, 2013). These findings underscore the important influence of light regime, as well as light intensity, quality, and circadian-related effects (reviewed in Seluzicki et al., 2017) on greening, factors that must be considered when observing plastid development. We suggest PLB reformation as an interesting field for future study, and underline that the use of diverse systems may both further clarify current understandings of PLB formation and dissolution, and suggest new directions for future works.

Using etiolated systems and knowledge to go ‘beyond the darkness’

The benefits of the standard seedling etiolation and/or de-etiolation systems means that they have been used often in recent years to study diverse topics including gravitropism (Yamamoto et al., 2017), phototropism (Sullivan et al., 2019), resource limitation (Avin-Wittenberg et al., 2015; Kósa et al., 2015), and metabolite or hormone signaling (Gupta et al., 2015). Furthermore, etiolated growth can promote development of (i) certain tissue and organ types (e.g. adventitious roots; Sorin et al., 2005; da Costa et al., 2018; Trinh et al., 2018), (ii) certain growth types (e.g. growth by cellular expansion in hypocotyls; Sinclair et al., 2017; Ilías et al., 2019), and (iii) specific responses (e.g. ethylene ‘triple response’; Guzmán and Ecker, 1990; Ma et al., 2018) that cannot be easily observed in light-grown plants. Growth in darkness can also induce arrest of the shoot apical meristem, and thus de-etiolation can be used to observe shoot apical meristem development (López-Juez et al., 2008; Mohammed et al., 2018; Dóczi et al., 2019).
Beyond the practicality of the system itself, the greatest value of etiolation/de-etiolation studies lies in the central role of light signaling in plant life. Indeed, the overlap between factors involved in light responses with those involved in other response and growth processes has allowed basic knowledge from etiolation studies to be used to understand diverse plant processes (reviewed in Liu et al., 2017; Hsieh and Okamoto, 2014; Casal and Qüesta, 2018). In the applied sector, associations have been made between light receptors or responses and desirable crop attributes such as dwarfism (Hou et al., 2017), fruit or flower chloroplast development (Pankratov et al., 2016), and abiotic stress response (Zhou et al., 2018). Shade avoidance responses bear similarity to etiolation (Wang et al., 2016a), while ‘photobiotechnology’, in which modulated expression results in improved crop yield and resistance, has recently been proposed for improved food security (Ganesan et al., 2017). Clearly, future attempts to improve photosynthesis will require a detailed understanding of the chloroplast membrane structures and their biogenesis, as well as a thorough understanding of the processes involved in regulating the expression of photosynthesis-related genes (Ort et al., 2015). Taken together, while there is still much more to be learnt about de-etiolation itself, it is also clear that etiolation and de-etiolation systems provide the ideal environments to gain insight into the establishment of one of the most important processes for plant growth.

Acknowledgements

We thank Ralph Bock for his support in writing this paper. Transmission electron microscopy images were performed in the Laboratory of Electron Microscopy, Nencki Institute of Experimental Biology of PAS (Warsaw, Poland), using a JEM 1400 electron microscope (Jeol).

References

Achkar NP, Cho SK, Poulsen C, et al. 2018. A quick HYL1-dependent reactivation of microRNA production is required for a proper developmental response after extended periods of light deprivation. Developmental Cell 46, 236–247.e6.

Armarego-Marriott T, Kowalewska Ł, Burgos A, et al. 2019. Highly resolved systems biology to dissect the etioloplast-to-chloroplast transition in tobacco leaves. Plant Physiology 180, 654–681.

Aronsson H, Schöttler MA, Kelly AA, Sundqvist C, Dörmann P, Fujii S, Kobayashi K, Nagata N, Masuda T, Wada H. 2018. Monogalactosyldiacylglycerol deficiency in Arabidopsis affects pigment composition in the prolamellar body and impacts chloroplast differentiation. Plant & Cell Physiology 59, 1436–1449.

