UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
PROGRAMA DE PÓS-GRADUAÇÃO EM
GENÉTICA E BIOLOGIA MOLECULAR

Estudo dos mecanismos de sinalização fotomorfogênica envolvendo a comunicação entre parte aérea e raízes em *Arabidopsis thaliana*

Study of shoot-to-root communication of photomorphogenic signaling in *Arabidopsis thaliana*

Autora: Cássia Fernanda Stafen

- Tese submetida ao Programa de Pós-Graduação em Genética e Biologia Molecular da Universidade Federal do Rio Grande do Sul como requisito parcial para a obtenção do grau de Doutor em Ciências -

Orientador: Prof. Dr. Felipe dos Santos Maraschin

Porto Alegre, setembro de 2022

"*Foi o tempo que dedicastes à tua rosa que a fez tão importante*" (Antoine de Saint-Exupéry)

- Sumário -

- Instituições e fontes financiadoras -

Esta tese de doutorado foi realizada no Laboratório de Fisiologia Vegetal do Departamento de Botânica do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil. O presente trabalho foi realizado com apoio da Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (Fapergs) e da CAPES, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil, no âmbito do Programa Pesquisador Visitante Especial (PVE) - 3º Cronograma de 2014 e com bolsa de Doutorado concedida à aluna.

- Agradecimentos -

Essa é a hora em que faltam palavras para agradacer... Gostaria de primeiramente agradecer meu orientador, Felipe, pela oportunidade e por todo o empenho, paciência e dedicação que depositou na minha pesquisa e em mim. Pelas incansáveis orientações e pela inigualável prestatividade, tu és um exemplo a ser seguido. Muito obrigada!

Ao presente do doutorado para a minha vida, Kelen de "*Homematte*" a uma amiga e irmã de coração. Minha querida colega, amiga e vizinha Cibele, de conselhos estatísticos, jardinagem e até empréstimos de bicicletas, rsrsrs, obrigada.

Tenho muito a agradecer também, aos meus colegas e amigos do laboratório, vocês têm uma participação especial nesse trabalho, sentirei muita saudade de todos. Agradecer em especial aos Maraschetxs e nossas reuniões maravilhosas. A Yohanna que me guiou nos meus primeiros passos durante o doutorado, aprendi muito com ela e sou eternamente grata. Ao Joninhas, e seu suporte como colega de profissão, amigo e conselheiro de mercado (melhores bolachas). Aos professores Arthur, Janete, Felipe R. e Márcia por serem exemplos profissionais e pessoais.

Aos meus pais, por sempre me apoiarem nas decisões que tomei, por acreditarem fielmente em mim, por serem meu porto seguro e meu abraço quentinho, amo vocês! À minha mãe, por ser o meu amor da vida todinha.

A todas as amizades que o doutorado me proporcionou, foram 4 lindos anos de experiências, crescimento profissional e pessoal. Por que, nada nessa vida acontece por acaso, tudo nela são escolhas e eu escolheria mil vezes vocês. Obrigada! **S2**

- Lista de abreviaturas -

ABA: do inglês, *abscisic acid*

ABFs: do inglês, *fatores bZIP responsivos a ABA*

ABRE*:* do inglês, *fator de ligação responsivo a ABA*

ABI5: do inglês, *abscisic acid 5*

AIA/IAA: *ácido indol-3-acético, do inglês, indole-3-acetic acid*

bHLH: do inglês, *basic helix-loop-helix*

bZIP: do inglês, *basic leucine-zipper*

cDNA: DNA complementar

Col-0: Columbia-0

COP1: do inglês, *constitutive photomorphogenic1*

cry1: do inglês, *cryptochrome 1*

CRYs: do inglês, *cryptochromes*

DNA: ácido desoxirribonucleico

D-root: do inglês, *dark-grown root*

FHY3: do inglês, *hypocotyl far-red elongated 3*

GFP: do inglês, *green fluorescent protein*

GO: do inglês, *gene ontology*

GUS: do inglês, *β-glucuronidase*

HFR1: do inglês, *long hypocotyl in far-red 1*

HY5: do inglês, *elongated hypocotyl 5*

HYH: do inglês, *HY5-homolog*

LB: meio de cultivo Luria Bertani

LD: do inglês, *light-protect roots*

LR: do inglês, *lateral root*

PIF: do inglês, *phytochrome interacting factors*

PHOT: do inglês, *phototropin*

PP2C: do inglês, *constitutive protein 2C phosphatase*

PP6: do inglês, *protein 6 phosphatase*

PYL1: do inglês, *pyrabactin-like resistance receptor 1*

RNA: ácido ribonucleico

ROS: do inglês, *reactive oxygen species*

RT-qPCR: do inglês, *reverse transcription - quantitative polymerase chain reaction*

SE: do inglês, *standard error*

SnRK2: do inglês, *non-fermenting sugar protein kinase 2*

SPA: do inglês, *supressor of phyA-105*

T-DNA: do inglês, *transferred*-DNA

UVR8: do inglês, *UV-B resistance 8*

WT: do inglês, *wild-type*

- Resumo -

A luz fornece uma entrada para o processo de fotossíntese e influencia diretamente o crescimento e desenvolvimento das plantas. O crescimento das raízes, em condições naturais, ocorre abaixo do solo na ausência de luz. Análises prévias demostram que, embora as raízes cresçam abaixo do solo na escuridão, a iluminação da parte aérea é essencial para que as raízes se desenvolvam normalmente. Plântulas de *Arabidopsis* cultivadas sob luz apresentam padrão de desenvolvimento fotomorfogênico, apresentando hipocótilo curto e raízes longas. As respostas transcricionais iniciais à luz que estimulam a comunicação entre a parte aérea e a raiz ainda não estão completamente esclarecidas. A correta regulação da expressão gênica é um dos mecanismos que possibilitam respostas nas plantas. Esta tese teve como objetivo o estudo dos mecanismos de sinalização fotomorfogênica envolvendo a comunicação entre parte aérea e raízes em *Arabidopsis thaliana*. Os apontamentos relatados nos capítulos II à IV mostram que à luz desempenha um papel chave no desenvolvimento da planta e na comunicação entre parte aérea e raiz. A presença de luz na parte aérea leva a alterações significativas no transcriptoma de plântulas, promovendo a montagem da maquinaria fotossintética, sinalização e respostas redox. Utilizando mutantes de perda de função, identificamos que a regulação da transcrição da resposta à luz precoce pode estar envolvida com o fator de transcrição ABA-Insensível 5 (ABI5) juntamente com os fatores bZIP responsivos a ABA (ABFs). Propomos que esta expressão gênica inicial reaproveita a transcrição de fatores bZIP ligados ao ABA, expressos na escuridão, para ativar respostas fotomorfogênicas.

- Abstract -

Light provides an input to the process of photosynthesis and directly influences the growth and development of plants. Root growth, under natural conditions, occurs below ground in the absence of light. Previous analyzes show that, although roots grow underground in the dark, shoot illumination is essential for roots to develop normally. *Arabidopsis* seedlings grown under light show a photomorphogenic pattern of development, with a short hypocotyl and long roots. The initial transcriptional responses to light that stimulate communication between the shoot and the root are not completely understood. The correct regulation of gene expression is one of the mechanisms that enable responses in plants. The work presented in this thesis aimed to study the photomorphogenic signaling mechanisms involving the communication between shoots and roots in *Arabidopsis thaliana*. The appointments presented in Chapters II to IV show that light plays a key role in plant development and in communication between shoots and roots. The presence of light in the shoot leads to significant changes in the transcriptome of seedlings, promoting the assembly of photosynthetic machinery, signaling and redox responses. Using loss-of-function mutants, we identified that transcriptional regulation of the early light response may be involved with the ABA-Insensitive transcription factor 5 (ABI5) along with the ABA-responsive bZIP factors (ABFs). We propose that this initial gene expression reuses the transcription of ABA-linked bZIP factors, expressed in the dark, to activate photomorphogenic responses.

Capítulo I

- Introdução -

1. Morfogênese Vegetal

As plantas desenvolveram várias estratégias e mecanismos para perceber as mudanças nas condições ambientais e adaptar-se a elas. Respostas rápidas, em âmbito arquitetônico e morfológico, são desencadeadas quando as plantas são expostas a luz ou escuridão. Durante a germinação, no escuro, as plântulas apresentam um padrão de desenvolvimento estiolado ou escotomorfogênico, guardando reservas de energia contidas nas sementes para o alongamento do hipocótilo em contrapartida ao desenvolvimento dos cotilédones e do sistema radicular. As dicotiledôneas como a *Arabidopsis thaliana*, alongam os hipocótilos, os cotilédones permanecem fechados, há a formação do gancho plumular (este facilita a passagem pela barreira do solo e protege o meristema apical e cotilédones), e a etapa de esverdeamento das folhas iniciada, todo esse processo é denominado fotomorfogênese (Figura 1). À medida que essas plantas vão se desenvolvendo, emergindo do solo e o hipocótilo é exposto à luz, alterações fotomorfogênicas ocorrem, como a parada do alongamento do hipocótilo, abertura dos cotilédones e esverdeamento das folhas. Essas características contribuem para o crescimento, desenvolvimento das plântulas jovens e o início do processo fotossintético (Lee et al. 2017a).

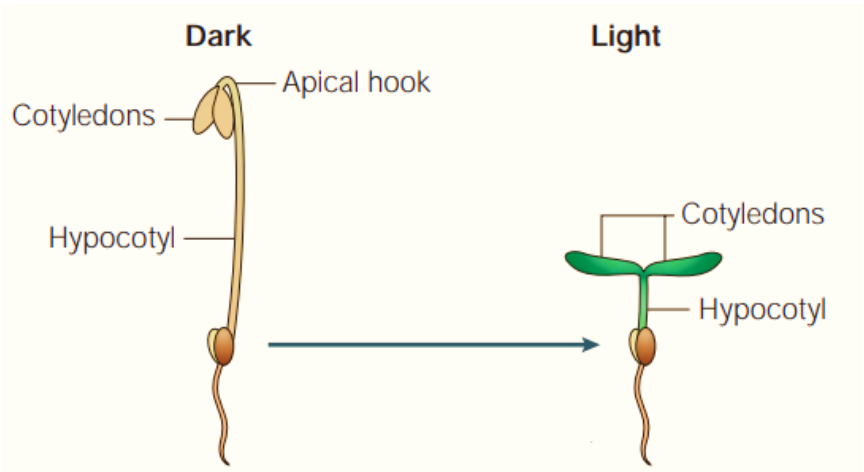


Figura 1. O efeito da luz em plântulas de *Arabidopsis thaliana* – Escotomorfogênese x Fotomorfogênese (Modificado de Mallappa et al. 2008).

O desencadeamento das respostas fotomorfogênicas depende da ativação de fotorreceptores específicos nas plantas. Sabe-se que as plantas captam a luz em diferentes comprimentos de onda, e estes ativam fotorreceptores específicos capazes de detectar com eficiência comprimentos de onda das faixas do vermelho, vermelho distante, azul e UV. Os fitocromos (PHYs) detectam luz vernmelha (R) e vermelha distante (FR), a luz causa mudanças conformacionais nos mesmos e estes passam a interagir com outras proteínas. Os criptocromos (CRYs), as fototropinas (PHOTs) e as proteínas ZEITLUPE detectam UV-A e luz azul, e estão associados com os processos de alongamento do hipocótilo, fototropismo e floração, respectivamente. Já o fotorreceptor de UV UVR8 também está presente nas plantas, sendo específico para UV-B e dando início a respostas fotomorfogênicas UV-B clássicas, como a indução da biossíntese de flavonóides e supressão do crescimento de hipocótilo. Os fotorreceptores estão em maior quantidade na parte aérea e também exercem função nas raízes (Lee et al. 2017; van Gelderen et al. 2018; Sanchez et al. 2020).

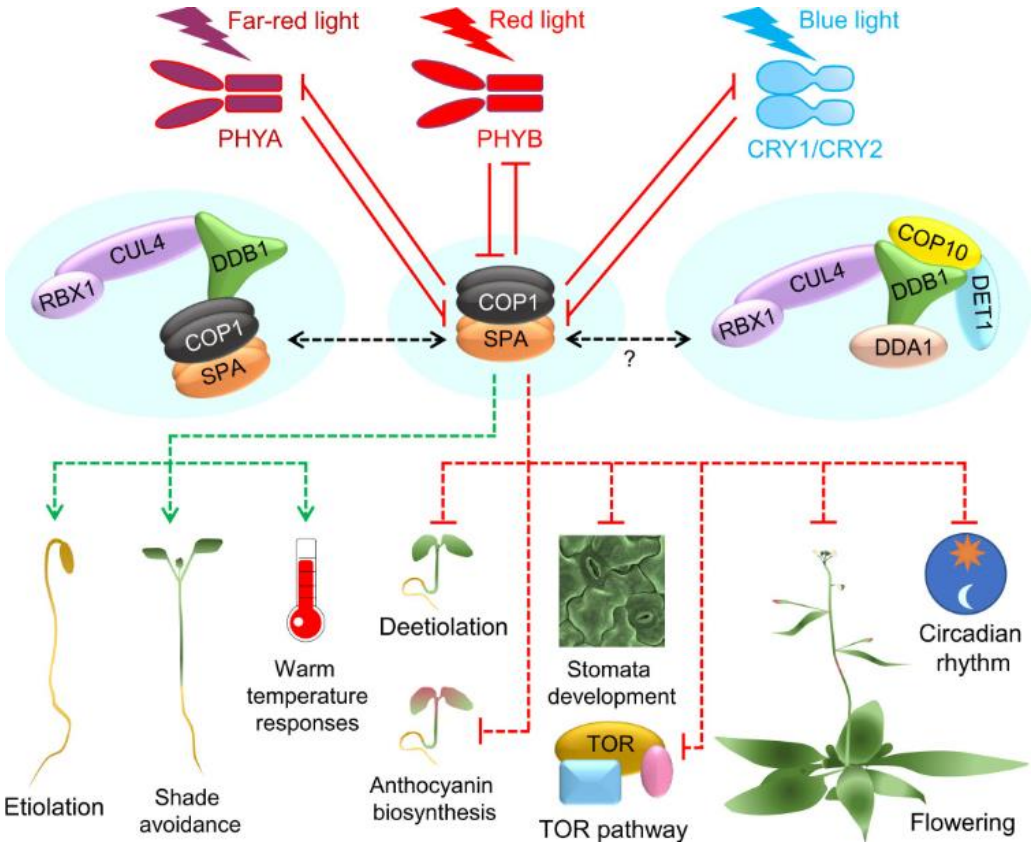


Figura 2. Ações e mecanismos pelos quais os fotorreceptores interagem e desencadeiam processos fisiológicos na planta (Figura retirada do paper Ponnu and Hoecker 2021).

2. Transdução da sinalização luminosa da parte aérea para as raízes

O desenvolvimento das raízes ocorre abaixo do solo com pouco acesso à iluminação direta. Entretanto, o drástico efeito da iluminação das folhas sobre o crescimento das raízes sugere que sinais à jusante da luz são enviados às raízes para promover seu crescimento.

São conhecidas três rotas dessa transdução de sinal na fotomorfogênese radicular: A primeira seria a transmissão de mensageiros de sinalização móvel para as raízes. Várias moléculas e metabólitos como fitohormônios, sacarose, RNAs e proteínas, são produzidas na parte aérea e translocadas para as raízes em resposta à luz e ativam respostas fotomorfogênicas tais como, crescimento da raiz primária, formação de nódulos radiculares e emergência das raízes laterais (revisado por Lee et al. 2017). A segunda seria pela percepção direta da luz pelas raízes, uma vez que essa luz pode penetrar no solo em condições ambientais normais. A passagem da luz pelo sistema caulinar do corpo da planta para as raízes seria a terceira proposta, este efeito conhecido como "*light piping*" ocorre quando a luz acima do solo é conduzida através do sistema vascular para as raízes em curtas distâncias. Este efeito foi sugerido como responsável por ativar a resposta gravitrópica de raízes laterais em um mecanismo dependente de phyB e HY5 (Lee et al. 2016; Lee et al. 2017; Lacek et al. 2021).

Apesar de muitas moléculas serem transportadas da parte aérea para a raiz, somente algumas foram relacionados à sinalização sistêmica do desenvolvimento de raízes, dentre os quais se destacam os açúcares derivados da fotossíntese (como a sacarose) e transportados através do floema, hormônios vegetais (auxina, ácido giberélico) e o fator de transcrição ELONGATED HYPOCOTYL 5 (HY5) (van Gelderen et al. 2018b).

3. Genes envolvidos na sinalização por luz

Independentemente de seu mecanismo de percepção, a luz desencadeia mudanças conformacionais nas proteínas fotorreceptoras, levando a eventos de sinalização a jusante. A partir da identificação de mutantes de resposta à luz em triagens mutagênicas destinadas a identificar fenótipos estiolados em plantas, os mutantes *hy* (hipocótilo longo) auxiliaram na caracterização de genes codificadores de reguladores positivos da fotomorfogênese, como fitocromos, criptocromos e o fator de transcrição HY5 (Möglich et al. 2010).

Os fotorreceptores ativados pela luz foram descritos como ativadores das respostas fotomorfogênicas tanto de forma sinérgica quanto antagônica (Jiao et al. 2007a), com componentes de sinalização a jusante convergindo para dois hubs principais compostos por CONSTITUTIVE PHOTOMORPHOGENIC/DE-ETIOLATED (COP1) (Deng and Quail 1992; Podolec and Ulm 2018) e PHYTOCHROME-INTERACTING FACTORS (PIFs) (Ni et al. 1998; Pham et al. 2018). Fenótipos mutantes e análises moleculares indicaram que fotorreceptores e fatores de transcrição atuam como reguladores fotomorfogênicos positivos com sua estabilidade e/ou atividade regulada por um conjunto de repressores fotomorfogênicos, compreendendo genes repressor CONSTITUTIVE PHOTOMORPHOGENIC/DE-ETIOLATED / FUSCA (COP/DET/FUS) (Chamovitz et al. 1996) e PIFs (Hellmann and Estelle 2002; Xu et al., 2015).

Os *loci* COP/DET/FUS estão associados a três complexos proteicos distintos: o COP1-SPA, as ligases COP10-DET1-DDB1 (CDD) Ubiquitina E3 e o sinalossoma CSN/COP9 (Lau and Deng 2012). Todas as fortes mutações cop/det/fus levam à letalidade das plântulas logo após a germinação, indicando que esses módulos são centrais para o desenvolvimento da planta (Kwok et al. 1996).

A caracterização molecular de DET1 mostrou que ele interage com COP10 e uma ligase CUL4-DDB1 Ub-E3 (conhecida como CUL4-CDD1) (Lau and Deng 2012). O complexo CUL4-CDD1 mostrou aumentar a atividade de ubiquitinação de outras ligases E3. Ele pode ter seus próprios alvos de ubiquitinação diretos (Lau and Deng 2012). Uma das atividades mais diretas do DET1 no controle da fotomorfogênese é a estabilização de proteínas PIF no escuro por meio de interação direta (Dong et al. 2014). Curiosamente, esta estabilização não envolve degradação proteassomal de PIFs, sugerindo que DET1 atua por uma via diferente. Isso coloca o DET1 como um repressor direto da fotomorfogênese tanto quanto um promotor de crescimento estiolado. O DET1 também pode interagir e reprimir a atividade de fatores de transcrição associados ao relógio circadiano (Lau et al. 2011), bem como estabilizar proteínas reguladoras do relógio inibindo sua ubiquitinação (Park et al. 2010).

Recentemente, foi identificado que DET1 interage com COP1 e promove sua degradação e atividade. O DET1 também favorece a interação COP1-HY5, de forma independente da luz, evitando a hiperacumulação de HY5 (Cañibano et al. 2021).

Desenvolvemos alguns experimentos com mutantes de fitocromos (*phyA, phyB, phyC, phyD, phyE*) e criptocromos (*cry1* e *cry2*) crescidos sob diferentes fontes de açúcar (glicose e sacarose) no meio e em condições de luz branca constantes, afim de investigar o comportamento destes mutantes (Anexo 1 A-D). Mutantes para *phyB* apresentaram maior comprimento de hipocótilo e raiz em todos os tratamentos e o oposto ocorreu com os mutantes *cry1* (Anexo 1 C). Esses resultados indicam que a ativação de fotorreceptores (fitocromos e criptocromos) em plântulas são necessários para desencadear o desenvolvimento tanto caulinar quanto radicular adequados.

4. O fitohormônio ABA

O crescimento e o desenvolvimento das plantas são influenciados por diversos fatores, tais como, luz, radiação solar, temperatura, umidade, ventos, nutrientes presentes na água e no solo, fitohormônios e outros. A luz interage com diferentes vias hormonais e em conjunto desempenha uma participação significativa no processo de crescimento e desenvolvimento que afeta a planta (Ullah et al. 2018). O fitohormônio ABA (Ácido Abscísico) é um dos fitohormônios que são alterados quando a planta entra em contato com a luz, sua sinalização regula a biossíntese de flavonóides. Isto é consistente com a alta integração do ABA e das vias de sinalização luminosa, que ocorre ao nível dos principais componentes de sinalização (Brunetti et al. 2019; Agurla et al. 2020). Os papéis da luz e ABA nos processos fisiológicos das plantas parecem ser contrários, pois por exemplo, a luz promove o crescimento das raízes por um curto período, enquanto o ABA em algumas quantidades suprime o crescimento das raízes (Wang et al. 2019).