Avin-Wittenberg T, Bajdzienko K, Wittenberg G, Alseekh S, Tohge T, Vázquez-Márquez G, Dóczi R, Hatzimasoura E, Burgos A, Dóczi R, Hatzimasoura E, Burgos A. 2017. Sugar and light effects on the condensation of monogalactosyldiacylglycerol in Arabidopsis. Plant, Cell & Environment 40, 161–168.

Borgez F, Martienssen RA. 2015. The expanding world of small RNAs in plants. Nature Reviews. Molecular cell biology 16, 727–741.

Borges F, Martienssen RA. 2015. The expanding world of small RNAs in plants. Nature Reviews. Molecular cell biology 16, 727–741.

Charuvi D, Kiss V, Nevo R, Shimoni E, Adam Z, Reich Z, Chen S, Kim C, Lee JM, Lee HA, Fei Z, Wang L, Apel K. 2015. Blocking the Qb-binding site of photosystem II by fenazine acid, a non-host-specific toxin of Alternaria alternata, activates singlet oxygen-mediated and EXECUTER-dependent signalling in Arabidopsis. Plant, Cell & Environment 38, 1069–1080.

Cho SK, Ben Chaabane S, Shah P, Poulsen CP, Yang SW. 2014. COP1 E3 ligase protects HYL1 to retain microRNA biogenesis. Nature Communications 5, 5867.

Cran DG, Possingham JV. 1973. The fine structure of avocado plastids. Annals of Botany 37, 993–997.

da Costa CT, Gaeta ML, de Araujo Mariath JE, Offringa R, Fett-Neto AG. 2018. Comparative adventitious root development in pretreated and flooded Arabidopsis hypocotyls exposed to different auxins. Plant Physiology and Biochemistry 127, 161–168.

Dóczi R, Hatzimasoura E, Farahi Bloncet S, Ahmad Z, Díte, J., Lopez-Juez E, Palme K, Bögre L. 2019. The MKK7-MPK6 MAP kinase module is a regulator of meristem quiescence or active growth in Arabidopsis. Frontiers in Plant Science 10, 202.

Dogra V, Duan J, Lee KP, Lv S, Liu R, Kim C. 2017. FtsH2-dependent proteolysis of EXECUTER1 is essential in mediating singlet oxygen-triggered retrograde signaling in Arabidopsis thaliana. Frontiers in Plant Science 8, 1145.

Do P, Li M, Singh S, Li M, Kim C. 2019. Oxidative post-translational modification of EXECUTER1 is required for singlet oxygen sensing in plastids. Nature Communications 10, 2834.

Dubreuil C, Jin X, Barajas-López JD, et al. 2018. Establishment of photosynthesis through chloroplast development is controlled by two distinct regulatory phases. Plant Physiology 176, 1199–1214.

Eckstein A, Zieba P, Gabrys H. 2012. Sugar and light effects on the condition of the photosynthetic apparatus of Arabidopsis thaliana cultured in vitro. Journal of Plant Growth Regulation 31, 90–101.

Evans JR, Clarke VC. 2019. The nitrogen cost of photosynthesis. Journal of Experimental Botany 70, 7–15.

Fujii S, Kobayashi K, Nagata N, Masuda T, Wada H. 2017. Monogalactosyldiacylglycerol facilitates synthesis of photoactive protochlorophyllide in etioplasts. Plant Physiology 174, 1143–1157.

Fujii S, Kobayashi K, Nakamura Y, Wada H. 2014. Inducible knockdown of MONOGLACOSYLDIACYLGLYCEROL SYNTHASE1 reveals roles of galactolipids in organelle differentiation in Arabidopsis cotyledons. Plant Physiology 166, 1436–1440.

Ganesan M, Lee HY, Kim Ji, Song PS. 2017. Development of transgenic crops based on photo-biotechnology. Plant, Cell & Environment 40, 2469–2486.
Leister D. 2019. Piecing the puzzle together: the central role of reactive oxygen species and redox hubs in chloroplast retrograde signaling. Antioxidants & Redox Signaling 30, 1206–1219.

Li L, Nelson CJ, Trösch J, Castleden I, Huang S, Millar AH. 2017a. Protein degradation rate in Arabidopsis thaliana leaf growth and development. The Plant Cell 29, 207–228.

Li LX, Song Y, Wang K, Dong P, Zhang XY, Li FG, Li ZG, Ren MZ. 2015. TOR-inhibitor insensitive-1 (TRI1) regulates cotyledons greening in Arabidopsis. Frontiers in Plant Science 6, 861.

Li M, Hensel G, Mascher M, et al. 2019. Leaf variegation and impaired chloroplast development caused by a truncated CCT domain gene in abostris barley. The Plant Cell 31, 1430–1445.

Li X, Cai W, Liu Y, Li H,Fu L, Liu Z, Xu L, Liu H, Xu T, Xiong Y. 2017b. Differential TOR activation and cell proliferation in Arabidopsis root and shoot apexes. Proceedings of the National Academy of Sciences, USA 114, 2765–2770.

Li Y, Varala K, Hudson ME. 2014. A survey of the small RNA population during far-red light-induced apical hook opening. Frontiers in Plant Science 5, 156.

Liang Z, Zhu N, Mai KK, Liu Z, Tzeng D, Osteryoung KW, Zhong S, Staehelin LA, Kang BH. 2018. Thylakoid-bound polysomes and a dynamin-related protein, FZL, mediate critical stages of the linear chloroplast biogenesis program in greening Arabidopsis cotyledons. The Plant Cell 30, 1476–1495.

Lin MC, Tsai HL, Lim SL, Jeng ST, Wu SH. 2017. Unraveling multifaceted contributions of small regulatory RNAs to photomorphogenic development in Arabidopsis. BMC Genomics 18, 859.

Lindquist E, Aronsson H. 2018. Chloroplast vesicle transport. Photosynthesis Research 138, 361–371.

Lindquist E, Solymosi K, Aronsson H. 2016. Vesicles are persistent features of different plastids. Traffic 17, 1125–1138.

Liu MJ, Wu SH, Chen HM, Wu SH. 2012. Widespread translational control contributes to the regulation of Arabidopsis photomorphogenesis. Molecular Systems Biology 8, 666.

Liu MJ, Wu SH, Wu JF, Lin WD, Wu YC, Tsai TY, Tsai HL, Wu SH. 2013. Translational landscape of photomorphogenic Arabidopsis. The Plant Cell 25, 3699–3710.

Liu QX, Li Y, Zhong SW. 2017. Interplay between light and plant hormones in the control of Arabidopsis seedling chlorophyll biosynthesis. Frontiers in Plant Science 8, 1433.

López-Juez E, Dillon E, Magyar Z, Khan S, Hazeldine S, de Jager SM, Murray JA, Bemster GT, Bögre L, Shanahan H. 2008. Distinct light-initiated gene expression and cell cycle programs in the shoot apex and cotyledons of Arabidopsis. The Plant Cell 20, 947–968.

Ma B, Zhou Y, Chen H, et al. 2018. Membrane protein MHZ3 stabilizes OsElN2 in rice by interacting with its Nram-like domain. Proceedings of the National Academy of Sciences, USA 115, 2520–2525.

Ma L, Li J, Qu L, Hager J, Chen Z, Zhao H, Deng XW. 2001. Light control of Arabidopsis development entails coordinated regulation of genome expression and cellular pathways. The Plant Cell 13, 2589–2607.

Maldonado-Bonilla LD. 2014. Composition and function of P bodies in Arabidopsis thaliana. Frontiers in Plant Science 5, 201.

Manavella PA, Yang SW, Palatnik J. 2019. Keep calm and carry on: mRNA biogenesis under stress. The Plant Journal 99, 832–843.