Sabe-se que o ABA está presente em diversos processos nas plantas, na germinação e desenvolvimento de sementes, na resposta ao estresse abiótico, sendo acompanhado por alterações no padrão de expressão dos genes ligados a ele (Brocard et al. 2002).

Por meio de uma via central de sinalização, onde o estresse é percebido pela planta, o ABA se liga ao PIRABACTIN-LIKE RESISTANCE RECEPTOR 1 (PYL1), reprimindo assim a ação das CONSTITUTIVE PROTEINS OF TYPE 2C PHOSPHATASES (PP2C), que atuam a jusante das NON-FERMENTING SUGAR PROTEIN KINASES (SnRK2) (Brunetti et al. 2019b; Chen et al. 2020). Devido ao estresse enfrentado durante o desenvolvimento da planta, o ABA acaba se acumulando

nas células e desencadeia a ligação do complexo receptor-ABA, inibindo a fosfatase PP2C, permitindo que SnRK2s fosforilem e controlem a atividade de fatores a jusante, causando respostas fisiológicas. Fatores de transcrição de domínio básico de zíper de leucina (bZIP), incluindo proteínas de ligação ABRE (AREBs), fatores de ligação ABRE (ABFs) e ABA INSENSITIVE 5 (ABI5) são alguns exemplos de elementos que podem se ligar a proteínas responsivas a ABA (Finkelstein 2013; Dejonghe et al. 2018; Agurla et al. 2020).

O ABA foi associado há muito tempo apenas com respostas ao estresse biótico e abiótico e como um inibidor do crescimento vegetal. Porém, algumas outras funções lhe foram atribuídas, como sendo um promotor no crescimento da parte aérea em várias situações fisiológicas e de desenvolvimento, levando a um novo conceito geral de controle químico, onde em baixas doses causa estimulação e em altas doses inibição (Zhang et al. 2010; Humplík et al. 2017).

A conexão entre a luz e o metabolismo do ABA já foi observada na inibição inicial da germinação dependente de PHYB por FR, onde ela é mediada no endosperma e envolve um sinal inibidor de ABA para o embrião evitar a germinação dependente de PHYA. A alta integração entre este fitohormônio e a luz explica a multiplicidade de funções reguladas pela via de sinalização do ABA. Essa relação tem sido relativamente bem estudada em nível molecular, especialmente no desenvolvimento inicial da semente. (De Wit et al. 2016).

Os papéis de alguns genes ligados à sinalização por luz como HY5, COP1, DET1 estão também ligados à sinalização ABA atuando na modulação no nível transcricional e pós-transcricional de ABI5 (Chen et al. 2008a; Yadukrishnan et al. 2020a). Estudos apontam que COP1 é co-localizado com ABI5 e os substratos do primeiro (HY5 e BBX21) influenciam os níveis de expressão de ABI5 ao se ligarem a seu promotor (Wang et al. 2019).

Nos últimos tempos, diversas pesquisas mostraram que a sinalização mediada por fotorreceptores envolve participação dos fitohormônios nas vias de a interação da luz com vias de sinalização mediadas por fitohormônios (Wang et al., 2013).

A interação de fitocromos e seus parceiros PIF1 ou PIL5 facilita a germinação após a ativação da luz, regulando a sinalização de ABA e GA através de seus alvos a jusante (Oh et al., 2009; Seo et al., 2009; de Wit et al., 2016). A degradação mediada

por fitocromo de PIF1 é proposta como o mecanismo crucial que controla a germinação de sementes induzida pela luz, alterando o metabolismo de ABA e GA nas sementes.

.

5. Interações entre ABA e a sinalização de luz

Nos últimos tempos, diversas pesquisas mostraram que a cascata da sinalização por luz mediada por fotorreceptores envolve também a participação da via dos fitohormônios. A luz parece influenciar significativamente a sensibilidade ao ABA em plântulas durante o desenvolvimento pós-germinação e a inibição causada por ele neste período é maior no escuro em comparação com condições de luz (Wang et al. 2019; Yadukrishnan and Datta 2021). Todos esses processos envolvem mudanças transcricionais e traducionais, a expressão de genes responsivos ao ABA é regulada pela ligação de fatores de transcrição à elementos de ação *cis* conservados, tais como o fator de ligação responsivo ao ABA (ABRE). Diferentes classes de genes reguladores ligados ao ABA foram identificados em *Arabidopsis*, dentre estes estão: o fator de transcrição ABA INSENSITIVE 5 (ABI5) que faz parte da subfamília de fatores de transcrição de domínio básico do tipo zíper de leucina (b-ZIP); os fatores de ligação ABRE (ABF1-4) e proteínas de ligação responsivas ao ABA (AREB1-3) que são induzidas após a exposição ao ABA (Agurla et al. 2020).

ABA promove a ligação de HY5 à ABI5, ou seja, o fator de transcrição HY5 liga-se ao promotor do gene do fator de transcrição ABI5 e é necessário para a expressão de ABI5 (Brunetti et al. 2019). Estudos demonstraram também, que o ABA vindo da parte aérea promove o crescimento das raízes. Níveis aumentados de auxina radicular (IAA) em enxertos de plantas deficientes em ABA sugerem que o mesmo, quando derivado das folhas, inibe o crescimento das raízes através da IAA (McAdam et al. 2016a).

O ABI5 desempenha um papel crucial na germinação e crescimento de sementes mediado por ABA, sua expressão é controlada no nível transcricional e pós-traducional (Skubacz et al. 2016). HY5 é conhecido por promover a fotomorfogênese, controla cerca de 300 genes alvo-verdadeiros no genoma da *Arabidopsis thaliana* (Burko et al. 2020) e, também atua como um importante fator de integração para as

vias de luz e ABA, apesar de ter efeitos contrastantes sobre o ABA (Xu et al. 2014). Ele está envolvido na sinalização de ABA ativando diretamente a expressão de ABI5 e é necessário para a expressão de ABI5 e seus genes alvo nas sementes (Osterlund et al. 2000; Chen et al. 2008; Xu et al. 2014).

Estudos observaram que a superexpressão de ABI5 restaura a sensibilidade do ABA em mutantes *hy5* e aumenta as respostas à luz em plantas (Chen et al. 2008). Em contraste, outros experimentos demonstraram que o HY5 suprime a inibição do desenvolvimento pós-germinação mediado pelo ABA e é altamente influenciado pelos níveis de dormência em diferentes lotes de sementes (Yadukrishnan e Datta 2021).

HY5 e ABI5 interagem fisicamente e formam heterodímeros no núcleo, afetando assim a sinalização por luz e processos relacionados ao ABA. Linhagens que superexpressam HY5 apresentam alta sensibilidade ao ABA durante o estágio de germinação, bem como uma maior repressão do alongamento do hipocótilo em resposta à luz. A linhagem *knockout* para ABI5 exibe hipocótilo ligeiramente mais curto do que Col-0 e *hy5*, indicando que este gene intensifica as respostas à luz. Isto dá maior robustez ao papel de HY5 na regulação positiva mediada por ABI5 nos processos de sinalização do ABA e no envolvimento de ABI5 na fotomorfogênese (Bhagat et al. 2021a).

Embora HY5 seja controlado em diferentes níveis, a abundância da proteína é altamente controlada pelas proteínas COP/DET/FUS, que atuam negativamente na fotomorfogênese (Osterlund et al. 2000; Huang et al. 2014). COP1 funciona como um dos mais importantes controladores do desenvolvimento fotomorfogênico interagindo com várias proteínas alvo diferentes. Ele atua como uma ubiquitina E3 ligase mediando a degradação de várias proteínas envolvidas na luz (Lau e Deng 2012; Kim et al. 2017).

COP1 promove a via de sinalização do ABA atuando a jusante de ABI5, reforçando a estagnação do crescimento que é mediada pelo ABA. Considerando a função canônica de COP1 como uma ubiquitina E3 ligase, estudos recentes indicaram que ele pode modular a função de outras proteínas por meio de interações físicas não proteolíticas ou poderia de fato interagir fisicamente com ABI5 (Sharma et al. 2019; Yadukrishnan et al. 2020b). Um estudo interessante relatou que o COP1 regula positivamente ABA promovendo a parada do desenvolvimento das plântulas, facilitando a ligação de ABI5 ao seu próprio promotor (Yadukrishnan et al. 2020). O

mutante para este gene apresenta pouca sensibilidade ao fitohormônio ABA e apresenta dificuldades na germinação em comparação a planta selvagem quando o meio contém adição de ABA (Balcerowicz et al., 2011). Entretanto o mecanismo molecular dessa interação ainda precisa ser melhor compreendido e estudado.

Outro fator importante na via de sinalização luminosa é DET1, que desempenha um papel direto na repressão transcricional (Lau e Deng 2012). DET1 é parceiro de COP1 durante a escotomorfogênese e tem um papel divergente na via ABI5. No escuro, DET1 promove a expressão de ABI5 estabilizando os fatores de transcrição PIFs. Enquanto que, na luz, DET1 interage com HYPOCOTYL FAR-RED ELONGATED 3 (FHY3) e se associa a regiões de seus alvos diretos, como ABI5, onde regula a transcrição dele e inibe a sua expressão (Agurla et al. 2020; Xu et al. 2020).

DET1 regula a expressão de ABI5 através de múltiplos mecanismos, além de interagir com FHY3, reduz a transcrição de ABI5 através de PHYA (PHYTOCRHOME A) e a consequente diminuição da inibição do *greening* mediada por ABA. O promotor ABI5, recruta uma histona desacetilase, promovendo mudanças na cromatina, que prejudicam a transcrição (Wang e Xing 2002; Tang et al. 2013; Yadukrishnan e Datta 2021). De fato, DET1 forma um complexo com uma proteína DAMAGED DNA BINDING 1A/B (DDB1A) /B) e outro com um complexo DDB1 contendo DWA1 e 2 (DWD 1/2 hipersensível ao ABA), ambos demonstraram regular negativamente a resposta do ABA. Além disso, a ação de DET1 sobre HY5 e sua degradação podem gerar alguma complexidade na inibição do *greening* mediado por ABA, uma vez que HY5 é envolvido na expressão de genes de biossíntese de clorofila ao mesmo tempo que regula ABI5 (Agurla et al. 2020). DET1 influencia a transcrição de ABI5 e outros aspectos das respostas ABA de diferentes maneiras. Todos esses estudos sugerem um importante papel regulador de ABI5 com sinalização luminosa no processo de fotomorfogênese.

6. Elementos *cis* ABRE e TFs AREB/ABF para expressão gênica dependente de ABA

Análises de promotores de genes induzidos por ABA, permitiram a descoberta de um elemento *cis* conservado, denominado elemento responsivo a ABA (ABRE); os

elementos *cis*-regulatórios responsáveis pela regulação da expressão gênica de ABA compartilham um motivo conservado, ACGTGGC. Existem cerca de 78 genes da família bZIP em todo o genoma de *Arabidopsis thaliana,* fatores de transcrição bZIP (TFs) ligam-se a G-boxes (CACGTG) com sequências centrais de ACGT como hetero ou homodímeros. A subfamília ABFs/AREB e ABI5 são homólogas e desempenham papéis específicos e redundantes durante o crescimento e desenvolvimento das plantas (Choi et al. 2005; Kurihara et al. 2020).

As proteínas b-ZIP induzíveis por ABA (ABFs) podem se ligar às caixas G e C e são induzidas por vários tipos de tratamentos de estresse. Existem 9 AREB/ABFs em *Arabidopsis*, e eles abrigam três domínios conservados N-terminal e um C-terminal (Choi et al. 2005; Yoshida et al. 2010). ABF1, AREB1/ABF2, ABF3 e AREB2/ABF4 são os TFs a jusante mais importantes envolvidos na sinalização do estresse osmótico mediado por ABA em tecidos vegetativos. ABF1–4 que atuam no núcleo da sinalização ABA de maneira parcialmente redundante (Hwang et al. 2019).

A sinalização de ABA leva à fosforilação de ABF1-4 pelas quinases SnRK ativando sua ligação aos elementos de resposta ao ABA (ABRE). A PROTEIN FOSFATASE 6 (PP6) é conhecida por interagir com ABI5. Onde, proteínas Ser/Thr FOSFATASE 1 (FyPP1) e FyPP3 associadas ao fitocromo codificam PP6 que por sua vez interage fisicamente com ABI5 e regula negativamente sua atividade de transativação. Assim, supõe-se que talvez a ação de PP6 possa ser modulada pela luz em função da participação de genes ligados ao fitocromo (Yoshida et al. 2015; Banerjee e Roychoudhury 2017).

A maioria dos estudos atualmente tem focado no desenvolvimento dos órgãos acima do solo e de certa forma acabam deixando de lado partes essenciais como as raízes formando um *gap* na compreensão do ciclo de crescimento das plântulas. A raiz abaixo do solo é fortemente influenciada pela presença de luz na parte aérea e, o esclarecimento destes processos a nível molecular e como se dá esta comunicação é imprescindível para o entendimento completo do desenvolvimento vegetal. Tendo em vista a falta de informação com relação ao envolvimento/efeito da luz na parte aérea e consequente crescimento das raízes na escuridão e buscando uma melhor compreensão dos mecanismos moleculares participantes nesta sinalização entre parte aérea e raízes, entra a presente pesquisa e respectiva tese.

- Objetivos -

1. Objetivo geral

A presente tese de doutorado se propôs a investigar/identificar sinais fotomorfogênicos móveis (fatores de transcrição, mRNAs, proteínias), oriundos da parte aérea, reguladores do desenvolvimento de raízes na planta modelo *Arabidopsis thaliana*.

2. Objetivos específicos

2.1 Identificar genes diferencialmente expressos em raízes em diferentes bases de dados de RNAseq coletados de plântulas cultivadas sob diferentes condições de luz

2.2 Identificar os potenciais fatores de transcrição que regulam os genes diferencialmente expressos;

2.3 Selecionar potenciais sinais móveis entre a parte aérea e as raízes;

2.4 Avaliar se a superexpressão e/ou o nocaute dos genes candidatos na parte aérea influencia o crescimento das raízes;

Capítulo II

- Signaling events for photomorphogenic root development-

Artigo publicado no periódico *Trends in Plant Science*

Cássia Fernanda Stafen, Jürgen Kleine-Vehn, Felipe dos Santos Maraschin

Signaling events for photomorphogenic root development

Signaling events for photomorphogenic root development

Cássia Fernanda Stafen[1], Jürgen Kleine-Vehn[3,4,5], Felipe dos Santos Maraschin[1,2*]

[1]PPGBM - Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil; [2] Departamento de Botânica, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil; [3]Department of Applied Genetics and Cell Biology, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria; [4]Institute of Biology, Department of Molecular Plant Physiology (MoPP), University of Freiburg, Freiburg, Germany; [5]Center for Integrative Biological Signalling Studies (CIBSS), University of Freiburg, 79104 Freiburg, Germany; *Correspondence : felipe.maraschin@ufrgs.br (F.S. Maraschin)

Keywords: photomorphogenesis, etiolation, photoreceptors, seedling development

Glossary

Photomorphogenesis – A developmental growth pattern of seedlings grown in light. This involves inhibition of the hypocotyl elongation, opening of the apical hook, cotyledon expansion, chloroplast differentiation and development of the shoot and root apical meristems. Photomorphogenic seedlings display a short and green shoot with expanded leaves and a well-developed root system.

Skotomorphogenesis – from the greek word "skotos" meaning darkness. A development pattern of seedlings germinated in the dark that triggers etiolated growth consisting of strong elongation of the embryonic stem (hypocotyl), formation of an apical hook and a repression of the expansion of the embryonic leaves (cotyledons), apical meristems, and root system. This strategy ensures that limited seed reserves are used for the quest for light, a prerequisite for photoautotrophic survival.

Etiolation - the developmental process triggered by skotomorphogenesis.

Photoreceptors – the plant photoreceptors are comprised of light sensitive proteins activated by a wide range of wavelengths: UVR8 for UV-B light (280–320 nm), cryptochromes CRY1 and CRY2, phototropins PHOT1 and PHOT2, F-box containing

Flavin binding proteins (e.g., ZEITLUPE, FKF1/LKP2) for blue/UV-A light (320–500 nm) and phytochromes phyA-E for red/far-red light (600–750 nm).

PIFs (Phytochrome Interacting Factors) – a class of basic helix-loop-helix (bHLH) transcription factors comprised of eight members (PIF1-8) in arabidopsis. PIFs act as negative regulators of light responses by repressing photomorphogenesis in darkness.

DELLA proteins - a group of GRAS transcription regulators that acts as repressors of gibberellin signaling as well as other signaling responses. They modulate gene expression via interaction with several proteins, mostly transcriptional factors, such as PIFs.

Cotyledons – embryonic leaves first emerged from the seed.

Meristem – a group of undifferentiated stem cells capable of cell division that control organ formation. The young germinating seedling grows from the mitotic activity of the shoot apical meristem (SAM) and the root apical meristem (RAM).

Hypocotyl – the stem of a germinating seedling, found below the cotyledons and above the radicle (root)

D-Root – "dark-root" system. An *in vitro* growing system for seedlings first described by Silva-Navas, et al. 2015, which allows the roots to be protected from direct illumination.

Abstract

A germinating seedling incorporates environmental signals such as light into developmental outputs. Light is not only a source of energy, but also a central coordinative signal in plants. Traditionally, most research focuses on aboveground organs' response to light, therefore our understanding of photomorphogenesis in roots is relatively scarce. However, root development underground is highly responsive to light signals from the shoot and understanding these signaling mechanisms will give a better insight into early seedling development. Here we review the central light signaling hubs and their role in root growth promotion of *Arabidopsis thaliana* seedlings.

Light signaling and photomorphogenesis

Photomorphogenic development drastically affects the entirety of plant architecture. By activating photosynthesis and enabling autotrophy, the early developmental program of a plant is centered in optimizing light capture. When grown in darkness, arabidopsis (*Arabidopsis thaliana*) seedlings favor hypocotyl elongation over root displaying an **etiolated** development, named **skotomorphogenesis**, which is energetically dependent on the seed's energy storage and is characterized by unexpanded **cotyledons,** a closed apical hook, and a short and thin root with a reduced apical **meristem**. Light, however, affects the morphology of all sections of the seedling, as it transitions to autotrophic growth by promoting hook opening, cotyledon expansion and primary root growth, while strongly inhibiting hypocotyl growth (Arsovski et al. 2012a; De Wit et al. 2016). A large amount of knowledge has accumulated over the past decades regarding the signaling events that control the shoot responses during photomorphogenesis (Arsovski et al. 2012a; Gommers and Monte 2018) as well as other adaptative light responses such as shade avoidance, phototropism and circadian rhythms which have been covered by excellent reviews(Mo et al. 2015b; Lee et al. 2017a; van Gelderen et al. 2018b; Wan et al. 2019; Sanchez et al. 2020; Fernández-Milmanda and Ballaré 2021). Shoot illumination stimulates primary root growth through shoot-to-root signaling. In this review, we highlight how photomorphogenesis regulates the growth of the primary root during early seedling development.

Photoreceptor signaling cascade

Besides fueling photosynthesis, light effects on plant development are largely dependent on the activity of cellular **photoreceptors**. Regardless of their perception mechanism, light triggers protein conformational changes in the photoreceptor protein leading to downstream signaling events (Möglich et al. 2010). The signaling outputs downstream of photoreceptor activation converge to suppress the activity/abundance of CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) (Deng and Quail 1992; Podolec and Ulm 2018a) and PHYTOCHROME-INTERACTING FACTORS (**PIFs**) (Ni et al. 1998b; Hellmann and Estelle 2002a; Xu et al. 2015a; Pham et al. 2018b), which results in the stabilization of positive transcriptional regulators (e.g. ELONGATED HYPOCOTYL 5, HY5; HY5 HOMOLOG, HYH, **DELLA proteins**

among other COP1 degradation targets) which are otherwise actively degraded by COP1 in darkness **(Figure 1)**.

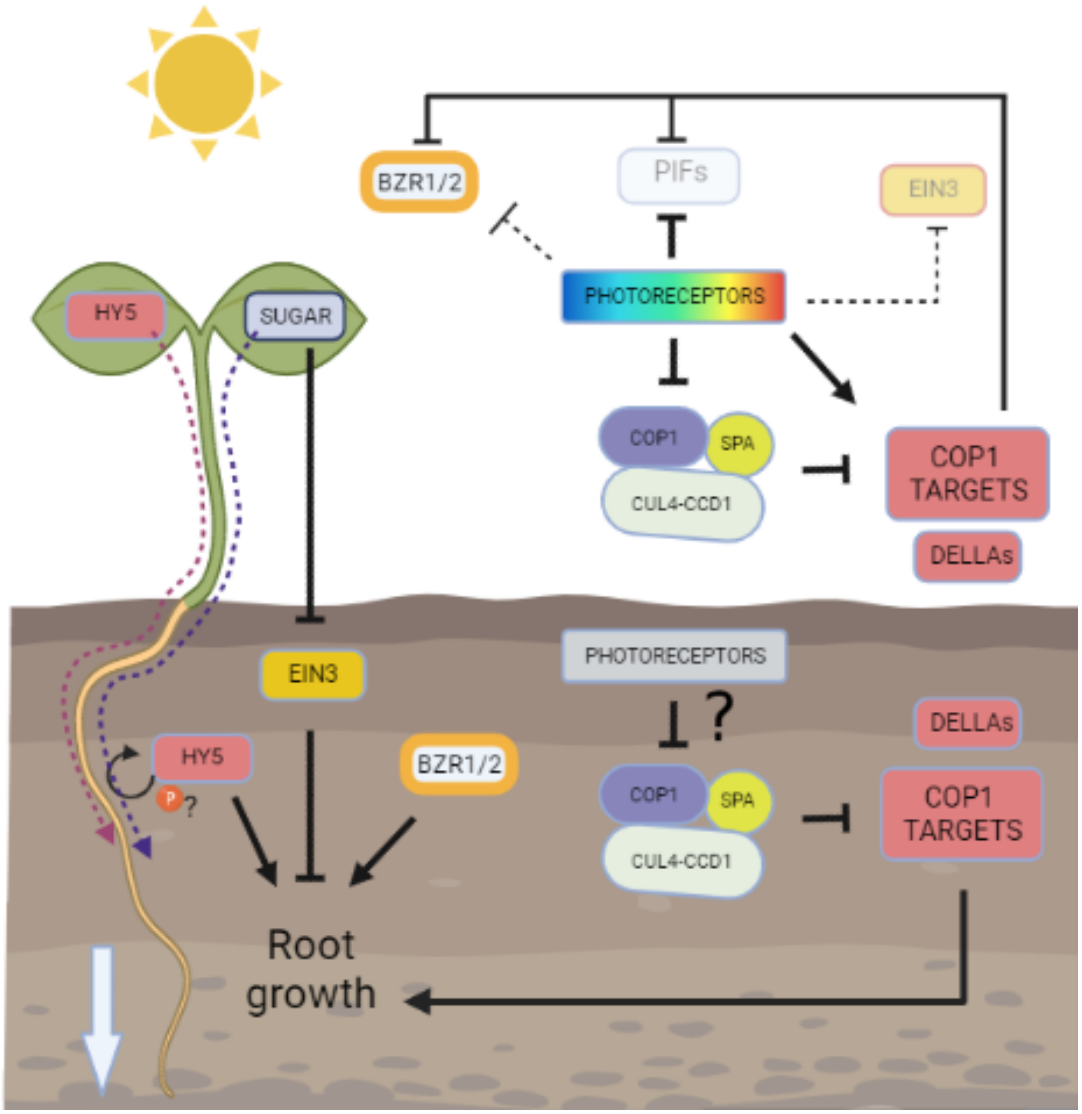


Figure 1 Shoot light signaling components and their effect on root growth. Seedlings grown in the dark (left panel) display skotomorphogenic development with elongated hypocotyls, a closed apical hook and a short primary root. COP1-SPA Ubiquitin-E3 ligase actively represses photomorphogenesis by targeting positive transcriptional regulators to proteasome dependent degradation. The main positive regulators of skotomorphogenesis are the PHYTOCRHOME INTERACTING FACTORS (PIFs) which activate hypocotyl elongation in the dark in association with the BR-responsive TFs BRASSINAZOLE-RESISTANT 1 and 2 (BZR1/2). PIFs are stabilized by COP1 which fine-tunes both PIFs and BRZ1 levels. BZR1/2 levels are also negatively regulated by COP1(Kim et al. 2014) but the root effects of this regulation are unknown. The ethylene response regulator ETHYLENE INSENSITIVE3/EIN3 acts alongside PIFs to maintain etiolated growth (An et al. 2012; Liu et al. 2017) both in the shoot and root and its levels are regulated by the $SCF^{EBF1/2}$ Ubiquitin-E3 ligase whose activity is repressed by COP1. Light grown seedlings (right panel) engage photomorphogenesis through activated photoreceptors that lead to opening of the apical hook, cotyledon expansion, repression of hypocotyl elongation and elongation of the

primary root. Activated phytoreceptors (PHYs and CRYs) strongly repress COP1 complexes via direct association and promote PIFs Ubiquitin-mediated degradation. SPA1-dependent phosphorylation of HY5 occurs both in light and dark conditions to fine tune its activity (Wang et al. 2021). Activated photoreceptors also enhance $SCF^{EBF1/2}$ Ubiquitin-E3 ligase activity towards EIN3 and PIFs promoting their destruction. Repression of the COP1 complex by light enhances the abundance of photomorphogenesis positive regulators (HY5, HYH, DELLAs among others) leading to transcriptional reprogramming in the whole seedling. Light stabilization of shoot HY5 leads to its shoot-to-root transport where it can self-activate and promote root growth. Processes unknown to operate in roots are labeled with a question mark. Abbreviations: BZR1/2, BRASSINAZOLE-RESISTANT1 and 2; CONSTITUTIVE PHOTOMORPHOGENIC1; COP1 TARGETS, COP1/SPA Ubiquitination targets (for an updated version see Ponnu 2021); CUL4-CCD1, CUL4–DDB1 Ubiquitin-E3 ligase; DELLAs, DELLA proteins; EIN3, ETHYLENE INSENSITIVE3; HY5, ELONGATED HYPOCOTYL 5; HYH, ELONGATED HYPOCOTYL 5-HOMOLOG; $SCF^{EBF1/2}$, EIN3-BINDING F BOX PROTEIN 1 AND 2 Ubiquitin-E3 ligases; PIFs, PHYTOCHROME INTERACTING FACTORS; PHOTORECEPTORS (cry1, cry2, phyA, phyB), SPA, SUPRESSOR OF PHYA; Created with BioRender.com

COP1 acts in the dark as a main repressor of photomorphogenesis. It was originally identified as a mutation leading to a constitutive photomorphogenic phenotype regardless the light condition (Deng et al. 1991; Deng and Quail 1992). From early observations, it was noted that the *cop1* mutants were affected in most photoreceptor-dependent responses consisting in a major switch from skoto- to photomorphogenic developmental programs. Mutant *cop1* seedlings display elongated roots in darkness (McNellis et al. 1994; Sassi et al. 2012), reinforcing that light signaling activates root growth.

COP1 functions along SUPPRESSOR OF PHYA-105 (SPA) proteins as the COP1/SPA Ubiquitin E3 ligase (Seo et al. 2003; Saijo et al. 2003; Han et al. 2020) complex that promotes the dark degradation of light response regulators through protein ubiquitination (Ang Lay Hong and Deng Xing Wang 1994; Ang et al. 1998; Osterlund et al. 2000; Ponnu and Hoecker 2021b). SPAs bridge activated photoreceptors to COP1 to repress its activity (Hoecker et al. 1999; Chen et al. 2010; Ponnu and Hoecker 2021b). Light-activated photoreceptors repress the COP1/SPA complex by promoting nuclear exclusion of COP1, disruption of the COP1/SPA interaction, and promoting SPA protein degradation (von Arnim and Deng 1994; Osterlund and Deng 1998; Pacín et al. 2014; Podolec and Ulm 2018b). More importantly, activated blue-light photoreceptors CRYPTOCHROME 1 and 2 (CRY1, CRY2) and the UVB activated receptor UV RESISTANCE LOCUS 8 (UVR8) directly inhibit COP1 by displacing its substrates, which seems to be the major

inhibitory mechanism for its ubiquitin ligase activity (Lau et al. 2019; Ponnu et al. 2019).

PIFs function in darkness and shade promoting etiolated growth as negative regulators of light responses (Leivar and Quail 2011; Leivar and Monte 2014; Pham et al. 2018b). PIFs are stabilized in the dark whereas phytochrome activation leads to repression of PIF activity through protein phosphorylation, protein-protein interactions and proteasome-dependent degradation (Xu et al. 2015b). The quadruple mutant *pif1pif3pif4pif5* (*pifQ*) has a *cop*-like phenotype (Leivar et al. 2008a; Shin et al. 2009a). The gene expression profiles of *cop1* and *spa1234* (*spaQ)* mutants overlaps with *pifQ* in the dark, with an overrepresentation of PIF direct target genes, suggesting that the *cop1* phenotypes are partially due to a reduced level of PIFs (Pham et al. 2018c).

Although roots are not usually studied in photomorphogenesis experiments, many COP1/SPA targets as well as the remaining components of the light signaling cascade are actively expressed in roots, which suggest roots have their own light sensing mechanisms. The expression of all the central photomorphogenic signaling genes in roots raises the question of what are the regulatory mechanisms acting in underground organs. In order to place the relative expression of photoreceptors and COP1 among root tissues, we plotted an heatmap derived from a root-specific expression atlas (Li et al. 2016) **(Figure 2)**. Interestingly, COP1, PHYB, PHOTOTROPIN 2 (PHOT2), CRY1 and CRY2 are mainly expressed in mature endodermis cells. It is hence tempting to speculate that the endodermis may comprise a major site for light responses in the root. Notably, PHYA and PHYTOCHROME C (PHYC) display increased expression in columella and quiescent center (QC) cells. Notably, some PIFs show preferential expression in the root endodermis and columella (PIF3), vasculature (PIF2, PIF4, PIF8) and cortex (PIF1, PIF7) **(**see online supplemental information **Figure S1B)**.

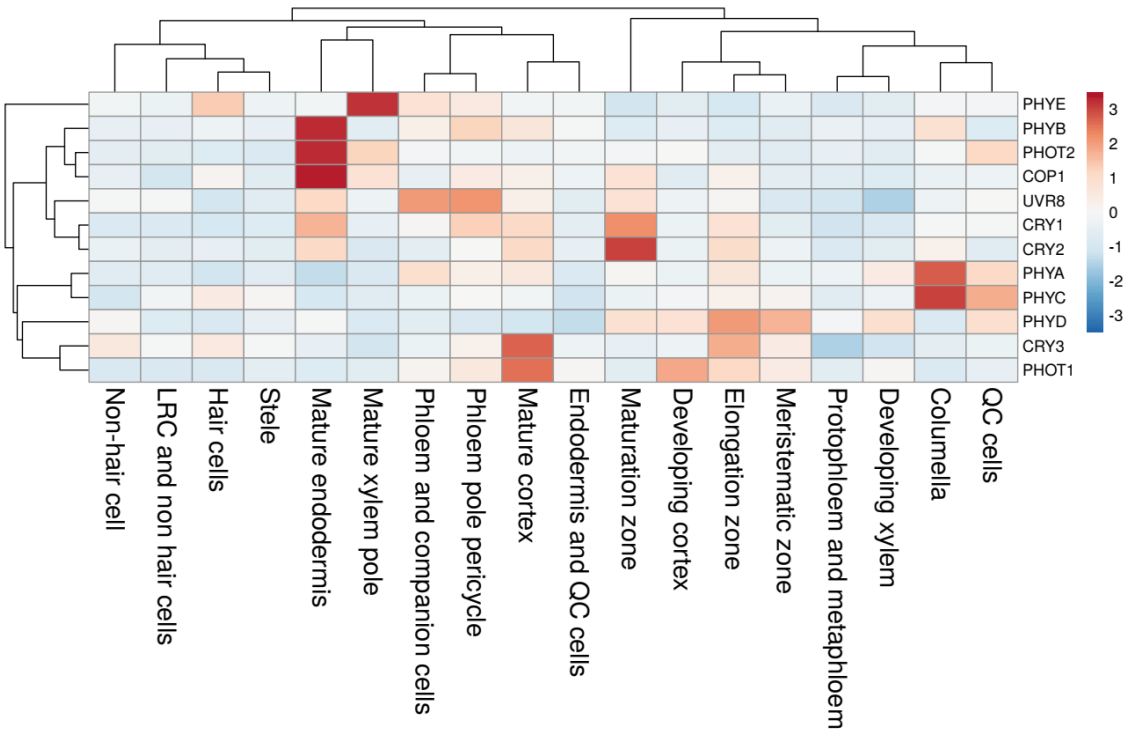


Figure 2 Root expression pattern of photoreceptors and COP1. Heat map of averaged expression for selected genes from a high-resolution root expression map of arabidopsis seedlings. Each column represents a root tissue and each line a single gene listed on the right. The color indicates the fold change average expression of each gene. The analysis was performed in Clustvis (Metsalu and Vilo 2015) with default settings and raw data from Table S5 from (Li et al. 2016).

A detailed description of all the genes mentioned in this review and their reported effects on root growth is listed on **Table 1** and their root-specific expression patterns are depicted in online supplemental information Figure S1.

Root responses to illumination

Direct root illumination is usually perceived as a stress by roots as direct blue light exposure affects root morphology and behavior leading to bursts of ROS and negative tropism (Yokawa et al. 2011; Yokawa et al. 2014; Mo et al. 2015a). Furthermore, root illumination represses root elongation through phytochromes (Correll and Kiss 2005a; Costigan et al. 2011a) and blue/UV-B light receptors cryptochromes (CRY1 and CRY2) and UVR8 (Kurata and Yamamoto 1997; Yokawa et al. 2011; Silva-Navas et al. 2016). UV-B has a strong inhibiting effect on root growth, either when supplied to the whole seedling or only to the root (Tong et al. 2008; Leasure et al. 2009; Silva-Navas et al. 2015; Li et al. 2017; van Gelderen et al. 2018b) whereas the lack of phyB

reduced root growth regardless the light condition (Silva-Navas et al. 2015). Except for the *phyd* mutant, all other phytochrome mutants display lower LR number suggesting an important role of phytochrome signaling for the adaptative development of the root (Salisbury et al. 2007a; Lee et al. 2016a). The responses downstream of specific wavelengths are complex as phyB inhibits root elongation in response to red light (Costigan et al. 2011b), whereas phyA promotes root elongation under red, far-red and blue light (Kurata and Yamamoto 1997). Interestingly, under far-red illumination, activation of root elongation is resistant to photosynthesis inhibitors, suggesting that a phyA also promotes root growth independently of photosynthesis (Kurata and Yamamoto 1997). The root activity of phyA and phyB seems is essential for proper root development (Correll and Kiss 2005b; Molas et al. 2006; Salisbury et al. 2007a; Costigan et al. 2011b) influencing responses to signals other than light such as jasmonic acid (JA) (Costigan et al. 2011b). Studies on shade-avoidance response (SAR) have been helpful in elucidating some long-distance shoot-to-root signaling (van Gelderen et al. 2018a; Rosado et al. 2021). Shaded light (low R:FR ratio) stimulus in shoots represses LR emergence through a shoot phyA and HY5 dependent mechanism (van Gelderen et al. 2018a). Shoot shade also promotes the root-specific expression of stress related WRKY transcription factors affecting primary and lateral root growth via ethylene signaling, suggesting that shade translates into a stressful signal for roots (Rosado et al. 2021).

In order to determine better experimental setups for evaluating how light perception is transduced to the roots grown in the darkness, different growing conditions were developed to reduce direct light exposure to roots, such as **D-Root** (Silva-Navas et al. 2015; van Gelderen et al. 2018b; Miotto et al. 2019a; Cabrera et al. 2022) dark-protected roots (Sassi et al. 2012; Xu et al. 2013; Yokawa et al. 2013; Novák et al. 2014; Lee et al. 2016a; Sakaguchi and Watanabe 2017a) and improved plant-growing method-IPG (Qu et al. 2017) which have been thoroughly reviewed recently (Lacek et al. 2021a; Cabrera et al. 2022). Shoot-only illumination promotes root growth and suggests that shoot-to-root signaling occurs in a photosynthesis-dependent fashion (Kurata and Yamamoto 1997; Kircher and Schopfer 2012; Sassi et al. 2012; Silva-Navas et al. 2015; Miotto et al. 2019a). Interestingly, monochromatic red light inhibits primary root growth solely in dark-grown roots (shoot illumination only) suggesting that, in arabidopsis, red light represses root growth by activation of shoot-localized

photoreceptors that influences shoot-to-root transport of signaling molecules (Spaninks et al. 2020). Moreover, shoot-localized phytochromes exhibit long-distance effects on root elongation (Salisbury et al. 2007a; Costigan et al. 2011b). Root phyB is necessary for HY5 protein accumulation in the root, whereas root illumination represses the main root growth via HY5 whose abundance is also regulated by light in decapitated seedlings, which suggest a root-autonomous process (Zhang et al. 2019). This effect is probably regulated by phytochromes, although recent data suggests that root-only light exposure is not sufficient to enhance HY5 accumulation in seedlings roots (Gao et al. 2021) which opens the question whether other factors than light could lead to root stabilization of HY5. The mechanisms leading to the activation of photoreceptors in roots shielded from direct light are still unclear as the penetrance of light in root tissues is limited. Some works suggest that phytochromes could be activated through stem light-piped light (Lee et al. 2016a; Lee et al. 2017a; Ko and Helariutta 2017). The significance of the light-pipe mechanism on the activation of root phytochromes is still debated as root-only illumination seems to affect shoot hypocotyl responses. Direct exposure of roots to red light did not counteract the far-red shoot effect in reducing lateral root (LR) emergence as well as it did not affect PHYB-GFP photobody accumulation (van Gelderen et al. 2018a). Nevertheless, it is feasible that various chemical signals (peptides, RNAs, hormones, metabolites, etc.) downstream of shoot-activated photoreceptors many transduce long distance information to promote root growth (Buer et al. 2007; Notaguchi et al. 2012; Matsubayashi 2014; Oh et al. 2018; Binenbaum et al. 2018; Kondhare et al. 2021).

Shoot illumination was shown to activate the translocation of the positive photomorphogenic regulator HY5 to roots where it induces NITRATE TRANSPORTER 2.1 (NRT2.1) expression, enhancing nitrate uptake to counterbalance photosynthetic carbon (Chen et al. 2016a). The interplay between carbon and nitrogen demand for plant growth is linked to photosynthetic capacity and photomorphogenic signaling. Sucrose alone does not activate NRT2.1 expression, which is dependent on light and HY5. Evidences support the hypothesis that shoot HY5 is transported to the roots both in arabidopsis and tomato (*Solanum lycopersicum*) where local activity of HY5 in the root promotes root gravitropism, strigolactone biosynthesis and activation of light-responsive genes (Chen et al. 2016a; Lee et al. 2016a; Sakuraba et al. 2018; Guo et al. 2021; Ge et al. 2022). In parallel, Pi

starvation response is dependent on shoot-to-root HY5 mobility activated downstream of shoot cryptochromes (Gao et al. 2021).

The hypothesis of root dependency on mobile, shoot-derived HY5 was challenged by the observation that a shoot-restricted version of HY5 (CAB3p::DOF-HY5) was able to complement root elongation, but not the LR phenotype of *hy5* mutants (Burko et al. 2020a). Accordingly, a shoot signal downstream of HY5 might be needed for shoot-to-root communication. The sugar-insensitive and abscisic acid (ABA) deficient mutant *sis4/aba2* has reduced NRT2.1 activation by HY5 (Chen et al. 2016a), suggesting a converging point between light, sugar, and ABA. HY5 activates the production of flavonoids to counterbalance reactive oxygen species (ROS) accumulation (Stracke et al. 2010; Silva-Navas et al. 2016; Zhang et al. 2019). Flavonoids are phloem mobile and highly abundant in root tissues (Buer et al. 2007) which might also participate in long distance signaling. Although the importance of HY5 connecting shoot-to-root light signaling is well documented, its role as a primary activator of root photomorphogenesis is still uncertain.

Metabolic demand and photomorphogenesis

The growth of the hypocotyl and the primary root compete for sucrose as an energy source (Kircher and Schopfer 2012; Lilley et al. 2012). Sucrose sustains the root primary metabolism and also functions as a major shoot-to-root signal, regulating nutrient uptake to counterbalance the shoot photosynthetic carbon input (Lejay et al. 2008; Li and Sheen 2016). The light effect on roots goes beyond photosynthetic sugar availability (Kircher and Schopfer; Kurata and Yamamoto 1997; Xiong et al. 2013) as sugar alone cannot fully activate root growth independently of an active photomorphogenic program (Kurata and Yamamoto 1997; García-González et al. 2021; Miotto et al. 2021).Although the photomorphogenic signaling networks are mainly regulated by light in shoots, it is feasible that they could be regulated by other signals in roots growing underground as several photoreceptor mutants are affected in root growth (Correll and Kiss 2005a; Canamero et al. 2006; Costigan et al. 2011b). Since the positive effect of sugars on root growth is not observed in excised roots, it has been suggested that additional mobile signals from the shoot are needed for root elongation (Kurata and Yamamoto 1997). Therefore, the activation of the root competence to act as an energy sink might be a central part of photomorphogenesis.