Matthews S. 2006. Phytochrome-mediated development in land plants: red light sensing evolves to meet the challenges of changing light environments. Molecular Ecology 15, 3483–3503.

Mazur R, Mostowska A, Szach J, Gieczewska LR, Wójcikowicz J, Bednarska K, Garstka M, Kowalewska L. 2019. Galactolipid deficiency disturbs spatial arrangement of the thylakoid network in Arabidopsis thaliana plants. Journal of Experimental Botany 70, 4689–4704.

Mechela A, Schwenkert S, Soll J. 2019. A brief history of thylakoid biogenesis. Open Biology 9, 180237.

Mochizuki N, Suske R, Chory J. 1996. An intracellular signal transduction pathway between the chloroplast and nucleus is involved in de-etiolation. Plant Physiology 112, 1465–1469.
Mohammed B, Biloei SF, Dóczi R, Grove E, Raison S, Palme K, Dítengou FA, Bögre L, López-Juez E. 2018. Converging light, energy and hormonal signaling control meristem activity, leaf initiation, and growth. Plant Physiology 176, 1365–1381.

Monselise EB, Levkovitz A, Kost D. 2015. Ultraviolet radiation induces stress in etiolated Landoltia punctata, as evidenced by the presence of alamine, a universal stress signal: a 11NMR study. Plant Biology 17 (Suppl 1), 101–107.

Muramoto T, Kohchi T, Yokota A, Hwang I, Goodman HM. 1999. The Arabidopsis photomorphogenic mutant hyt is deficient in phytocrome chromophore biosynthesis as a result of a mutation in a plastid heme oxygenase. The Plant Cell 11, 335–348.

Ning DL, Liu KH, Liu CC, Liu JW, Qian CR, Yu Y, Wang YF, Wang YC, Wang BC. 2016. Large-scale comparative phosphoprotein analysis of maize seedling leaves during greening. PLoS ONE 11, 501–517.

Ort DR, Merchant SS, Alric J, et al. 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. Proceedings of the National Academy of Sciences, USA 112, 8520–8536.

Page MT, McCormac AC, Smith AG, Terry MJ. 2017. Singlet oxygen initiates a plastid signal controlling photosynthetic gene expression. New Phytologist 213, 1168–1180.

Pankratov I, McQuinn R, Schwartz J, Bar E, Fei Z, Lewinsohn E, Zamir D, Giovannoni JN, Hirschberg J. 2016. Fruit carotenoid-deficient mutants in tomato reveal a function of the plastididopentylphosphate isomerase (IDI1) in carotenoid biosynthesis. The Plant Journal 88, 82–94.

Patil M, Seifert S, Seiler F, Soli J, Schwenkert S. 2018. EZL is primarily localized to the inner chloroplast membrane however influences thylakoid maintenance. Plant Molecular Biology 97, 421–435.

Peng YL, Zou T, Li LM, Tang SW, Li Q, Zhang J, Chen YJ, Wang XC, Yang GT, Hu YG. 2019. Map-based cloning and functional analysis of YET1 in rice, which is involved in light-dependent chlorophyll biogenesis and photoperiodic flowering pathway. International Journal of Molecular Sciences 20, E758.

Pesaresi P, Kim C. 2019. Current understanding of GUN1: a key mediator involved in biogenic retrograde signalling. Plant Cell Reports 38, 819–823.

Pham VN, Kathare PK, Huq E. 2018. Phytochromes and phytochrome interacting factors. Plant Physiology 176, 1025–1038.

Podolec R, Urm L. 2018. Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Current Opinion in Plant Biology 45, 18–25.

Pogson B, Ganguly D, Abrech-Borth V. 2015. Insights into chloroplast biogenesis and development. Biochimica et Biophysica Acta 1847, 1017–1024.