During germination, sucrose increases hypocotyl elongation (Stewart et al. 2011) via the sucrose dependent stabilization of PIFs leading to increased auxin transport and synthesis. This response is impaired in the *pifQ* mutant, as PIFs were shown to integrate growth with metabolic demands during photomorphogenesis (Lilley et al. 2012). Alongside sugars, light enhances shoot-derived auxin transport (Bhalerao et al. 2002b), which promotes root growth by activating GA responses (Fu and Harberd 2003). Whereas light reduces GA levels in hypocotyls, roots highly depend on GA to establish photomorphogenic growth (Ubeda-Tomás et al. 2008; Ubeda-Tomás et al. 2009). Photosynthesis derived sugars transported from shoots affect DELLA root responses as sucrose inhibits DELLA degradation and promotes anthocyanin accumulation (Li et al. 2014), a common phenotype observed in *cop*, *spaQ* and *pifQ* mutants. The developmental trade-off between shoot/root growth during the transition from skoto- to photomorphogenesis places PIFs as essential players for the primary root growth, as seen for PIF4 in the control of root thermomorphogenesis (Gaillochet et al. 2020).

Photosynthetic carbon fixation by the shoots must be coordinated with water and mineral uptake by the roots (Forde 2002; Liu et al. 2009), this way DELLA and PIF counterbalance sugar-hormone cross-regulation networks (de Lucas et al. 2008; Feng et al. 2008; Ljung et al. 2015), adjusting growth rates in shoots according to the carbon input. Therefore, PIFs repress the sucrose- and glucose-induced auxin biosynthesis, which promotes root growth (Sairanen et al. 2013a). Interestingly, the root responses to compensate for the nutrient acquisition in higher C/N ratios are not PIF-dependent (Lilley et al. 2012), indicating that shoots and roots operate separate carbon sensing mechanisms. The higher sugar/auxin transport to the roots induces N-uptake to equilibrate the C/N balance [52] in response to shoot light. Although PIFs play a central role mediating hypocotyl elongation in the dark, their roles in root photomorphogenic development are still unknown. For one part, PIFs are about 5-fold less expressed in roots when compared to shoot tissues (Jeong and Choi 2013).

While photomorphogenesis drastically affects both shoot and root growth, there is a major representation of hypocotyl over root growth measurements in the published literature, so the root-specific effects of light signaling remain largely to be elucidated. A detailed description of the signaling events triggered by light in the seedling's root are depicted in **Figure 3.**

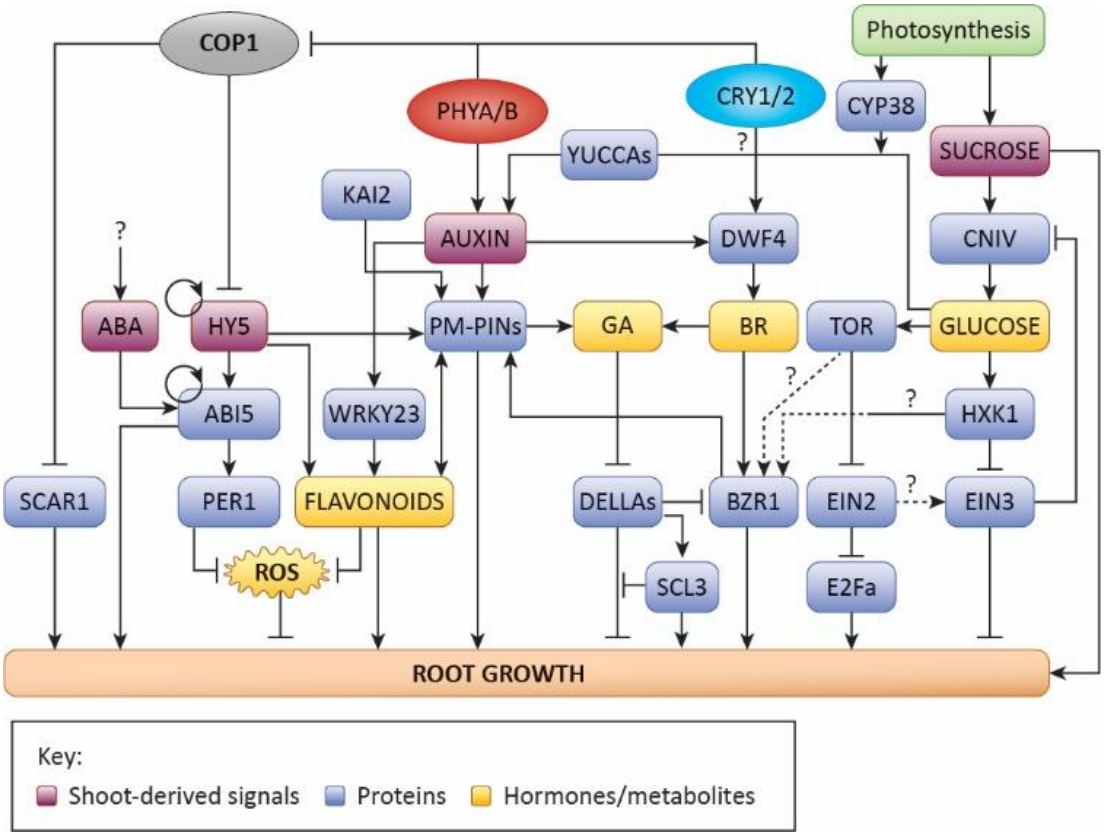


Figure 3. Effects of shoot illumination for the control of primary root growth. Shoot illumination activates the main photomorphogenesis photoreceptors: Phytochromes (phyA and phyB) and cryptochromes (cry1 and cry2), that suppress the activity of the photomorphogenic repressor COP1 (Podolec and Ulm 2018b). Suppression of COP1 enhances the stability of its degradation targets such as HY5 and SCAR1 which act as positive regulators of root growth (Dyachok et al. 2011; Zhang et al. 2019; Ponnu and Hoecker 2021b). In the shoot, activated phyB enhances HY5 stability that activates ABI5 leading to the to the production of a mobile signal (ABA?) to the roots that activate ABI5-dependent expression of a hydrogen peroxidase (PER1) that detoxifies ROS (Ha et al. 2018b). HY5 also directly induces root accumulation of flavonoids (Stracke et al. 2010) alongside the auxin-responsive WRKY23 transcription factor that promotes root growth by ROS detoxification and regulation of polar auxin transport (PAT) (Grunewald et al. 2012; Prát et al. 2018). One centralizing effect of shoot illumination is the enhancement of PAT and the stabilization of PINs in the plasma membrane (PM-PINs)(Laxmi et al. 2008a; Sassi et al. 2012), which is promoted by HY5 (Laxmi et al. 2008a), KAI2 (Hamon-Josse et al. 2022) and BR (Bao et al. 2004; Li et al. 2005) and induces GA root responses through DELLAs degradation in the endodermis(Fu and Harberd 2003; Ubeda-Tomás et al. 2008; Ubeda-Tomás et al. 2009; Shani et al. 2013). DELLAs enhance SCL3 transcription which stimulates root growth (Zhang et al. 2011b; Heo et al. 2011). Shoot blue light, acting via cryptochromes (CRY1/2), induces the root expression of DWF4, a BR biosynthetic gene, via an unknown mobile signal (Sakaguchi and Watanabe 2017a; Sakaguchi et al. 2019). Activation of photosynthesis increases sucrose transported to the root to fuel heterotrophic metabolism and growth. Sucrose is hydrolyzed in roots by invertases (CNIV) activating glucose sensing mechanisms that suppress EIN3 expression via HXK1 (Meng et al. 2020) and promote BZR1/2 stabilization via TOR (Zhang et al. 2016; Wu et al. 2019). TOR also activates E2Fa via EIN2-repression leading to RAM activation (Fu et al. 2021). Glucose enhances root auxin biosynthesis by promoting YUCCAs expression (Sairanen et al. 2013b). Shoot expressed CYP38 increases root IAA biosynthesis downstream of photosynthetic output (Duan et al. 2021). Processes unknown to operate in roots are labeled with a question mark. Abbreviations: ABI5, ABA INSENSITIVE5; BR, brassinosteroids; BZR1, BRASSINAZOLE-

RESISTANT1; COP1, CONSTITUTIVE PHOTOMORPHOGENIC 1; cry1 and cry2, CRYPTOCHROME 1 and 2; CYP38, CYCLOPHYLIN38; CINV, CYTOSOLIC INVERTASE; DELLAs, DELLA proteins; DWF4, DWARF4; E2Fa, TRANSCRIPTION FACTOR E2FA; EIN2, ETHYLENE-INSENSITIVE PROTEIN2; EIN3, ETHYLENE INSENSITIVE3; GA, gibberellins; HY5, ELONGATED HYPOCOTYL 5; HXK1, HEXOKINASE1; KAI2, KARRIKIN INSENSITIVE2; PER1, PEROXIDASE1; phyA and phyB, PHYTOCHROME A and B; PM-PINs, plasma membrane PINs; ROS, reactive oxygen species; SCAR1, Suppressor of cAMP receptor; SCL3, SCARECROW-LIKE3; TOR, TARGET OF RAPAMYCIN; WRKY23, WRKY DNA-binding protein23; YUCCAs, Flavin Monooxygenase-Like Enzymes.

Seedlings germinated in photosynthesis-constrained and sugar-free conditions can activate photomorphogenesis but such conditions trigger the root meristem to enter a mitotic quiescent state with arrested meristematic activity. Growth reactivation is dependent on photosynthesis-derived sugars (sucrose, glucose, fructose) and TARGET OF RAPAMYCIN (TOR) kinase but are uncoupled from glucose-sensing HEXOKINASE 1 (HXK1) signaling (Xiong et al. 2013). Sugar also promotes BR signaling through TOR-dependent stabilization of BZR1 (Zhang et al. 2016). In addition, sugar represses ETHYLENE INSENSITIVE 2 (EIN2) signaling in roots to allow activation of the root apical meristem (RAM) via E2F TRANSCRIPTION FACTOR 3 (E2Fa) (Fu et al. 2021) (Figure 3). The reactivation of mitotic activity in the root meristem after glucose depletion in so called "mitotic quiescent seedlings" seems to be dependent of light and auxin in shoots but only dependent on glucose in roots (Xiong et al. 2013; Li et al. 2017). The stimulation of the TOR kinase that leads to shoot meristem activation was shown to be dependent on auxin activation of the RHO-RELATED PROTEIN FROM PLANTS 2 (ROP2) GTPase (Li et al. 2017; Schepetilnikov et al. 2017). Moreover, auxin activation of TOR is repressed by COP1 in the darkness leading to an overall suppression of translation, restraining photomorphogenesis in the shoot (Chen et al. 2018). It is however unknown whether a similar pathway operates for the activation of root growth during deetiolation. Considering that glucose seems to be sufficient for TOR activation in the RAM, the direct light effects on TOR remains to be addressed in roots. In roots, TOR shows localized enhanced expression in the QC and columella cells (see online supplemental information Figure S1B). Transcriptomic analysis of roots from photomorphogenic seedlings (Miotto et al. 2019a) shows ~25% common upregulated genes with Glucose-TOR target genes (Xiong et al. 2013), suggesting that TOR signaling in roots is an important step for the activation of the photomorphogenic developmental program.

It is also tempting to hypothesize that shoot-derived sugars activate root growth via suppression of ETHYLENE INSENSITIVE 3 (EIN3), which acts repressing the primary root growth and promoting skotomorphogeneis (An et al. 2012; Jeong et al. 2016; Liu et al. 2017; Harkey et al. 2018; Vaseva et al. 2018). EIN3 acts in the root as a transcriptional repressor of CYTOSOLIC INVERTASE 1 (CINV), which is essential for sucrose assimilation (Meng et al. 2020). EIN3 expression is further repressed by glucose accumulation, creating a sugar sensing loop (Figure 3). Ethylene seems to be central for root growth repression under shade conditions (Rosado et al. 2021) and its signaling also feedbacks with auxin in the root epidermis (Vaseva et al. 2018) although this relationship to photomorphogenic root growth remains to be evaluated.

BOX 1 - Phytohormones as promoters of root photomorphogenic growth

Light grown seedlings activate auxin synthesis in young leaves which is polarly transported to the roots activating the primary and lateral root development (Bhalerao et al. 2002b; Salisbury et al. 2007a; Swarup et al. 2008). Shoot-synthesized auxin promotes RAM activity, induces PIN-FORMED 1 (PIN1) and PIN-FORMED 2 (PIN2) transcription and the plasma membrane (PM) stabilization of their proteins in the root tip. Seedlings grown in increasing shoot light intensities progressively attenuated auxin transport chemical inhibition effects supporting that shoot light increases auxin polar transport to induce primary root growth (Miotto et al. 2021). PIN2 stabilization is impaired in *hy5-1* mutants and enhanced in *cop9-1* (Laxmi et al. 2008a). Light repression of COP1 increases PINs gene expression to sustain shoot-derived auxin as a mobile signal to stabilize root PIN1 and PIN2 in dark grown roots, showing that light-dependent root growth depends on shoot signals (Sassi et al. 2012). The *cop1* mutants display higher PIN1 hypocotyl and root expression in darkness as well as stabilization of PM PIN2 in a proteasome-dependent fashion. Furthermore, *cop1* RAM size is more sensitive to auxin transport inhibitors than WT, suggesting that COP1 affects auxin-dependent responses (Sassi et al. 2012). These observations place COP1 in a central role in the root regulation of auxin transport to sustain RAM activity and primary root growth **(Figure 3)**. Although the hypothesis that shoot-derived polar transported auxin would have a major role as a signal to trigger root growth, accumulated evidence suggests that root derived auxin might be even more

important for the promotion of root development (Ljung et al. 2001; Ljung et al. 2005; Petersson et al. 2009; Chen et al. 2014) and meristem maintenance (Brumos et al. 2018) as the root becomes progressively independent from the shoot on its own auxin synthesis during early development (Bhalerao et al. 2002b; Ljung et al. 2005). Both sucrose and glucose promote IAA root biosynthesis, where the auxin biosynthetic gene YUCCA9 (YUC9) acts as a PIF-repressed, sugar-induced converging point for auxin accumulation in roots in response to shoot light (Sairanen et al. 2013a). High endogenous auxin levels in the *yucca-D* mutant partially phenocopies sucrose treatment on root elongation (Lilley et al. 2012) whereas inhibition of auxin transport blocks sucrose induced hypocotyl elongation. The shoot-expressed CYCLOPHYLIN 38 (CYP38) was found to be involved in shoot-to-root signaling downstream of photosynthetic activity by increasing root IAA levels (Duan et al. 2021) and KARRIKIN INSENSITIVE 2 (KAI2) was identified promoting light-induced PIN-dependent activation of rootward auxin transport (Hamon-josse et al. 2021).

Paclobutrazol inhibition of gibberellin (GA) biosynthesis drastically represses root growth (Zhang et al. 2011b) and the GA-DELLA response in the root endodermis was demonstrated to be crucial for root meristem size and growth (Ubeda-Tomás et al. 2008; Ubeda-Tomás et al. 2009; Shani et al. 2013) acting partially through SCARECROW-LIKE3 (SCL3) (Heo, 2011; Zhang 2011) a GRAS-type transcription factor. PIF3 and PIF4 are major activators of GA transcriptional responses, and their activity in hypocotyls is specifically repressed by DELLA proteins (de Lucas et al. 2008; Feng et al. 2008). DELLAs, in its turn, are highly expressed in roots (see online supplemental information **Figure S1A**). Although their repressive action on PIFs during shoot etiolation places DELLAs as promoters of photomorphogenesis (Achard et al. 2007), their roles on light dependence of root GA-responses are not clear. A possible link might lie on the DELLA repression of BZR1-dependent BR responses (Bai et al. 2012; Li et al. 2012; Li et al. 2014), as BZR1 is highly expressed in root tissues and its activity is counterbalanced by auxin and other factors (Chaiwanon and Wang 2015; Chaiwanon et al. 2016). SINA OF ARABIDOPSIS THALIANA (SINAT) Ubiquitin E3 ligases promote degradation of BZR1/2 in the light to reduce hypocotyl elongation (Yang et al. 2017a). However, the light responsive BR effect on root growth is opposite to hypocotyls as local BR biosynthesis and signaling was described to be essential for primary root growth (Chaiwanon and Wang 2015;

Vukašinović et al. 2021). BR signaling induces GA biosynthesis (Unterholzner et al. 2015), possibly linking both hormones to root growth in response to light. DWARF 4 (DWF4), a BR biosynthetic gene, shows root-specific expression which is controlled by shoot-perceived blue light, acting though cryptochromes to promote BR accumulation in roots (Sakaguchi and Watanabe 2017b; Sakaguchi et al. 2019).

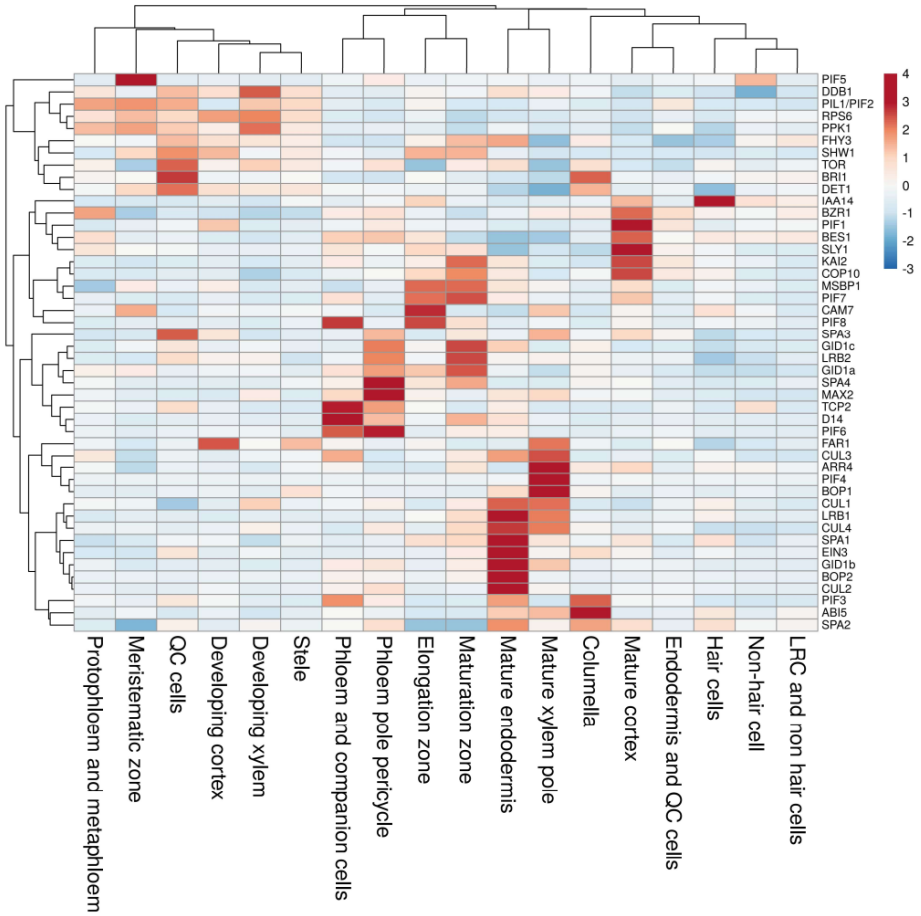


Figure S1: Root expression pattern of COP1 targets and light signaling genes. Heat map of averaged expression for selected genes from a high-resolution root expression map of arabidopsis seedlings. Each column represents a root tissue and each line a single gene listed on the right. The color indicates the fold change average expression of each gene. (A) COP1/SPA Ubiquitination-targets, (B) Selected light signaling genes. The analysis was performed in Clustvis (Metsalu and Vilo 2015) with default settings and raw data from Table S5 from (Li et al. 2016).

Shoot-produced abscisic acid (ABA) was described as a mobile promotor of root growth in many species (McAdam et al. 2016b; Gil et al. 2018). Interestingly, a shoot-to-root mobile signal might be produced downstream a phyB-dependent ABA INSENSITIVE 5 (ABI5) signaling module that represses ROS production in the primary roots to promote root elongation (Ha et al. 2018b). Altogether, this suggests that ABI5 or other ABA-related signals might also play a role in the root responses to

shoot illumination. *hy5* mutants show ABA hypersensitivity whereas *cop1* mutants show ABA hyposensitivity during postgermination development (Yadukrishnan et al. 2020a), with COP1 acting as an enhancer of the ABA signal (Yadukrishnan et al. 2020b) during early seedling establishment. The role of ABA as a promoter of growth is still debated (Humplík et al. 2017) as it has essential roles both to sustain etiolation and photomorphogenesis.

Concluding Remarks and Future Perspectives

The past decade has been extremely exciting for plant photobiology and remarkable discoveries have been made on shoot photomorphogenic responses and its underlying photoreceptors. On the other hand, the signaling events controlling root photomorphogenesis have been largely overlooked and are just now surfacing. Recent findings have shown that long distance communication plays a major role for photomorphogenesis, abiotic and biotic stresses, nutrient signaling, thermomorphogenesis, and circadian entrainment between shoots and roots. Tissue specific expression of light signaling components can now be evaluated in a single cell context. Tissue-specific gene knockouts and targeted gene ablation techniques allow for unprecedented discoveries without the need for more invasive experimentation such as grafting or cotyledon excision. We encourage the community of photomorphogenesis to extent their focus on unlighted aspects of root development.

Acknowledgements

This project was financially supported by Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul - FAPERGS, The Brazilian National Council of State Funding Agencies – CONFAP, the National Council for Scientific and Technological Development (CNPq) and European Research Council (Auxin ER-ERC starting grant 639478). We would like to thank Fernanda Lazzarotto and Stefan Kircher for comments on the final draft of this manuscript.

Supplemental information associated with this article can be found at doi: https://doi.org/10.1016/j.tplants.2022.08.002

REFERENCES

Abbas N, Maurya JP, Senapati D, Gangappa SN and Chattopadhyaya S (2014) Arabidopsis CAM7 and HY5 physically interact and directly bind to the HY5 promoter to regulate its expression and thereby promote photomorphogenesis. Plant

Cell 26:1036–1052. doi: 10.1105/tpc.113.122515

Achard P, Liao L, Jiang C, Desnos T, Bartlett J, Fu X and Harberd NP (2007) DELLAs contribute to plant photomorphogenesis. Plant Physiol 143:1163–1172. doi: 10.1104/pp.106.092254

Achard P, Renou J-P, Berthomé R, Harberd NP and Genschik P (2008) Plant DELLAs Restrain Growth and Promote Survival of Adversity by Reducing the Levels of Reactive Oxygen Species. Curr Biol 18:656–660. doi: 10.1016/J.CUB.2008.04.034

Agurla S, Gahir S, Munemasa S, Murata Y, Raghavendra AS, Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I et al. (2020) Light and abscisic acid coordinately regulate greening of seedlings. Plant Physiol 183:1281–1294. doi: 10.1104/pp.20.00503

Al-Sady B, Ni W, Kircher S, Schäfer E and Quail PH (2006) Photoactivated Phytochrome Induces Rapid PIF3 Phosphorylation Prior to Proteasome-Mediated Degradation. Mol Cell 23:439–446. doi: 10.1016/j.molcel.2006.06.011

Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I, Nambara E and Lorenzo O (2015) S-nitrosylation triggers ABI5 degradation to promote seed germination and seedling growth. Nat Commun 6:1–10. doi: 10.1038/ncomms9669

Ali F, Qanmber G, Li F and Wang Z (2022) Updated role of ABA in seed maturation, dormancy, and germination. J Adv Res 35:199–214. doi: 10.1016/J.JARE.2021.03.011

An F, Zhang X, Zhu Z, Ji Y, He W, Jiang Z, Li M and Guo H (2012) Coordinated regulation of apical hook development by gibberellins and ethylene in etiolated Arabidopsis seedlings. Cell Res 2012 225 22:915–927. doi: 10.1038/cr.2012.29

Ang Lay Hong and Deng Xing Wang (1994) Regulatory hierarchy of photomorphogenic loci: Allele-specific and light-dependent interaction between the HY5 and COP1 loci. Plant Cell 6:613–628. doi: 10.1105/tpc.6.5.613

Ang LH, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A and Deng XW (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. Mol Cell 1:213–222. doi: 10.1016/S1097-2765(00)80022-2

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012a) Photomorphogenesis. Arab B 10:e0147. doi: 10.1199/tab.0147

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012b) Photomorphogenesis Photomorphogenesis. Society. doi: 10.1199/tab.0147

Bai MY, Shang JX, Oh E, Fan M, Bai Y, Zentella R, Sun TP and Wang ZY (2012) Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. Nat Cell Biol 14:810–817. doi: 10.1038/ncb2546

Bai S, Yao T, Li M, Guo X, Zhang Y, Zhu S and He Y (2014) PIF3 Is Involved in the Primary Root Growth Inhibition of Arabidopsis Induced by Nitric Oxide in the Light. Mol Plant 7:616–625. doi: 10.1093/MP/SST142

Balcerowicz M, Fittinghoff K, Wirthmueller L, Maier A, Fackendahl P, Fiene G, Koncz C and Hoecker U (2011) Light exposure of Arabidopsis seedlings causes rapid de-stabilization as well as selective post-translational inactivation of the repressor of photomorphogenesis SPA2. Plant J 65:712–723. doi: 10.1111/J.1365-313X.2010.04456.X

Balcerowicz M, Kerner K, Schenkel C and Hoecker U (2017) SPA proteins affect the subcellular localization of COP1 in the COP1/SPA ubiquitin ligase complex during photomorphogenesis. Plant Physiol 174:1314–1321. doi: 10.1104/pp.17.00488

Banerjee A and Roychoudhury A (2017) Abscisic-acid-dependent basic leucine zipper (bZIP) transcription factors in plant abiotic stress. Protoplasma 254:3–16. doi: 10.1007/S00709-015-0920-4/FIGURES/1

Bao F, Shen J, Brady SR, Muday GK, Asami T and Yang Z (2004) Brassinosteroids interact with auxin to promote lateral root development in arabidopsis. Plant Physiol 134:1624–1631. doi: 10.1104/pp.103.036897

Bhagat PK, Verma D, Sharma D and Sinha AK (2021a) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z/FIGURES/6

Bhagat PK, Verma D, Sharma D and Sinha AK (2021b) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z

Bhalerao RP, Eklo J, Ljung K, Marchant A, Bennett M and Sandberg È (2002a) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. 29:

Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett M and Sandberg G (2002b) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. Plant J 29:325–332. doi: 10.1046/j.0960-7412.2001.01217.x

Bhatia S, Gangappa SN, Kuswaha R, Kundu S and Chattopadhyay S (2008) Short Hypocotyl in White Light1, a serine-arginine-aspartate-rich protein in Arabidopsis, acts as a negative regulator of photomorphogenic growth. Plant Physiol 147:169–178. doi: 10.1104/pp.108.118174

Bhatnagar A, Singh S, Khurana JP and Burman N (2020) HY5-COP1: the central module of light signaling pathway. J Plant Biochem Biotechnol 29:590–610. doi: 10.1007/s13562-020-00623-3

Binder BM, Walker JM, Gagne JM, Emborg TJ, Hemmann G, Bleecker AB and Vierstra RD (2007) The Arabidopsis EIN3 Binding F-Box Proteins EBF1 and EBF2 Have Distinct but Overlapping Roles in Ethylene Signaling. Plant Cell 19:509–523. doi: 10.1105/TPC.106.048140

Binenbaum J, Weinstain R and Shani E (2018) Gibberellin Localization and Transport in Plants. Trends Plant Sci 23:410–421. doi: 10.1016/J.TPLANTS.2018.02.005

Bouché F, D'Aloia M, Tocquin P, Lobet G, Detry N and Périlleux C (2016) Integrating roots into a whole plant network of flowering time genes in Arabidopsis thaliana. Sci Reports 2016 61 6:1–12. doi: 10.1038/srep29042

Brumos J, Robles LM, Yun J, Vu TC, Jackson S, Alonso JM and Stepanova Correspondence AN (2018) Local Auxin Biosynthesis Is a Key Regulator of Plant Development. Dev Cell 47:306–318. doi: 10.1016/j.devcel.2018.09.022

Brunetti C, Sebastiani F and Tattini M (2019) Review: ABA, flavonols, and the evolvability of land plants. Plant Sci 280:448–454. doi: 10.1016/j.plantsci.2018.12.010

Buer CS, Muday GK and Djordjevic MA (2007) Flavonoids are differentially taken up and transported long distances in Arabidopsis. Plant Physiol 145:478–490. doi:

10.1104/pp.107.101824

Bulgakov VP and Koren OG (2022) Basic Protein Modules Combining Abscisic Acid and Light Signaling in Arabidopsis. Front Plant Sci 12:2986. doi: 10.3389/FPLS.2021.808960/BIBTEX

Burko Y, Gaillochet C, Seluzicki A, Chory J and Busch W (2020a) Local HY5 Activity Mediates Hypocotyl Growth and Shoot-to-Root Communication. Plant Commun 1:100078. doi: 10.1016/j.xplc.2020.100078

Burko Y, Seluzicki A, Zander M, Pedmale U V., Ecker JR and Chory J (2020b) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/TPC.19.00772

Burko Y, Seluzicki A, Zander M, Pedmale U V, Ecker JR and Chory J (2020c) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/tpc.19.00772

Cabrera J, Conesa CM and Pozo JC (2022) May the dark be with roots: a perspective on how root illumination may bias in vitro research on plant–environment interactions. New Phytol 233:1988–1997. doi: 10.1111/nph.17936

Canamero RC, Bakrim N, Bouly J-P, Garay A, Dudkin EE, Habricot Y and Ahmad M (2006) Cryptochrome photoreceptors cry1 and cry2 antagonistically regulate primary root elongation in Arabidopsis thaliana. Planta 2006 2245 224:995–1003. doi: 10.1007/S00425-006-0280-6

Cañibano E, Bourbousse C, García-León M, Garnelo Gómez B, Wolff L, García-Baudino C, Lozano-Durán R, Barneche F, Rubio V and Fonseca S (2021) DET1-mediated COP1 regulation avoids HY5 activity over second-site gene targets to tune plant photomorphogenesis. Mol Plant 14:963–982. doi: 10.1016/j.molp.2021.03.009

Caño-Delgado A, Lee J-Y and Demura T (2010) Regulatory Mechanisms for Specification and Patterning of Plant Vascular Tissues. Annu Rev Cell Dev Biol 26:605–637. doi: 10.1146/annurev-cellbio-100109-104107

Carella P, Merl-Pham J, Wilson DC, Dey S, Hauck SM, Vlot AC and Cameron RK (2016) Comparative Proteomics Analysis of Phloem Exudates Collected during the Induction of Systemic Acquired Resistance. Plant Physiol 171:1495. doi: 10.1104/PP.16.00269

Chaiwanon J, Wang W, Zhu J-Y, Oh E and Wang Z-Y (2016) Information Integration and Communication in Plant Growth Regulation. Cell 164:1257–1268. doi: 10.1016/j.cell.2016.01.044

Chaiwanon J and Wang ZY (2015) Spatiotemporal brassinosteroid signaling and antagonism with auxin pattern stem cell dynamics in Arabidopsis roots. Curr Biol 25:1031–1042. doi: 10.1016/j.cub.2015.02.046

Chamovitz D a, Wei N, Osterlund MT, von Arnim a G, Staub JM, Matsui M and Deng XW (1996) The COP9 complex, a novel multisubunit nuclear regulator involved in light control of a plant developmental switch. Cell 86:115–21.

Chen G-H, Liu M-J, Xiong Y, Sheen J and Wu S-H (2018) TOR and RPS6 transmit light signals to enhance protein translation in deetiolating Arabidopsis seedlings. Proc Natl Acad Sci 115:12823–12828. doi: 10.1073/pnas.1809526115

Chen H, Huang X, Gusmaroli G, Terzaghi W, Lau OS, Yanagawa Y, Zhang Y, Li J, Lee JH, Zhu D et al. (2010) Arabidopsis CULLIN4-damaged DNA binding protein 1

interacts with CONSTITUTIVELY PHOTOMORPHOGENIC1-SUPPRESSOR OF PHYA complexes to regulate photomorphogenesis and flowering time. Plant Cell 22:108–123. doi: 10.1105/tpc.109.065490

Chen H, Zhang J, Neff MM, Hong S-WW, Zhang H, Deng X-WW, Xiong L and Korea S (2008a) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen H, Zhang J, Neff MM, Hong SW, Zhang H, Deng XW and Xiong L (2008b) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen Q, Dai X, De-Paoli H, Cheng Y, Takebayashi Y, Kasahara H, Kamiya Y and Zhao Y (2014) Auxin overproduction in shoots cannot rescue auxin deficiencies in arabidopsis roots. Plant Cell Physiol 55:1072–1079. doi: 10.1093/pcp/pcu039

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016a) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016b) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Cheng ZJ, Zhao XY, Shao XX, Wang F, Zhou C, Liu YG, Zhang Y and Zhang XS (2014) Abscisic acid regulates early seed development in arabidopsis by ABI5-Mediated transcription of SHORT HYPOCOTYL UNDER BLUE1. Plant Cell 26:1053–1068. doi: 10.1105/tpc.113.121566

Chory J (1993) Out of darkness: mutants reveal pathways controlling light-regulated development in plants. Trends Genet 9:167–172. doi: 10.1016/0168-9525(93)90163-C

Christians MJ, Gingerich DJ, Hua Z, Lauer TD and Vierstra RD (2012) The Light-Response BTB1 and BTB2 Proteins Assemble Nuclear Ubiquitin Ligases That Modify Phytochrome B and D Signaling in Arabidopsis. Plant Physiol 160:118–134. doi: 10.1104/pp.112.199109

Christie JM, Blackwood L, Petersen J and Sullivan S (2015) Plant Flavoprotein Photoreceptors. Plant Cell Physiol 56:401–413. doi: 10.1093/pcp/pcu196

Collin A, Daszkowska-Golec A and Szarejko I (2021) Updates on the Role of ABSCISIC ACID INSENSITIVE 5 (ABI5) and ABSCISIC ACID-RESPONSIVE ELEMENT BINDING FACTORs (ABFs) in ABA Signaling in Different Developmental Stages in Plants. Cells 2021, Vol 10, Page 1996 10:1996. doi: 10.3390/CELLS10081996

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C et al. (2007) FT protein movement contributes to long-distance signaling in floral induction of Arabidopsis. Science 316:1030–1033. doi: 10.1126/SCIENCE.1141752

Correll MJ and Kiss JZ (2005a) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Correll MJ and Kiss JZ (2005b) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Cosme M, Fernández I, Declerck S, van der Heijden MGA and Pieterse CMJ (2021) A coumarin exudation pathway mitigates arbuscular mycorrhizal incompatibility in Arabidopsis thaliana. Plant Mol Biol 1:3. doi: 10.1007/s11103-021-01143-x

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011a) Root-localized phytochrome chromophore synthesis is required for photoregulation of root elongation and impacts root sensitivity to jasmonic acid in Arabidopsis. Plant Physiol 157:1138–50. doi: 10.1104/pp.111.184689

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011b) Root-Localized Phytochrome Chromophore Synthesis Is Required for Photoregulation of Root Elongation and Impacts Root Sensitivity to Jasmonic Acid in Arabidopsis. Plant Physiol 157:1138–1150. doi: 10.1104/pp.111.184689

da Silva SR, Perrone GC, Dinis JM and de Almeida RM (2014a) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics 15:1181. doi: 10.1186/1471-2164-15-1181

da Silva SRM, Perrone GC, Dinis JM and de Almeida RMC (2014b) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics. doi: 10.1186/1471-2164-15-1181

Datta S, Hettiarachchi GHCM, Deng X-W and Holm M (2006) Arabidopsis CONSTANS-LIKE3 Is a Positive Regulator of Red Light Signaling and Root Growth. Plant Cell 18:70–84. doi: 10.1105/TPC.105.038182

de Lucas M, Davière J-M, Rodríguez-Falcón M, Pontin M, Iglesias-Pedraz JM, Lorrain S, Fankhauser C, Blázquez MA, Titarenko E and Prat S (2008) A molecular framework for light and gibberellin control of cell elongation. Nature 451:480–484. doi: 10.1038/nature06520

de Wit M, Keuskamp DH, Bongers FJ et al. (2016) Integration of Phytochrome and Cryptochrome Signals Determines Plant Growth during Competition for Light. Curr Biol 26:3320–3326. doi: 10.1016/j.cub.2016.10.031

De Wit M, Galvão VC and Fankhauser C (2016) Light-Mediated Hormonal Regulation of Plant Growth and Development. Annu Rev Plant Biol 67:513–537. doi: 10.1146/annurev-arplant-043015-112252

Deng X-WX -W and Quail PH (1992) Genetic and phenotypic characterization of cop1 mutants of Arabidopsis thaliana. Plant J 2:83–95. doi: 10.1111/j.1365-313X.1992.00083.x

Deng XW, Caspar T and Quail PH (1991) cop1: a regulatory locus involved in light-controlled development and gene expression in Arabidopsis. Genes Dev 5:1172–1182. doi: 10.1101/GAD.5.7.1172

Dobin A, Davis CA, Schlesinger F, Drenkow J, Zaleski C, Jha S, Batut P, Chaisson M and Gingeras TR (2013) Sequence analysis STAR: ultrafast universal RNA-seq aligner. 29:15–21. doi: 10.1093/bioinformatics/bts635

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017a) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017b) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Tang D, Gao Z, Yu R, Li K, He H, Terzaghi W, Deng XW and Chen H (2014) Arabidopsis DE-ETIOLATED1 Represses Photomorphogenesis by Positively Regulating Phytochrome-Interacting Factors in the Dark. Plant Cell 26:3630–3645. doi: 10.1105/tpc.114.130666

Du M, Daher FB, Liu Y, Steward A, Tillmann M, Zhang X, Wong JH, Ren H, Cohen JD, Li C et al. (2022) Biphasic control of cell expansion by auxin coordinates etiolated seedling development. Sci Adv 8:1570. doi: 10.1126/SCIADV.ABJ1570/SUPPL_FILE/SCIADV.ABJ1570_MOVIES_S1_TO_S8.ZIP

Duan L, Pérez-Ruiz JM, Cejudo FJ and Dinneny JR (2021) Characterization of CYCLOPHILLIN38 shows that a photosynthesis-derived systemic signal controls lateral root emergence. Plant Physiol 185:503–518. doi: 10.1093/PLPHYS/KIAA032

Durinck S, Spellman PT, Birney E and Huber W (2009) Mapping identifiers for the integration of genomic datasets with the R/ Bioconductor package biomaRt. Nat Protoc 4:1184–1191. doi: 10.1038/nprot.2009.97

Dyachok J, Zhu L, Liao F, He J, Huq E and Blancaflor EB (2011) SCAR Mediates Light-Induced Root Elongation in Arabidopsis through Photoreceptors and Proteasomes. Plant Cell 23:3610–3626. doi: 10.1105/tpc.111.088823

Feng S, Martinez C, Gusmaroli G, Wang Y, Zhou J, Wang F, Chen L, Yu L, Iglesias-Pedraz JM, Kircher S et al. (2008) Coordinated regulation of Arabidopsis thaliana development by light and gibberellins. Nature 451:475–479. doi: 10.1038/nature06448

Fernández-Milmanda GL and Ballaré CL (2021) Shade Avoidance: Expanding the Color and Hormone Palette. Trends Plant Sci 26:509–523. doi: 10.1016/j.tplants.2020.12.006

Fernando VCD, Al Khateeb W, Belmonte MF and Schroeder DF (2018) Role of Arabidopsis ABF1/3/4 during det1 germination in salt and osmotic stress conditions. Plant Mol Biol 97:149–163. doi: 10.1007/S11103-018-0729-6/FIGURES/10

Forde BG (2002) Local and long-range signaling pathways regulating plant responses to nitrate. Annu Rev Plant Biol 53:203–224. doi: 10.1146/annurev.arplant.53.100301.135256

Franceschini A, Szklarczyk D, Frankild S, Kuhn M, Simonovic M, Roth A, Lin J, Minguez P, Bork P, von Mering C et al. (2012) STRING v9.1: protein-protein interaction networks, with increased coverage and integration. Nucleic Acids Res 41:D808–D815. doi: 10.1093/nar/gks1094

Fu L, Liu Y, Qin G, Wu P, Zi H, Xu Z, Zhao X, Wang Y, Li Y, Yang S et al. (2021) The TOR–EIN2 axis mediates nuclear signalling to modulate plant growth. Nature 591:288–292. doi: 10.1038/s41586-021-03310-y

Fu X and Harberd NP (2003) Auxin promotes Arabidopsis root growth by modulating gibberellin response. Nature 421:740–743. doi: 10.1038/nature01387

Fukaki H, Taniguchi N and Tasaka M (2006) PICKLE is required for SOLITARY-ROOT/IAA14-mediated repression of ARF7 and ARF19 activity during Arabidopsis lateral root initiation. Plant J 48:380–389. doi: 10.1111/J.1365-313X.2006.02882.X

Gaillochet C, Burko Y, Platre MP, Zhang L, Simura J, Willige BC, Kumar SV, Ljung K, Chory J and Busch W (2020) HY5 and phytochrome activity modulate shoot to root coordination during thermomorphogenesis. Development. doi:

10.1242/dev.192625

Galen C, Rabenold JJ and Liscum E (2007) Functional ecology of a blue light photoreceptor: effects of phototropin-1 on root growth enhance drought tolerance in Arabidopsis thaliana. New Phytol 173:91–99. doi: 10.1111/J.1469-8137.2006.01893.X

Galvã VC and Fankhauser C (2015) Sensing the light environment in plants: photoreceptors and early signaling steps. Curr Opin Neurobiol 34:46–53. doi: 10.1016/j.conb.2015.01.013

Gangappa SN, Crocco CD, Johansson H, Datta S, Hettiarachchi C, Holm M and Botto JF (2013a) The Arabidopsis B-BOX Protein BBX25 Interacts with HY5, Negatively Regulating BBX22 Expression to Suppress Seedling Photomorphogenesis. Plant Cell 25:1243–1257. doi: 10.1105/TPC.113.109751

Gangappa SN, Holm M and Botto JF (2013b) Molecular interactions of BBX24 and BBX25 with HYH, HY5 HOMOLOG, to modulate Arabidopsis seedling development. Plant Signal Behav. doi: 10.4161/psb.25208

Gao YQ, Bu LH, Han ML, Wang YL, Li ZY, Liu HT and Chao DY (2021) Long-distance blue light signalling regulates phosphate deficiency-induced primary root growth inhibition. Mol Plant 14:1539–1553. doi: 10.1016/j.molp.2021.06.002