Pomeranc MZ, Hah C, Lin PC, Kang SG, Finer JJ, Blackshear PJ, Jang JC. 2018. Regulation of light-dependent pathways by non-coding RNAs. Sánchez-Retuerta C, Suaréz-López P, Henriques R. 2017. Establishing of an Arabidopsis callus system to study the interactions of bioregulation, degradation and accumulation of carotenoids. PLoS ONE 13, e0192158.

Schmied J, Hou Z, Hedtke B, Grimm B. 2018. Controlled partitioning of glutamyl-tRNA reductase in stroma- and membrane-associated fractions affects the synthesis of 5-aminolevulenic acid. Plant & Cell Physiology 59, 2204–2213.

Schoefs B, Franck F. 2008. The photoenzymatic cycle of NADPH: protochlorophyllide oxidoreductase in primary bean leaves (Phaseolus vulgaris) during the first days of photoperiodic growth. Photosynthesis Research 96, 15–26.

Selstam E, Sandelius AS. 1984. A comparison between prolamellar bodies and prothylakoid membranes of etioplasts of dark-grown wheat concerning lipid and polypeptide composition. Plant Physiology 76, 1036–1040.

Seluzicki A, Burko Y, Chory J. 2017. Dancing in the dark: darkness as a signal in plants. Plant, Cell & Environment 40, 2487–2501.

Semenova GA, Fomina IR, Kosobryukhov AA, Lyubimov YV, Nadezhkina ES, Balakhnina TI. 2017. Mesophyll cell ultrastructure of wheat leaves etiolated by lead and selenium. Journal of Plant Physiology 219, 37–44.

Shen Z, Li P, Ni RJ, et al. 2009. Label-free quantitative proteomics analysis of etiolated maize seedling leaves during greening. Molecular & Cellular Proteomics 8, 2443–2460.

Shevda D, Ananyev G, Vatland AK, Arnold J, Mamedov F, Eichacker LA, Dismukes GC, Messinger J. 2019. ‘Birth defects’ of photosystem II make it highly susceptible to photodamage during chloroplast biogenesis. Physiology Plantarum 166, 165–180.

Sinclair SA, Larue C, Bonk L, et al. 2017. Etiolated seedling development requires repression of photophoresisogenesis by a small cell-wall-derived dark signal. Current Biology 27, 3403–3418.e7.

Singh A, Gautam V, Singh S, Sarkar Das S, Verma S, Mishra V, Mukherjee S, Sarkar AK. 2018. Plant small RNAs: advancement in the understanding of biogenesis and role in plant development. Planta 248, 545–558.

Skupień J, Wójtowicz J, Kowalewska Ł, Mazur R, Garstka M, Gieczewska K, Mostowska A. 2017. Dark-chilling induces substantial structural changes and modifies galactolipid and carotenoid composition during chloroplast biogenesis in cucumber (Cucumis sativus L.) cotyledons. Plant Physiology and Biochemistry 111, 107–118.

Solymosi K, Aronsson H. 2013. Etioplasts and their significance in chloroplast biogenesis. In: Biwaa B, Krupinska K, Biwaa UC, eds. Plastid development in leaves during growth and senescence. Berlin, Heidelberg: Springer, 39–71.

Solymosi K, Böddi B. 2006. Optical properties of bud scales and protochlorophyllide forms in leaf primordia of closed and opened buds. Tree Physiology 26, 1075–1085.

Solymosi K, Bóka B, Böddi B. 2006. Transient etiolation: protochlorophyllide and chlorophyll forms in differentiating plasids of closed and breaking leaf buds of horse chestnut (Aesculus hippocastanum). Tree Physiology 26, 1087–1096.

Solymosi K, Morandi D, Bóka B, Böddi B, Schoefs B. 2012. High biochemical variability of plasids, photosynthetic pigments and pigment forms of leaf primordia in buds. Planta 233, 1035–1043.