García-González J, Lacek J, Weckwerth W and Retzer K (2021) Exogenous carbon source supplementation counteracts root and hypocotyl growth limitations under increased cotyledon shading, with glucose and sucrose differentially modulating growth curves. Plant Signal Behav. doi: 10.1080/15592324.2021.1969818

Gautier L, Cope L, Bolstad BM and Irizarry RA (2004) affy-analysis of Affymetrix GeneChip data at the probe level. BIOINFORMATICS 20:307–315. doi: 10.1093/bioinformatics/btg405

Ge S, He L, Jin L, Xia X, Li L, Ahammed GJ, Qi Z, Yu J and Zhou Y (2022) Light-dependent activation of HY5 promotes mycorrhizal symbiosis in tomato by systemically regulating strigolactone biosynthesis. New Phytol 233:1900–1914. doi: 10.1111/nph.17883

Gil K-E, Ha J-H and Park C-M (2018) Abscisic acid-mediated phytochrome B signaling promotes primary root growth in Arabidopsis. Plant Signal Behav 13:e1473684. doi: 10.1080/15592324.2018.1473684

Gommers CMM and Monte E (2018) Seedling Establishment: A Dimmer Switch-Regulated Process between Dark and Light Signaling. Plant Physiol 176:1061–1074. doi: 10.1104/pp.17.01460

Grunewald W, De Smet I, Lewis DR, Löfke C, Jansen L, Goeminne G, Vanden Bossche R, Karimi M, De Rybel B, Vanholme B et al. (2012) Transcription factor WRKY23 assists auxin distribution patterns during Arabidopsis root development through local control on flavonol biosynthesis. Proc Natl Acad Sci U S A 109:1554–9. doi: 10.1073/pnas.1121134109

Guo Z, Xu J, Wang Y, Hu C, Shi K, Zhou J, Xia X, Zhou Y, Foyer CH and Yu J (2021) The phyB-dependent induction of HY5 promotes iron uptake by systemically activating FER expression. EMBO Rep 22:e51944. doi: 10.15252/embr.202051944

Ha J-HH, Kim J-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-HJ-IIJH and Park C-MM (2018a) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant

J 94:790–798. doi: 10.1111/tpj.13902

Ha J-HH, Kim J-IJ-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-IJ-HJ-IIJH and Park C-MM (2018b) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant J 94:790–798. doi: 10.1111/tpj.13902

Hacham Y, Holland N, Butterfield C, Ubeda-Tomas S, Bennett MJ, Chory J and Savaldi-Goldstein S (2011) Brassinosteroid perception in the epidermis controls root meristem size. Development 138:839–848. doi: 10.1242/DEV.061804

Ham B-K and Lucas WJ (2017a) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Ham B-K and Lucas WJ (2017b) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Hamon-josse M, Villaecija-aguilar JA, Ljung K and Leyser O (2021) KAI2 regulates seedling development by mediating light- induced remodelling of auxin transport. bioRxiv 2021.05.06.443001. doi: 10.1101/2021.05.06.443001

Hamon-Josse M, Villaécija-Aguilar JA, Ljung K, Leyser O, Gutjahr C and Bennett T (2022) KAI2 regulates seedling development by mediating light-induced remodelling of auxin transport. New Phytol 235:126–140. doi: 10.1111/NPH.18110

Han X, Huang X and Deng XW (2020) The Photomorphogenic Central Repressor COP1: Conservation and Functional Diversification during Evolution. Plant Commun 1:100044. doi: 10.1016/j.xplc.2020.100044

Hannapel DJ, Sharma P and Lin T (2013) Phloem-mobile messengerRNAs and root development. Front Plant Sci 4:257. doi: 10.3389/FPLS.2013.00257/BIBTEX

Harkey AF, Watkins JM, Olex AL, DiNapoli KT, Lewis DR, Fetrow JS, Binder BM and Muday GK (2018) Identification of Transcriptional and Receptor Networks That Control Root Responses to Ethylene. Plant Physiol 176:2095–2118. doi: 10.1104/PP.17.00907

Hartmann L, Drewe-Boß P, Wießner T, Wagner G, Geue S, Lee H-C, Obermüller DM, Kahles A, Behr J, Sinz FH et al. (2016) Alternative Splicing Substantially Diversifies the Transcriptome during Early Photomorphogenesis and Correlates with the Energy Availability in Arabidopsis. Plant Cell 28:2715–2734. doi: 10.1105/tpc.16.00508

He S-B, Wang W-X, Zhang J-Y, Xu F, Lian H-L, Li L and Yang H-Q (2015a) The CNT1 Domain of Arabidopsis CRY1 Alone Is Sufficient to Mediate Blue Light Inhibition of Hypocotyl Elongation. Mol Plant 8:822–825. doi: 10.1016/J.MOLP.2015.02.008

He SB, Wang WX, Zhang JY, Xu F, Lian HL, Li L and Yang HQ (2015b) The CNT1 domain of arabidopsis CRY1 alone is sufficient to mediate blue light inhibition of hypocotyl elongation. Mol Plant 8:822–825. doi: 10.1016/j.molp.2015.02.008

He Z, Zhao X, Kong F, Zuo Z and Liu X (2016) TCP2 positively regulates HY5/HYH and photomorphogenesis in Arabidopsis. J Exp Bot 67:775–785. doi: 10.1093/JXB/ERV495

Hellmann H and Estelle M (2002a) Plant development: regulation by protein degradation. Science 297:793–7. doi: 10.1126/science.1072831

Hellmann H and Estelle M (2002b) Plant development: Regulation by protein degradation. Science (80-) 297:793–797. doi: 10.1126/science.1072831

Heo J-O, Chang KS, Kim IA, Lee M-H, Lee SA, Song S-K, Lee MM and Lim J (2011) Funneling of gibberellin signaling by the GRAS transcription regulator SCARECROW-LIKE 3 in the Arabidopsis root. Proc Natl Acad Sci 108:2166–2171. doi: 10.1073/pnas.1012215108

Hoecker U and Quail PH (2001) The Phytochrome A-specific Signaling Intermediate SPA1 Interacts Directly with COP1, a Constitutive Repressor of Light Signaling inArabidopsis. J Biol Chem 276:38173–38178. doi: 10.1074/jbc.M103140200

Hoecker U, Tepperman JM and Quail PH (1999) SPA1, a WD-Repeat Protein Specific to Phytochrome A Signal Transduction. Science (80-) 284:496–499. doi: 10.1126/science.284.5413.496

Holm M, Ma LG, Qu LJ and Deng XW (2002) Two interacting bZIP proteins are direct targets of COP1-mediated control of light-dependent gene expression in Arabidopsis. Genes Dev 16:1247–1259. doi: 10.1101/gad.969702

Holtan HE, Bandong S, Marion CM, Adam L, Tiwari S, Shen Y, Maloof JN, Maszle DR, Ohto M, Preuss S et al. (2011) BBX32, an Arabidopsis B-Box Protein, Functions in Light Signaling by Suppressing HY5-Regulated Gene Expression and Interacting with STH2/BBX21. Plant Physiol 156:2109–2123. doi: 10.1104/PP.111.177139

Hornitschek P, Kohnen M V., Lorrain S, Rougemont J, Ljung K, López-Vidriero I, Franco-Zorrilla JM, Solano R, Trevisan M, Pradervand S et al. (2012) Phytochrome interacting factors 4 and 5 control seedling growth in changing light conditions by directly controlling auxin signaling. Plant J 71:699–711. doi: 10.1111/j.1365-313X.2012.05033.x

Hu W, Su Y-S and Lagarias JC (2009a) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant • 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009b) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009c) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Humplík JF, Bergougnoux V and Van Volkenburgh E (2017) To Stimulate or Inhibit? That Is the Question for the Function of Abscisic Acid. Trends Plant Sci 22:830–841. doi: 10.1016/j.tplants.2017.07.009

Jaillais Y and Vert G (2016) Brassinosteroid signaling and BRI1 dynamics went underground. Curr Opin Plant Biol 33:92–100. doi: 10.1016/J.PBI.2016.06.014

Jeong J and Choi G (2013) Phytochrome-interacting factors have both shared and distinct biological roles. Mol Cells 35:371–380. doi: 10.1007/s10059-013-0135-5

Jeong J, Kim K, Kim ME, Kim HG, Heo GS, Park OK, Park Y Il, Choi G and Oh E (2016) Phytochrome and ethylene signaling integration in Arabidopsis occurs via the transcriptional regulation of genes co-targeted by PIFs and EIN3. Front Plant Sci 7:1055. doi: 10.3389/fpls.2016.01055

Jiang K, Yung V, Chiba T and Feldman LJ (2017) Longitudinal patterning in roots: a

GATA2–auxin interaction underlies and maintains the root transition domain. Planta 2017 2474 247:831–843. doi: 10.1007/S00425-017-2831-4

Jiao Y, Lau OS and Deng XW (2007a) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jiao Y, Lau OS and Deng XW (2007b) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jing Y and Lin R (2013) Plant Signaling & Behavior PICKLE is a repressor in seedling de-etiolation pathway. doi: 10.4161/psb.25026

Jing Y and Lin R (2020) Transcriptional regulatory network of the light signaling pathways. New Phytol 227:683–697. doi: 10.1111/nph.16602

Jing Y, Zhang D, Wang X, Tang W, Wang W, Huai J, Xu G, Chen D, Li Y and Lin R (2013) Arabidopsis chromatin remodeling factor PICKLE interacts with transcription factor HY5 to regulate hypocotyl cell elongation. Plant Cell 25:242–256. doi: 10.1105/tpc.112.105742

Job N and Datta S (2021) PIF3/HY5 module regulates BBX11 to suppress protochlorophyllide levels in dark and promote photomorphogenesis in light. New Phytol 230:190–204. doi: 10.1111/nph.17149

Job N, Yadukrishnan P, Bursch K, Datta S and Johansson H (2018) Two B-Box Proteins Regulate Photomorphogenesis by Oppositely Modulating HY5 through their Diverse C-Terminal Domains. Plant Physiol 176:2963–2976. doi: 10.1104/PP.17.00856

Khanna R, Huq E, Kikis EA, Al-Sady B, Lanzatella C and Quail PH (2004) A novel molecular recognition motif necessary for targeting photoactivated phytochrome signaling to specific basic helix-loop-helix transcription factors. Plant Cell 16:3033–3044. doi: 10.1105/tpc.104.025643

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J and Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363. doi: 10.1111/j.1365-313X.2007.03052.x

Kim B, Jeong YJ, Corvalán C, Fujioka S, Cho S, Park T and Choe S (2014) Darkness and gulliver2/phyB mutation decrease the abundance of phosphorylated BZR1 to activate brassinosteroid signaling in Arabidopsis. Plant J 77:737–747. doi: 10.1111/tpj.12423

Kim J, Kang H, Park J, Kim W, Yoo J, Lee N, Kim J, Yoon T-Y and Choi G (2016) PIF1-Interacting Transcription Factors and Their Binding Sequence Elements Determine the in Vivo Targeting Sites of PIF1. doi: 10.1105/tpc.16.00125

Kircher S and Schopfer P (2012) Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. Proc Natl Acad Sci U S A 109:11217–11221. doi: 10.1073/pnas.1203746109

Kircher S and Schopfer P Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. doi: 10.1073/pnas.1203746109

Ko D and Helariutta Y (2017) Shoot–Root Communication in Flowering Plants. Curr

Biol 27:R973–R978. doi: 10.1016/j.cub.2017.06.054

Kondhare KR, Patil NS and Banerjee AK (2021) A historical overview of long-distance signalling in plants. J Exp Bot 72:4218–4236. doi: 10.1093/JXB/ERAB048

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010a) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/j.devcel.2010.05.008

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010b) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/J.DEVCEL.2010.05.008

Kulkarni SR, Vaneechoutte D, de Velde J Van and Vandepoele K (2018) TF2Network: predicting transcription factor regulators and gene regulatory networks in Arabidopsis using publicly available binding site information. Nucleic Acids Res.

Kumar P, Montgomery CE and Kiss JZ (2008) The role of phytochrome C in gravitropism and phototropism in Arabidopsis thaliana. Funct Plant Biol 35:298–305. doi: 10.1071/FP08013

Kumari S, Yadav S, Patra D, Singh S, Sarkar AK and Panigrahi KCS (2019) Uncovering the molecular signature underlying the light intensity-dependent root development in Arabidopsis thaliana. BMC Genomics 20:1–23. doi: 10.1186/s12864-019-5933-5

Kurata T and Yamamoto KT (1997) Light-stimulated root elongation in Arabidopsis thaliana. J Plant Physiol 151:346–351. doi: 10.1016/S0176-1617(97)80263-5

Kurihara Y, Makita Y, Shimohira H and Matsui M (2020) Time-Course Transcriptome Study Reveals Mode of bZIP Transcription Factors on Light Exposure in Arabidopsis. Int J Mol Sci 21:1993. doi: 10.3390/ijms21061993

Kushwaha R, Singh A and Chattopadhyay S (2008) Calmodulin7 Plays an Important Role as Transcriptional Regulator in Arabidopsis Seedling Development. Plant Cell 20:1747–1759. doi: 10.1105/TPC.107.057612

Kwok SF, Piekos B, Miśera S and Deng XW (1996) A complement of ten essential and pleiotropic arabidopsis COP/DET/FUS genes is necessary for repression of photomorphogenesis in darkness. Plant Physiol 110:731–742. doi: 10.1104/pp.110.3.731

Lacek J, García-González J, Weckwerth W and Retzer K (2021a) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 22:12784. doi: 10.3390/ijms222312784

Lacek J, García-González J, Weckwerth W and Retzer K (2021b) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 2021, Vol 22, Page 12784 22:12784. doi: 10.3390/IJMS222312784

Lau K, Podolec R, Chappuis R, Ulm R and Hothorn M (2019) Plant photoreceptors and their signaling components compete for COP1 binding via VP peptide motifs. EMBO J 38:e102140. doi: 10.15252/embj.2019102140

Lau OS and Deng XW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci 17:584–593. doi: 10.1016/J.TPLANTS.2012.05.004

Lau OS, Huang X, Charron J-B, Lee J-H, Li G and Deng XW (2011) Interaction of

Arabidopsis DET1 with CCA1 and LHY in mediating transcriptional repression in the plant circadian clock. Mol Cell 43:703. doi: 10.1016/J.MOLCEL.2011.07.013

Laxmi A, Pan J, Morsy M and Chen R (2008a) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Laxmi A, Pan J, Morsy M and Chen R (2008b) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Leasure CD, Tong H, Yuen G, Hou X, Sun X and He ZH (2009) Root UV-B sensitive2 acts with root UV-B sensitive1 in a root ultraviolet B-sensing pathway. Plant Physiol 150:1902–1915. doi: 10.1104/pp.109.139253

Lee H-J, Ha J-H, Kim S-G, Choi H-K, Kim ZH, Han Y-J, Kim J-I, Oh Y, Fragoso V, Shin K et al. (2016a) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal 9:1–9. doi: 10.1126/scisignal.aaf6530

Lee HJ, Ha JH, Kim SG, Choi HK, Kim ZH, Han YJ, Kim J Il, Oh Y, Fragoso V, Shin K et al. (2016b) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal. doi: 10.1126/SCISIGNAL.AAF6530

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017a) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/j.tplants.2017.06.009

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017b) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/J.TPLANTS.2017.06.009

Lee S, Wang W and Huq E (2021) Spatial regulation of thermomorphogenesis by HY5 and PIF4 in Arabidopsis. Nat Commun 2021 121 12:1–12. doi: 10.1038/s41467-021-24018-7

Leivar P and Monte E (2014) PIFs: Systems Integrators in Plant Development. Plant Cell 26:56–78. doi: 10.1105/TPC.113.120857

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008a) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi: 10.1016/j.cub.2008.10.058

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008b) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi: 10.1016/J.CUB.2008.10.058

Leivar P and Quail PH (2011) PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci 16:19–28. doi: 10.1016/j.tplants.2010.08.003

Leivar P, Tepperman JM, Monte E, Calderon RH, Liu TL and Quail PH (2009) Definition of early transcriptional circuitry involved in light-induced reversal of PIF-imposed repression of photomorphogenesis in young Arabidopsis seedlings. Plant Cell 21:3535–3553. doi: 10.1105/tpc.109.070672

Lejay L, Wirth J, Pervent M, Cross JMF, Tillard P and Gojon A (2008) Oxidative pentose phosphate pathway-dependent sugar sensing as a mechanism for regulation

of root ion transporters by photosynthesis. Plant Physiol 146:2036–2053. doi: 10.1104/pp.107.114710

Li L, Ljung K, Breton G, Schmitz RJ, Pruneda-Paz J, Cowing-Zitron C, Cole BJ, Ivans LJ, Pedmale U V, Jung HS et al. (2012) Linking photoreceptor excitation to changes in plant architecture. Genes Dev 26:785–790. doi: 10.1101/gad.187849.112

Li L and Sheen J (2016) Dynamic and diverse sugar signaling. Curr Opin Plant Biol 33:116–125. doi: 10.1016/j.pbi.2016.06.018

Li L, Xu J, Xu ZH and Xue HW (2005) Brassinosteroids stimulate plant tropisms through modulation of polar auxin transport in Brassica and Arabidopsis. Plant Cell 17:2738–2753. doi: 10.1105/tpc.105.034397

Li S, Yamada M, Han X, Ohler U and Benfey PN (2016) High-Resolution Expression Map of the Arabidopsis Root Reveals Alternative Splicing and lincRNA Regulation. Dev Cell 39:508–522. doi: 10.1016/j.devcel.2016.10.012

Li T, Lei W, He R, Tang X, Han J, Zou L, Yin Y, Lin H and Zhang D (2020) Brassinosteroids regulate root meristem development by mediating BIN2-UPB1 module in Arabidopsis. PLOS Genet 16:e1008883. doi: 10.1371/JOURNAL.PGEN.1008883

Li X, Cai W, Liu Y, Li H, Fu L, Liu Z, Xu L, Liu H, Xu T and Xiong Y (2017) Differential TOR activation and cell proliferation in Arabidopsis root and shoot apexes. Proc Natl Acad Sci 114:2765–2770. doi: 10.1073/pnas.1618782114

Li Y, Ende W Van den and Rolland F (2014) Sucrose Induction of Anthocyanin Biosynthesis Is Mediated by DELLA. Mol Plant 7:570–572. doi: 10.1093/MP/SST161

Liang S, Gao X, Wang Y, Zhang H, Yin K, Chen S, Zhang M and Zhao R (2020) Phytochrome-interacting factors regulate seedling growth through ABA signaling. Biochem Biophys Res Commun 526:1100–1105. doi: 10.1016/j.bbrc.2020.04.011

Liao Y, Smyth GK and Shi W (2014) featureCounts: an efficient general purpose program for assigning sequence reads to genomic features. Bioinformatics 30:923–930. doi: 10.1093/bioinformatics/btt656

Lilley JLS, Gee CW, Sairanen I, Ljung K and Nemhauser JL (2012) An endogenous carbon-sensing pathway Triggers increased auxin flux and hypocotyl elongation. Plant Physiol 160:2261–2270. doi: 10.1104/pp.112.205575

Liu G, Gao S, Tian H, Wu W, Robert HS and Ding Z (2016) Local Transcriptional Control of YUCCA Regulates Auxin Promoted Root-Growth Inhibition in Response to Aluminium Stress in Arabidopsis. PLOS Genet 12:e1006360. doi: 10.1371/journal.pgen.1006360

Liu M-J, Wu S-H, Chen H-M and Wu S-H (2012) Widespread translational control contributes to the regulation of Arabidopsis photomorphogenesis. Mol Syst Biol 8:566. doi: 10.1038/msb.2011.97

Liu TY, Chang CY and Chiou TJ (2009) The long-distance signaling of mineral macronutrients. Curr Opin Plant Biol 12:312–319. doi: 10.1016/j.pbi.2009.04.004

Liu X, Liu R, Li Y, Shen X, Zhong S and Shi H (2017) EIN3 and PIF3 form an interdependent module that represses chloroplast development in buried seedlings. Plant Cell 29:3051–3067. doi: 10.1105/tpc.17.00508

Ljung K, Bhalerao RP and Sandberg G (2001) Sites and homeostatic control of auxin

biosynthesis in Arabidopsis during vegetative growth. Plant J 28:465–474. doi: 10.1046/j.1365-313X.2001.01173.x

Ljung K, Hull AK, Celenza J, Yamada M, Estelle M, Normanly J and Sandberg G (2005) Sites and regulation of auxin biosynthesis in arabidopsis roots. Plant Cell 17:1090–1104. doi: 10.1105/tpc.104.029272

Ljung K, Nemhauser JL and Perata P (2015) New mechanistic links between sugar and hormone signalling networks. Curr Opin Plant Biol 25:130–137. doi: 10.1016/j.pbi.2015.05.022

Luo X-M, Lin W-H, Zhu S, Zhu J-Y, Sun Y, Fan X-Y, Cheng M, Hao Y, Oh E, Tian M et al. (2010) Integration of Light- and Brassinosteroid-Signaling Pathways by a GATA Transcription Factor in Arabidopsis. Dev Cell 19:872–883. doi: 10.1016/J.DEVCEL.2010.10.023