Solymosi K, Vitáni B, Hideg E, Böddi B. 2007. Etiolation symptoms in sunflower (Helianthus annuus) cotyledons partially covered by the pericarp of the achene. Annals of Botany 99, 857–867.

Sorin C, Bussell JD, Camus I, et al. 2005. Auxin and light control of adventitious rooting in Arabidopsis require ARGONAUTE1. The Plant Cell 17, 1343–1359.

Sullivan S, Kharkhiing E, Laird J, Sakai T, Christie JM. 2019. Deetiolation enhances phototropism by modulating NON- PHOTOTROPIC HYPOCOTYL3 phosphorylation status. Plant Physiology 180, 1119–1131.

Sun L, Yu Y, Hu W, Min Q, Kang H, Li Y, Hong Y, Wang X, Hong Y. 2016. Ribosomal protein S6 kinase1 coordinates with TOR-Raptor2 to regulate thylakoid membrane biosynthesis in rice. Biochimica et Biophysica Acta 1861, 639–649.

Sun YY, Zhu SC, Yang X, Weston MV, Wang K, Shen ZQ, Xu HW, Chen LS. 2018a. Nitrogen diagnosis based on dynamic characteristics of leaves and prothylakoid membranes of etioplasts of dark-grown wheat concerning lipid and polypeptide composition. Plant Physiology 176, 1036–1040.

Sulaiman H, Harishree T, Khandil K, Sakai T, Christie JM. 2019. Deetiolation enhances phototropism by modulating NON- PHOTOTROPIC HYPOCOTYL3 phosphorylation status. Plant Physiology 180, 1119–1131.

Sun ZF, Li M, Zhou Y, Guo TT, Liu Y, Zhang H, Fang YD. 2018b. Coordinated regulation of Arabidopsis microRNA biogenesis and red light signaling through Dicer-like 1 and phytochrome-interacting factor 4. PLoS Genetics 14.
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Susek RE, Ausubel FM, Chory J. 1993. Signal transduction mutants of Arabidopsis uncouple nuclear CAB and RBCS gene expression from chloroplast development. Cell 74, 787–799.

Trinh HK, Verstraten I, Geelen D. 2018. In vitro assay for induction of adventitious rooting on intact Arabidopsis hypocotyls. Methods in Molecular Biology 1761, 95–102.

Tsai HL, Li YH, Hsieh WP, Lin MC, Ahn JH, Wu SH. 2014. HUA ENHANCER1 is involved in posttranscriptional regulation of positive and negative regulators in Arabidopsis photomorphogenesis. The Plant Cell 26, 2858–2872.

Uberegui E, Hall M, Lorenzo O, Schröder WP, Balsera M. 2015. An Arabidopsis soluble chloroplast proteomic analysis reveals the participation of the Executer pathway in response to increased light conditions. Journal of Experimental Botany 66, 2067–2077.

Ugly B, Karlický V, Dlouhý O, Javorník U, Materová Z, Zsiros O, Šket P, Plavec J, Špunda V, Garab G. 2019. Lipid-polymorphism of plant thylakoid membranes. Enhanced non-bilayer lipid phases associated with increased membrane permeability. Physiologia Plantarum 166, 278–287.

Vitányi B, Kósa A, Solymos K, Bóddi B. 2013. Etioplasts with protochlorophyll and protochlorophyllide forms in the under-soil epicotyl segments of pea (Pisum sativum) seedlings grown under natural light conditions. Physiologia Plantarum 148, 307–315.

Wang H, Wu GX, Zhao BB, Wang BB, Lang ZH, Zhang CY, Wang HY. 2016a. Regulatory modules controlling early shade avoidance response in maize seedlings. BMC Genomics 17, 269.

Wang L, Apel K. 2019. Dose-dependent effects of O2 in chloroplasts are determined by its timing and localization of production. Journal of Experimental Botany 70, 29–40.