Lyu G, Li D, Li S and Hu H (2019) STO and GA negatively regulate UV-B-induced Arabidopsis root growth inhibition. Plant Signal Behav. doi: 10.1080/15592324.2019.1675471

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008a) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008b) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Yadav V, Negi P and Chattopadhyay S (2006) A basic leucine zipper transcription factor, G-box-binding factor 1, regulates blue light-mediated photomorphogenic growth in Arabidopsis. J Biol Chem 281:22190–22199. doi: 10.1074/jbc.M601172200

Mancini E, Sanchez SE, Romanowski A, Schlaen RG, Sanchez-Lamas M, Cerdán PD and Yanovsky MJ (2016) Acute Effects of Light on Alternative Splicing in Light-Grown Plants. Photochem Photobiol 92:126–133. doi: 10.1111/php.12550

Marchant A, Bhalerao R, Casimiro I, Eklöf J, Casero PJ, Bennett M and Sandberg G (2002) AUX1 promotes lateral root formation by facilitating indole-3-acetic acid distribution between sink and source tissues in the Arabidopsis seedling. Plant Cell 14:589–597. doi: 10.1105/tpc.010354

Matsubayashi Y (2014) Posttranslationally Modified Small-Peptide Signals in Plants. http://dx.doi.org/101146/annurev-arplant-050312-120122 65:385–413. doi: 10.1146/ANNUREV-ARPLANT-050312-120122

McAdam SAM, Brodribb TJ and Ross JJ (2016a) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McAdam SAM, Brodribb TJ and Ross JJ (2016b) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McNellis TW, von Arnim AG, Araki T, Komeda Y, Misera S and Deng X-W (1994) Genetic and Molecular Analysis of an Allelic Series of cop1 Mutants Suggests Functional Roles for the Multiple Protein Domains. Plant Cell 6:487. doi: 10.2307/3869929

Meng LS, Wei ZQ, Cao XY, Tong C, Lv MJ, Yu F and Loake GJ (2020) Cytosolic invertase-mediated root growth is feedback regulated by a glucose-dependent signaling loop. Plant Physiol 184:895–908. doi: 10.1104/pp.20.00778

Metsalu T and Vilo J (2015) ClustVis: A web tool for visualizing clustering of multivariate data using Principal Component Analysis and heatmap. Nucleic Acids Res 43:W566–W570. doi: 10.1093/nar/gkv468

Miotto YE, da Costa CT, Offringa R, Kleine-Vehn J and Maraschin F dos S (2021) Effects of Light Intensity on Root Development in a D-Root Growth System. Front Plant Sci 12:1–9. doi: 10.3389/fpls.2021.778382

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019a) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019b) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Mo M, Yokawa K, Wan Y and Baluska F (2015a) How and why do root apices sense light under the soil surface? Front Plant Sci 6:1–8. doi: 10.3389/fpls.2015.00775

Mo M, Yokawa K, Wan Y and Baluška F (2015b) How and why do root apices sense light under the soil surface? Front Plant Sci 6:775. doi: 10.3389/fpls.2015.00775

Möglich A, Yang X, Ayers RA and Moffat K (2010) Structure and function of plant photoreceptors. Annu Rev Plant Biol 61:21–47. doi: 10.1146/annurev-arplant-042809-112259

Molas ML, Kiss JZ and Correll MJ (2006) Gene profiling of the red light signalling pathways in roots. J Exp Bot 57:3217–3229. doi: 10.1093/jxb/erl086

Moni A, Lee A-Y, Briggs WR and Han I-S (2015) The blue light receptor Phototropin 1 suppresses lateral root growth by controlling cell elongation. Plant Biol 17:34–40. doi: 10.1111/PLB.12187

Morais DA DR (2017) Bioconductor - transcriptogramer. In: Morais DA, Dalmolin RJ (2017). Transcr. Transcr. Anal. based Transcr. doi 10.18129/B9.bioc.transcriptogramer, R Packag. https://bioconductor.org/packages/release/bioc/html/transcriptogramer.html. Accessed 12 Dec 2018

Mostafavi S, Ray D, Warde-Farley D, Grouios C and Morris Q (2008) GeneMANIA: A real-time multiple association network integration algorithm for predicting gene function. Genome Biol 9:S4. doi: 10.1186/gb-2008-9-s1-s4

Murashige T and Skoog F (1962) A Revised Medium for Rapid Growth and Bio Assays with Tobacco Tissue Cultures. Physiol Plant 15:473–497. doi: 10.1111/J.1399-3054.1962.TB08052.X

Ni M, Tepperman JM and Quail PH (1998a) PIF3, a phytochrome-interacting factor necessary for normal photoinduced signal transduction, is a novel basic helix-loop-helix protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Ni M, Tepperman JM and Quail PH (1998b) PIF3, a Phytochrome-Interacting Factor Necessary for Normal Photoinduced Signal Transduction, Is a Novel Basic Helix-

Loop-Helix Protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Notaguchi M, Wolf S and Lucas WJ (2012) Phloem-Mobile Aux/IAA Transcripts Target to the Root Tip and Modify Root ArchitectureF. J Integr Plant Biol 54:760–772. doi: 10.1111/J.1744-7909.2012.01155.X

Novák J, Černý M, Pavlů J, Zemánková J, Skalák J, Plačková L and Brzobohatý B (2014) Roles of proteome dynamics and cytokinin signaling in root to hypocotyl ratio changes induced by shading roots of arabidopsis seedlings. Plant Cell Physiol 56:1006–1018. doi: 10.1093/pcp/pcv026

Oh E, Kang H, Yamaguchi S, Park J, Lee D, Kamiya Y and Choi G (2009) Genome-wide analysis of genes targeted by PHYTOCHROME INTERACTING FACTOR 3-LIKE5 during seed germination in arabidopsis. Plant Cell 21:403–419. doi: 10.1105/tpc.108.064691

Oh E, Seo PJ and Kim J (2018) Signaling Peptides and Receptors Coordinating Plant Root Development. Trends Plant Sci 23:337–351. doi: 10.1016/J.TPLANTS.2017.12.007/ATTACHMENT/BD6CC66E-2342-46C7-8AA9-996959725A60/MMC2.PDF

Oh J, Park E, Song K, Bae G and Choi G (2019) PHYTOCHROME INTERACTING FACTOR 8 Inhibits Phytochrome A-mediated Far-red Light Responses in Arabidopsis. Plant Cell Adv Publ. doi: 10.1105/tpc.19.00515

Osterlund MT and Deng XW (1998) Multiple photoreceptors mediate the light-induced reduction of GUS-COP1 from Arabidopsis hypocotyl nuclei. Plant J 16:201–208. doi: 10.1046/j.1365-313X.1998.00290.x

Osterlund MT, Hardtke CS, Ning W and Deng XW (2000) Targeted destabilization of HY5 during light-regulated development of Arabidopsis. Nature 405:462–466. doi: 10.1038/35013076

Oyama T, Shimura Y and Okada K (1997) The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus- induced development of root and hypocotyl. Genes Dev 11:2983–2995. doi: 10.1101/gad.11.22.2983

Pacín M, Legris M and Casal JJ (2014) Rapid decline in nuclear COSTITUTIVE PHOTOMORPHOGENESIS1 abundance anticipates the stabilization of its target ELONGATED HYPOCOTYL5 in the light. Plant Physiol 164:1134–1138. doi: 10.1104/pp.113.234245

Paik I, Chen F, Ngoc Pham V, Zhu L, Kim J Il and Huq E (2019) A phyB-PIF1-SPA1 kinase regulatory complex promotes photomorphogenesis in Arabidopsis. Nat Commun 10:1–17. doi: 10.1038/s41467-019-12110-y

Pan Y and Shi H (2017) Stabilizing the Transcription Factors by E3 Ligase COP1. Trends Plant Sci 22:999–1001. doi: 10.1016/j.tplants.2017.09.012

Park BS, Eo HJ, Jang I-C, Kang H-G, Song JT and Seo HS (2010) Ubiquitination of LHY by SINAT5 regulates flowering time and is inhibited by DET1. Biochem Biophys Res Commun 398:242–246. doi: 10.1016/j.bbrc.2010.06.067

Peng P, Yan Z, Zhu Y and Li J (2008) Regulation of the Arabidopsis GSK3-like Kinase BRASSINOSTEROID-INSENSITIVE 2 through Proteasome-Mediated Protein Degradation. Mol Plant 1:338–346. doi: 10.1093/MP/SSN001

Petersson S V., Johansson AI, Kowalczyk M, Makoveychuk A, Wang JY, Moritz T, Grebe M, Benfey PN, Sandberg G and Ljung K (2009) An Auxin Gradient and

Maximum in the Arabidopsis Root Apex Shown by High-Resolution Cell-Specific Analysis of IAA Distribution and Synthesis. Plant Cell 21:1659–1668. doi: 10.1105/tpc.109.066480

Pham VN, Kathare PK and Huq E (2018a) Phytochromes and phytochrome interacting factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Kathare PK and Huq E (2018b) Phytochromes and phytochrome interacting factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Paik I, Hoecker U and Huq E (2020) Genomic evidence reveals SPA-regulated developmental and metabolic pathways in dark-grown Arabidopsis seedlings. Physiol Plant 169:380–396. doi: 10.1111/PPL.13095

Pham VN, Xu X and Huq E (2018c) Molecular bases for the constitutive photomorphogenic phenotypes in Arabidopsis. Development. doi: 10.1242/dev.169870

Podolec R and Ulm R (2018a) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Podolec R and Ulm R (2018b) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Ponnu J and Hoecker U (2021a) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/FPLS.2021.662793/BIBTEX

Ponnu J and Hoecker U (2021b) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/fpls.2021.662793

Ponnu J, Riedel T, Penner E, Schrader A and Hoecker U (2019) Cryptochrome 2 competes with COP1 substrates to repress COP1 ubiquitin ligase activity during Arabidopsis photomorphogenesis. Proc Natl Acad Sci U S A 116:27133–27141. doi: 10.1073/PNAS.1909181116/-/DCSUPPLEMENTAL

Prát T, Hajný J, Grunewald W, Vasileva M, Molnár G, Tejos R, Schmid M, Sauer M and Friml J (2018) WRKY23 is a component of the transcriptional network mediating auxin feedback on PIN polarity. PLOS Genet 14:e1007177. doi: 10.1371/journal.pgen.1007177

Qi L, Liu S, Li C, Fu J, Jing Y, Cheng J, Li H, Zhang D, Wang X, Dong X et al. (2020) PHYTOCHROME-INTERACTING FACTORS Interact with the ABA Receptors PYL8 and PYL9 to Orchestrate ABA Signaling in Darkness. Mol Plant 13:414–430. doi: 10.1016/j.molp.2020.02.001

Qu Y, Liu S, Bao W, Xue X, Ma Z, Yokawa K, Baluška F and Wan Y (2017) Expression of root genes in Arabidopsis seedlings grown by standard and improved growing methods. Int J Mol Sci 18:951. doi: 10.3390/ijms18050951

Quail PH (2007) Phytochrome-regulated Gene Expression. J Integr Plant Biol. doi: 10.1111/j.1672-9072.2007.00422.x

Ram H, Priya P, Jain M and Chattopadhyay S (2014) Genome-wide DNA binding of GBF1 is modulated by its heterodimerizing protein partners, HY5 and HYH. Mol Plant 7:448–451. doi: 10.1093/mp/sst143

Ranjan A, Fiene G, Fackendahl P and Hoecker U (2011) The Arabidopsis repressor of light signaling SPA1 acts in the phloem to regulate seedling de-etiolation, leaf

expansion and flowering time. Development 138:1851–1862. doi: 10.1242/dev.061036

Regnault T, Davière J-M, Wild M, Sakvarelidze-Achard L, Heintz D, Carrera Bergua E, Lopez Diaz I, Gong F, Hedden P and Achard P (2015) The gibberellin precursor GA_{12}acts as a long-distance growth signal in <italic>Arabidopsis</italic>. doi: 10.1038/NPLANTS.2015.73

Ritchie ME, Phipson B, Wu D, Hu Y, Law CW, Shi W and Smyth GK (2015) limma powers differential expression analyses for RNA-sequencing and microarray studies. Nucleic Acids Res. doi: 10.1093/nar/gkv007

Rolland F, Moore B and Sheen J (2002) Sugar sensing and signaling in plants. Plant Cell 14 Suppl:S185-205. doi: 10.1105/TPC.010455

Rosado D, Ackermann A, Spassibojko O, Rossi M and Pedmale U V (2021) WRKY transcription factors and ethylene signaling modify root growth during the shade-avoidance response. Plant Physiol. doi: 10.1093/PLPHYS/KIAB493

Rybarczyk-Filho JL, Castro MAA, Dalmolin RJS, Moreira JCF, Brunnet LG and de Almeida RMC (2011) Towards a genome-wide transcriptogram: the Saccharomyces cerevisiae case. Nucleic Acids Res 39:3005–16. doi: 10.1093/nar/gkq1269

Saijo Y, Sullivan J a, Wang H, Yang J, Shen Y, Rubio V, Ma L, Hoecker U and Deng XW (2003) The COP1-SPA1 interaction defines a critical step in phytochrome A-mediated regulation of HY5 activity. Genes Dev 17:2642–7. doi: 10.1101/gad.1122903

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013a) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013b) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sakaguchi J, Matsushita T and Watanabe Y (2019) DWARF4 accumulation in root tips is enhanced via blue light perception by cryptochromes. Plant Cell Environ 42:1615–1629. doi: 10.1111/pce.13510

Sakaguchi J and Watanabe Y (2017a) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakaguchi J and Watanabe Y (2017b) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakamoto K and Briggs WR (2002) Cellular and Subcellular Localization of Phototropin 1. Plant Cell 14:1723–1735. doi: 10.1105/TPC.003293

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K and Yamaguchi-Shinozaki K (2006) Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. Plant Cell 18:1292–1309. doi: 10.1105/tpc.105.035881

Sakuraba Y, Kanno S, Mabuchi A, Monda K, Iba K and Yanagisawa S (2018) A phytochrome-B-mediated regulatory mechanism of phosphorus acquisition. Nat Plants 4:1089–1101. doi: 10.1038/s41477-018-0294-7

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007a) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007b) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Sanchez SE, Rugnone ML and Kay SA (2020) Light Perception: A Matter of Time. Mol Plant 13(3):363–385. doi: 10.1016/j.molp.2020.02.006

Sassi M, Lu Y, Zhang Y, Wang J, Dhonukshe P, Blilou I, Dai M, Li J, Gong X, Jaillais Y et al. (2012) COP1 mediates the coordination of root and shoot growth by light through modulation of PIN1- and PIN2-dependent auxin transport in Arabidopsis. Development 139:3402–3412. doi: 10.1242/dev.078212

Schepetilnikov M, Makarian J, Srour O, Geldreich A, Yang Z, Chicher J, Hammann P and Ryabova LA (2017) GTPase ROP2 binds and promotes activation of target of rapamycin TOR in response to auxin. EMBO J 36:886–903. doi: 10.15252/embj.201694816

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992a) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992b) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Senapati D, Kushwaha R, Dutta S, Maurya JP, Biswas S, Gangappa SN and Chattopadhyay S (2019) COP1 regulates the stability of CAM7 to promote photomorphogenic growth. Plant Direct 3:1–14. doi: 10.1002/pld3.144

Seo HS, Yang J, Ishikawa M and Bolle C (2003) LAF1 ubiquitination by COP1 controls photomorphogenesis and is stimulated by SPA1. Nature 8:995–999. doi: 10.1038/nature01751.1.

Shaikhali J, Norén L, De Dios Barajas-López J, Srivastava V, König J, Sauer UH, Wingsle G, Dietz KJ and Strand Å (2012) Redox-mediated mechanisms regulate DNA binding activity of the G-group of basic region leucine zipper (bZIP) transcription factors in Arabidopsis. J Biol Chem 287:27510–27525. doi: 10.1074/jbc.M112.361394

Shani E, Weinstain R, Zhang Y, Castillejo C, Kaiserli E, Chory J, Tsien RY and Estelle M (2013) Gibberellins accumulate in the elongating endodermal cells of Arabidopsis root. Proc Natl Acad Sci U S A 110:4834–4839. doi: 10.1073/pnas.1300436110

Shannon P, Markiel A, Ozier O, Baliga NS, Wang JT, Ramage D, Amin N, Schwikowski B and Ideker T (2003) Cytoscape: A software Environment for integrated models of biomolecular interaction networks. Genome Res 13:2498–2504. doi: 10.1101/gr.1239303

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015a) Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant

Cell 27:189–201. doi: 10.1105/tpc.114.134775

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015b) Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant Cell 27:189–201. doi: 10.1105/tpc.114.134775

Shi H, Liu R, Xue C, Shen X, Wei N, Deng XW and Zhong S (2016) Seedlings Transduce the Depth and Mechanical Pressure of Covering Soil Using COP1 and Ethylene to Regulate EBF1/EBF2 for Soil Emergence. Curr Biol 26:139–149. doi: 10.1016/J.CUB.2015.11.053

Shi QM, Yang X, Song L and Xue HW (2011) Arabidopsis MSBP1 is activated by HY5 and HYH and is involved in photomorphogenesis and brassinosteroid sensitivity regulation. Mol Plant 4:1092–1104. doi: 10.1093/mp/ssr049

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009a) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009b) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Silva-Navas J, Moreno-Risueno MA, Manzano C, Pallero-Baena M, Navarro-Neila S, Téllez-Robledo B, Garcia-Mina JM, Baigorri R, Gallego FJ and Del Pozo JC (2015) D-Root: A system for cultivating plants with the roots in darkness or under different light conditions. Plant J 84:244–255. doi: 10.1111/tpj.12998

Silva-Navas J, Moreno-Risueno MA, Manzano C, Téllez-Robledo B, Navarro-Neila S, Carrasco V, Pollmann S, Gallego FJ and Del Pozo JC (2016) Flavonols mediate root phototropism and growth through regulation of proliferation-to-differentiation transition. Plant Cell 28:1372–1387. doi: 10.1105/tpc.15.00857

Singh A, Ram H, Abbas N and Chattopadhyay S (2012a) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Singh A, Ram H, Abbas N and Chattopadhyay S (2012b) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Skubacz A, Daszkowska-Golec A and Szarejko I (2016) The role and regulation of ABI5 (ABA-insensitive 5) in plant development, abiotic stress responses and phytohormone crosstalk. Front Plant Sci 7:1–18. doi: 10.3389/fpls.2016.01884

Spaninks K, van Lieshout J, van Ieperen W and Offringa R (2020) Regulation of Early Plant Development by Red and Blue Light: A Comparative Analysis Between Arabidopsis thaliana and Solanum lycopersicum. Front Plant Sci. doi: 10.3389/fpls.2020.599982

Spiegelman Z, Ham BK, Zhang Z, Toal TW, Brady SM, Zheng Y, Fei Z, Lucas WJ and Wolf S (2015) A tomato phloem-mobile protein regulates the shoot-to-root ratio by mediating the auxin response in distant organs. Plant J 83:853–863. doi: 10.1111/TPJ.12932

Srivastava AK, Senapati D, Srivastava A, Chakraborty M, Gangappa SN and Chattopadhyay S (2015) Short Hypocotyl in White Light1 Interacts with Elongated Hypocotyl5 (HY5) and Constitutive Photomorphogenic1 (COP1) and Promotes COP1-Mediated Degradation of HY5 during Arabidopsis Seedling Development. Plant Physiol 169:2922–2934. doi: 10.1104/PP.15.01184

Stewart JL, Maloof JN and Nemhauser JL (2011) PIF Genes Mediate the Effect of Sucrose on Seedling Growth Dynamics. PLoS One 6:e19894. doi: 10.1371/JOURNAL.PONE.0019894

Stracke R, Favory JJ, Gruber H, Bartelniewoehner L, Bartels S, Binkert M, Funk M, Weisshaar B and Ulm R (2010) The Arabidopsis bZIP transcription factor HY5 regulates expression of the PFG1/MYB12 gene in response to light and ultraviolet-B radiation. Plant, Cell Environ 33:88–103. doi: 10.1111/j.1365-3040.2009.02061.x

Sun N, Wang J, Gao Z, Dong J, He H, Terzaghi W, Wei N, Deng XW and Chen H (2016) Arabidopsis SAURs are critical for differential light regulation of the development of various organs. Proc Natl Acad Sci U S A 113:6071–6. doi: 10.1073/pnas.1604782113

Supek F, Bošnjak M, Škunca N and Šmuc T (2011) REVIGO Summarizes and Visualizes Long Lists of Gene Ontology Terms. PLoS One 6:e21800. doi: 10.1371/journal.pone.0021800

Swarup K, Benková E, Swarup R, Casimiro I, Péret B, Yang Y, Parry G, Nielsen E, De Smet I, Vanneste S et al. (2008) The auxin influx carrier LAX3 promotes lateral root emergence. Nat Cell Biol 10:946–954. doi: 10.1038/ncb1754

Szklarczyk D, Morris JH, Cook H, Kuhn M, Wyder S, Simonovic M, Santos A, Doncheva NT, Roth A, Bork P et al. (2017) The STRING database in 2017: quality-controlled protein-protein association networks, made broadly accessible. Nucleic Acids Res 45:D362–D368. doi: 10.1093/nar/gkw937