Wang L, Kim C, Xu X, Piskurewicz U, Dogra V, Singh S, Maher H, Apel K. 2016b. Singlet oxygen- and EXECUTER1-mediated signaling is initiated in grana margins and depends on the protease FtsH2. Proceedings of the National Academy of Sciences, USA 113, E3792–E3800.

Wu GZ, Chalvin C, Hoelscher M, Meyer EH, Wu XN, Bock R. 2018. Control of retrograde signaling by rapid turnover of GENOMES UNCOUPLED1. Plant Physiology 176, 2472–2495.

Wu GZ, Meyer EH, Richter AS, et al. 2019. Control of retrograde signaling by protein import and cytosolic folding stress. Nature Plants 5, 525–538.

Xiong F, Zhang R, Meng Z, Deng K, Que Y, Zhuo F, Feng L, Guo S, Datla R, Ren M. 2017. Brassinosteroid Insensitive 2 (BIN2) acts as a downstream effector of the Target of Rapamycin (TOR) signaling pathway to regulate photoautotrophic growth in Arabidopsis. New Phytologist 213, 233–249.

Xiong Y, Sheen J. 2014. The role of target of rapamycin signaling networks in plant growth and metabolism. Plant Physiology 164, 499–512.

Xu J, Bräutigam A, Weber AP, Zhu XG. 2016. Systems analysis of cis-regulatory motifs in C4 photosynthesis genes using maize and rice leaf transcriptomic data during a process of de-etiolation. Journal of Experimental Botany 67, 5105–5117.

Xu J, Chua NH. 2009. Arabidopsis decapping 5 is required for mRNA decapping, P-body formation, and translational repression during postembryonic development. The Plant Cell 21, 3270–3279.

Xu J, Chua NH. 2011. Processing bodies and plant development. Current Opinion in Plant Biology 14, 88–93.

Xu J, Li Y, Wang Y, Liu X, Zhu XG. 2017. Altered expression profiles of microRNA families during de-etiolation of maize and rice leaves. BMC Research Notes 10, 108.

Yamamoto KT, Watahiki MK, Matsuzaki J, Satoh S, Shimizu H. 2017. Space-time analysis of gravitropism in etiolated Arabidopsis hypocotyls using bioluminescence imaging of the IAA19 promoter fusion with a destabilized luciferase reporter. Journal of Plant Research 130, 765–777.

Zavafer A, Cheah MH, Hillier W, Chow WS, Takahashi S. 2015. Photodamage to the oxygen evolving complex of photosystem II by visible light. Scientific Reports 5, 16363.

Zhang H, He H, Wang X, Wang X, Yang X, Li L, Deng XW. 2011. Genome-wide mapping of the HY5-mediated gene networks in Arabidopsis that involve both transcriptional and post-transcriptional regulation. The Plant Journal 65, 346–358.

Zhang Y, Zhang Y, McFarlane HE, Obata T, Richter AS, Lohse M, Grimm B, Persson S, Fernie AR, Giavalisco P. 2018. Inhibition of TOR represses nutrient consumption, which improves greening after extended periods of etiolation. Plant Physiology 178, 101–117.

Zhang Z, Zhu JY, Roh J, Marchive C, Kim SK, Meyer C, Sun Y, Wang W, Wang ZY. 2016. TOR signaling promotes accumulation of BZR1 to balance growth with carbon availability in Arabidopsis. Current Biology 26, 1854–1860.

Zhang ZW, Zhang GC, Zhu F, Zhang DW, Yuan S. 2015. The roles of tetrapyrroles in plastid retrograde signaling and tolerance to environmental stresses. Planta 242, 1263–1276.

Zhou T, Meng L, Ma Y, Liu Q, Zhang Y, Yang Z, Yang D, Bian M. 2018. Overexpression of sweet sorghum cryptochrome 1a confers hypersensitivity to blue light, abscisic acid and salinity in Arabidopsis. Plant Cell Reports 37, 251–264.