Tabata R, Sumida K, Yoshii T, Ohyama K, Shinohara H and Matsubayashi Y (2014) Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. Science 346:343–346. doi: 10.1126/SCIENCE.1257800

Tan H, Man C, Xie Y, Yan J, Chu J and Huang J (2019) A Crucial Role of GA-Regulated Flavonol Biosynthesis in Root Growth of Arabidopsis. Mol Plant 12:521–537. doi: 10.1016/j.molp.2018.12.021

Tang W, Ji Q, Huang Y, Jiang Z, Bao M, Wang H and Lin R (2013) FAR-RED ELONGATED HYPOCOTYL3 and FAR-RED IMPAIRED RESPONSE1 Transcription Factors Integrate Light and Abscisic Acid Signaling in Arabidopsis 1[C][W][OPEN]. doi: 10.1104/pp.113.224386

Tepperman JM, Hudson ME, Khanna R, Zhu T, Chang SH, Wang X and Quail PH (2004) Expression profiling of phyB mutant demonstrates substantial contribution of other phytochromes to red-light-regulated gene expression during seedling de-etiolation. Plant J 38:725–739. doi: 10.1111/j.1365-313X.2004.02084.x

Tepperman JM, Zhu T, Chang H-S, Wang X and Quail PH (2001) Multiple transcription-factor genes are early targets of phytochrome A signaling. Proc Natl Acad Sci 98:9437–9442. doi: 10.1073/pnas.161300998

Thieme CJ, Rojas-Triana M, Stecyk E, Schudoma C, Zhang W, Yang L, Miñambres M, Walther D, Schulze WX, Paz-Ares J et al. (2015) Endogenous Arabidopsis messenger RNAs transported to distant tissues. Nat Plants 2015 14 1:1–9. doi:

10.1038/nplants.2015.25

Tian T, Liu Y, Yan H, You Q, Yi X, Du Z, Xu W and Su Z (2017) agriGO v2.0: a GO analysis toolkit for the agricultural community, 2017 update. Nucleic Acids Res 45:W122–W129. doi: 10.1093/nar/gkx382

Tilbrook K, Arongaus AB, Binkert M, Heijde M, Yin R and Ulm R (2013) The UVR8 UV-B Photoreceptor: Perception, Signaling and Response. Arab B 11:e0164. doi: 10.1199/tab.0164

Tong H, Leasure CD, Hou X, Yuen G, Briggs W and He ZH (2008) Role of root UV-B sensing in Arabidopsis early seedling development. Proc Natl Acad Sci U S A 105:21039–21044. doi: 10.1073/pnas.0809942106

Ubeda-Tomás S, Federici F, Casimiro I, Beemster GTS, Bhalerao R, Swarup R, Doerner P, Haseloff J and Bennett MJ (2009) Gibberellin Signaling in the Endodermis Controls Arabidopsis Root Meristem Size. Curr Biol 19:1194–1199. doi: 10.1016/j.cub.2009.06.023

Ubeda-Tomás S, Swarup R, Coates J, Swarup K, Laplaze L, Beemster GTS, Hedden P, Bhalerao R and Bennett MJ (2008) Root growth in Arabidopsis requires gibberellin/DELLA signalling in the endodermis. Nat Cell Biol 10:625–628. doi: 10.1038/ncb1726

Unterholzner SJ, Rozhon W, Papacek M, Ciomas J, Lange T, Kugler KG, Mayer KF, Sieberer T and Poppenberger B (2015) Brassinosteroids are master regulators of gibberellin biosynthesis in Arabidopsis. Plant Cell 27:2261–2272. doi: 10.1105/tpc.15.00433

van Gelderen K, Kang C, Paalman R, Keuskamp D, Hayes S and Pierik R (2018a) Far-red light detection in the shoot regulates lateral root development through the HY5 transcription factor. Plant Cell 30:101–116. doi: 10.1105/tpc.17.00771

van Gelderen K, Kang C and Pierik R (2018b) Light Signaling, Root Development, and Plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Van Gelderen K, Kang C and Pierik R (2018) Light signaling, root development, and plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Vaseva II, Qudeimat E, Potuschak T, Du Y, Genschik P, Vandenbussche F and Van Der Straeten D (2018) The plant hormone ethylene restricts Arabidopsis growth via the epidermis. Proc Natl Acad Sci 115:E4130–E4139. doi: 10.1073/pnas.1717649115

von Arnim AG and Deng X-W (1994) Light inactivation of arabidopsis photomorphogenic repressor COP1 involves a cell-specific regulation of its nucleocytoplasmic partitioning. Cell 79:1035–1045. doi: 10.1016/0092-8674(94)90034-5

Vukašinović N, Wang Y, Vanhoutte I, Fendrych M, Guo B, Kvasnica M, Jiroutová P, Oklestkova J, Strnad M and Russinova E (2021) Local brassinosteroid biosynthesis enables optimal root growth. Nat Plants 7:619–632. doi: 10.1038/s41477-021-00917-x

Wan Y, Jasik J, Wang L, Hao H, Volkmann D, Menzel D, Mancuso S, Baluška F and Lin J (2012) The signal transducer NPH3 integrates the phototropin1 photosensor with PIN2-based polar auxin transport in Arabidopsis root phototropism. Plant Cell 24:551–565. doi: 10.1105/tpc.111.094284

Wan Y, Yokawa K and Baluška F (2019) Arabidopsis Roots and Light: Complex

Interactions. Mol Plant 12:1428–1430. doi: 10.1016/j.molp.2019.10.001

Wan YL, Eisinger W, Ehrhardt D, Kubitscheck U, Baluska F and Briggs W (2008) The subcellular localization and blue-light-induced movement of phototropin 1-GFP in etiolated seedlings of Arabidopsis thaliana. Mol Plant 1:103–117. doi: 10.1093/mp/ssm011

Wang W, Chen Q, Botella JR and Guo S (2019) Beyond light: Insights into the role of constitutively photomorphogenic1 in plant hormonal signaling. Front Plant Sci 10:557. doi: 10.3389/FPLS.2019.00557/BIBTEX

Wang W, Paik I, Kim J, Hou X, Sung S and Huq E (2021) Direct phosphorylation of HY5 by SPA kinases to regulate photomorphogenesis in Arabidopsis. New Phytol 230:2311–2326. doi: 10.1111/nph.17332

Wei N, Kwok SF, von Arnim AG, Lee A, McNellis TW, Piekos B, Deng XW, Deng XW and Chen H (1994) Arabidopsis COP8, COP10, and COP11 Genes Are Involved in Repression of Photomorphogenic Development in Darkness. PLANT CELL ONLINE 6:629–643. doi: 10.1105/tpc.6.5.629

Wieczorek K, Golecki B, Gerdes L, Heinen P, Szakasits D, Durachko DM, Cosgrove DJ, Kreil DP, Puzio PS, Bohlmann H et al. (2006) Expansins are involved in the formation of nematode-induced syncytia in roots of Arabidopsis thaliana. Plant J 48:98–112. doi: 10.1111/J.1365-313X.2006.02856.X

Willige BC, Zander M, Yoo CY, Phan A, Garza RM, Trigg SA, He Y, Nery JR, Chen H, Chen M et al. (2021) PHYTOCHROME-INTERACTING FACTORs trigger environmentally responsive chromatin dynamics in plants. Nat Genet 53:955–961. doi: 10.1038/s41588-021-00882-3

Wilson K, Long D, Swinburne J and Coupland G (1996) A Dissociation insertion causes a semidominant mutation that increases expression of TINY, an arabidopsis gene related to APETALA2. Plant Cell 8:659–671. doi: 10.1105/tpc.8.4.659

Woerlen N, Allam G, Popescu A, Corrigan L, Pautot V and Hepworth SR (2017) Repression of BLADE-ON-PETIOLE genes by KNOX homeodomain protein BREVIPEDICELLUS is essential for differentiation of secondary xylem in Arabidopsis root. Planta 2017 2456 245:1079–1090. doi: 10.1007/S00425-017-2663-2

Wu Y, Shi L, Li L, Fu L, Liu Y, Xiong Y and Sheen J (2019) Integration of nutrient, energy, light, and hormone signalling via TOR in plants. J Exp Bot 70:2227–2238. doi: 10.1093/jxb/erz028

Xie Z, Nolan T, Jiang H, Tang B, Zhang M, Li Z and Yin Y (2019) The AP2/ERF transcription factor TINY modulates brassinosteroid-regulated plant growth and drought responses in arabidopsis. Plant Cell 31:1788–1806. doi: 10.1105/tpc.18.00918

Xiong Y, McCormack M, Li L, Hall Q, Xiang C and Sheen J (2013) Glucose–TOR signalling reprograms the transcriptome and activates meristems. Nature 496:181–186. doi: 10.1038/nature12030

Xiong Y and Sheen J (2012) Rapamycin and glucose-target of rapamycin (TOR) protein signaling in plants. J Biol Chem 287:2836–2842. doi: 10.1074/jbc.M111.300749

Xu D, Jiang Y, Li J, Holm M and Deng XW (2018) The B-Box Domain Protein BBX21 Promotes Photomorphogenesis. Plant Physiol 176:2365–2375. doi:

10.1104/PP.17.01305

Xu D, Jiang Y, Li J, Lin F, Holm M and Deng XW (2016) BBX21, an Arabidopsis B-box protein, directly activates HY5 and is targeted by COP1 for 26S proteasome-mediated degradation. Proc Natl Acad Sci 113:7655–7660. doi: 10.1073/PNAS.1607687113

Xu D, Li J, Gangappa SN, Hettiarachchi C, Lin F, Andersson MX, Jiang Y, Deng XW and Holm M (2014a) Convergence of Light and ABA Signaling on the ABI5 Promoter. PLoS Genet 10:e1004197. doi: 10.1371/journal.pgen.1004197

Xu P, Chen H, Li T, Xu F, Mao Z, Cao X, Miao L, Du S, Hua J, Zhao J et al. Blue light-dependent interactions of CRY1 with GID1 and DELLA proteins regulate gibberellin signaling and photomorphogenesis in Arabidopsis. doi: 10.1093/plcell/koab124

Xu W, Ding G, Yokawa K, Baluška F, Li QF, Liu Y, Shi W, Liang J and Zhang J (2013) An improved agar-plate method for studying root growth and response of Arabidopsis thaliana. Sci Rep 3:1–7. doi: 10.1038/srep01273

Xu X, Kathare PK, Pham VN, Bu Q, Nguyen A and Huq E (2017) Reciprocal proteasome-mediated degradation of PIFs and HFR1 underlies photomorphogenic development in Arabidopsis. Dev 144:1831–1840. doi: 10.1242/dev.146936

Xu X, Paik I, Zhu L, Bu Q, Huang X, Deng XW and Huq E (2014b) PHYTOCHROME INTERACTING FACTOR1 enhances the E3 ligase activity of CONSTITUTIVE PHOTOMORPHOGENIC1 to synergistically repress photomorphogenesis in Arabidopsis. Plant Cell 26:1992–2006. doi: 10.1105/tpc.114.125591

Xu X, Paik I, Zhu L and Huq E (2015a) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. Trends Plant Sci 20:641–650. doi: 10.1016/j.tplants.2015.06.010

Xu X, Paik I, Zhu L and Huq E (2015b) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. doi: 10.1016/j.tplants.2015.06.010

Yadukrishnan P and Datta S (2021) Light and abscisic acid interplay in early seedling development. New Phytol 229:763–769. doi: 10.1111/NPH.16963

Yadukrishnan P, Rahul PV and Datta S (2020a) HY5 Suppresses, Rather Than Promotes, Abscisic Acid-Mediated Inhibition of Postgermination Seedling Development. Plant Physiol 184:574–578. doi: 10.1104/pp.20.00783

Yadukrishnan P, Rahul PV, Ravindran N, Bursch K, Johansson H and Datta S (2020b) CONSTITUTIVELY PHOTOMORPHOGENIC1 promotes ABA-mediated inhibition of post-germination seedling establishment. Plant J 103:481–496. doi: 10.1111/tpj.14844

Yang M, Li C, Cai Z, Hu Y, Nolan T, Yu F, Yin Y, Xie Q, Tang G and Wang X (2017a) SINAT E3 Ligases Control the Light-Mediated Stability of the Brassinosteroid-Activated Transcription Factor BES1 in Arabidopsis. Dev Cell 41:47. doi: 10.1016/J.DEVCEL.2017.03.014

Yang X, Song L and Xue H-W (2008) Membrane Steroid Binding Protein 1 (MSBP1) Stimulates Tropism by Regulating Vesicle Trafficking and Auxin Redistribution. Mol Plant 1:1077–1087. doi: 10.1093/MP/SSN071

Yang Y and Liu H (2020) Coordinated Shoot and Root Responses to Light Signaling

in Arabidopsis. Plant Commun 1:100026. doi: 10.1016/j.xplc.2020.100026

Yang Y, Zhang L, Chen P, Liang T, Li X and Liu H (2020) UV-B photoreceptor UVR8 interacts with MYB73/MYB77 to regulate auxin responses and lateral root development. EMBO J. doi: 10.15252/embj.2019101928

Yang Z, Liu B, Su J, Liao J, Lin C and Oka Y (2017b) Cryptochromes Orchestrate Transcription Regulation of Diverse Blue Light Responses in Plants. Photochem Photobiol 93:112–127. doi: 10.1111/php.12663

Yeh C-M, Kobayashi K, Fujii S, Fukaki H, Mitsuda N and Ohme-Takagi M (2020) Blue Light Regulates Phosphate Deficiency-Dependent Primary Root Growth Inhibition in Arabidopsis. Front Plant Sci 0:1803. doi: 10.3389/FPLS.2019.01803

Yokawa K, Fasano R, Kagenishi T and BaluÅ¡ka F (2014) Light as stress factor to plant roots â€“ case of root halotropism. Front Plant Sci 5:1–9. doi: 10.3389/fpls.2014.00718

Yokawa K, Kagenishi T and Baluška F (2013) Root photomorphogenesis in laboratory-maintained Arabidopsis seedlings. Trends Plant Sci 18:117–119. doi: 10.1016/j.tplants.2013.01.002

Yokawa K, Kagenishi T, Kawano T, Mancuso S and Baluška F (2011) Illumination of arabidopsis roots induces immediate burst of ROS production. Plant Signal Behav 6:1460–1464. doi: 10.4161/psb.6.10.18165

Yu X, Liu H, Klejnot J and Lin C (2010) The Cryptochrome Blue Light Receptors. Arab B 8:e0135. doi: 10.1199/tab.0135

Yuan X, Xu P, Yu Y and Xiong Y (2020) Glucose-TOR signaling regulates PIN2 stability to orchestrate auxin gradient and cell expansion in Arabidopsis root. Proc Natl Acad Sci U S A 117:32223–32225. doi: 10.1073/pnas.2015400117

Zdanio M, Boron AK, Balcerowicz D, Schoenaers S, Markakis MN, Mouille G, Pintelon I, Suslov D, Gonneau M, Höfte H et al. (2020) The Proline-Rich Family Protein EXTENSIN33 Is Required for Etiolated Arabidopsis thaliana Hypocotyl Growth. Plant Cell Physiol 61:1191–1203. doi: 10.1093/PCP/PCAA049

Zeng J, Wang Q, Lin J, Deng K, Zhao X, Tang D and Liu X Arabidopsis cryptochrome-1 restrains lateral roots growth by inhibiting auxin transport. JI Plant Physiol 167:670–673. doi: 10.1016/j.jplph.2009.12.003

Zhang B, Holmlund M, Lorrain S, Norberg M, Bakó LS, Fankhauser C and Nilsson O (2017a) BLADE-ON-PETIOLE proteins act in an E3 ubiquitin ligase complex to regulate PHYTOCHROME INTERACTING FACTOR 4 abundance. Elife. doi: 10.7554/eLife.26759

Zhang H, He H, Wang X, Wang X, Yang X, Li L and Deng XW (2011a) Genome-wide mapping of the HY5-mediated genenetworks in Arabidopsis that involve both transcriptional and post-transcriptional regulation. Plant J 65:346–358. doi: 10.1111/J.1365-313X.2010.04426.X

Zhang Y, Li C, Zhang J, Wang J, Yang J, Lv Y, Yang N, Liu J, Wang X, Palfalvi G et al. (2017b) Dissection of HY5/HYH expression in Arabidopsis reveals a root-autonomous HY5-mediated photomorphogenic pathway. PLoS One 12:e0180449. doi: 10.1371/journal.pone.0180449

Zhang Y, Wang C, Xu H, Shi X, Zhen W, Hu Z, Huang J, Zheng Y, Huang P, Zhang KX et al. (2019) HY5 Contributes to Light-Regulated Root System Architecture

Under a Root-Covered Culture System. Front Plant Sci 10:1490. doi: 10.3389/FPLS.2019.01490/BIBTEX

Zhang Z, Zhu J-Y, Roh J, Marchive C, Kim S-K, Meyer C, Sun Y, Wang W and Wang Z-Y (2016) TOR Signaling Promotes Accumulation of BZR1 to Balance Growth with Carbon Availability in Arabidopsis. Curr Biol 26:1854–1860. doi: 10.1016/j.cub.2016.05.005

Zhang ZL, Ogawa M, Fleet CM, Zentella R, Hu J, Heo JO, Lim J, Kamiya Y, Yamaguchi S and Sun TP (2011b) SCARECROW-LIKE 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in Arabidopsis. Proc Natl Acad Sci U S A 108:2160–2165. doi: 10.1073/pnas.1012232108

Zhong M, Zeng B, Tang D, Yang J, Qu L, Yan J, Wang X, Li X, Liu X and Zhao X (2021) The blue light receptor CRY1 interacts with GID1 and DELLA proteins to repress GA signaling during photomorphogenesis in Arabidopsis. Mol Plant 14:1328–1342. doi: 10.1016/J.MOLP.2021.05.011

Zhu L, Bu Q, Xu X, Paik I, Huang X, Hoecker U, Deng XW and Huq E (2015) CUL4 forms an E3 ligase with COP1 and SPA to promote light-induced degradation of PIF1. Nat Commun 6:1–10. doi: 10.1038/ncomms8245

Table 1. Root effects of light signaling components

Gene	AGI code	Protein identity	Signaling role	Processes involved in roots	Refs
CRY1	AT4G08920	cryptochrome 1(CRY1)	Photoperception	Shoot activated CRY1 positively controls primary root growth and restrains lateral root growth by inhibiting auxin transport. Blue light promotes DWF4 expression and BR biosynthesis in root tips	
CRY2	AT1G04400	cryptochrome 2(CRY2)	Photoperception	CRY2 negatively controls primary root elongation under higher blue light intensity	(Canamero et al. 2006)
CRY3	AT5G24850	cryptochrome 3(CRY3)	Photoperception	N/A	
PHOT1	AT3G45780	phototropin 1(PHOT1)	Photoperception	PHOT1 is expressed in the root elongation zone stele and cortex. PHOT1 is involved in negative root phototropism and suppresses lateral root growth	(Sakamoto and Briggs 2002; Galen et al. 2007; Wan et al. 2008; Wan et al. 2012; Silva-Navas et al. 2015; Moni et al. 2015)
PHOT2	AT5G58140	phototropin 2(PHOT2)	Photoperception	N/A	
PHYA	AT1G09570	phytochrome A(PHYA)	Photoperception	Shoot activated PHYA induces shoot-derived auxin transport to promote LR growth	(Salisbury et al. 2007a; Silva-Navas et al. 2015; Kumari et al. 2019)
PHYB	AT2G18790	phytochrome B(PHYB)	Photoperception	Both shoot and root-activated PHYB promote primary root growth	(Salisbury et al. 2007a; Silva-Navas et al. 2015; Kumari et al. 2019)
PHYC	AT5G35840	phytochrome C(PHYC)	Photoperception	PHYC attenuates the positive red-light phototropic response in roots.	(Kumar et al. 2008)
PHYD	AT4G16250	phytochrome D(PHYD)	Photoperception	PHYD acts in root growth inhibition in response to direct red light alongside PHYA and PHYB	(Correll and Kiss 2005a)
PHYE	AT4G18130	phytochrome E(PHYE)	Photoperception	N/A	
UVR8	AT5G63860	Ultraviolet-B receptor (UVR8)	Photoperception	UVR8 inhibits auxin responses in a tissue-autonomous manner and thereby regulates lateral root growth.	(Yang and Liu 2020)(Yang et al. 2020)
COP1	AT2G32950	Transducin/WD40 repeat-like superfamily protein(COP1)	Photoperception	COP1 represses root growth by inhibiting PIN1 and PIN2 in the root as well as maintaining low levels of positive photomorphogenic transcriptional regulators in the dark	(Sassi et al. 2012)(Bhatnagar et al. 2020)(Ponnu and Hoecker 2021b)
DET1	AT4G10180	deetiolated1	Ubiquitin-Proteasome	Represses photomorphogenesis maintaining low levels of positive photomorphogenic transcriptional regulators in the dark	(Cañibano et al. 2021)
BBX21	AT1G75540	salt tolerance homolog2 (STH2/BBX21)	COP1 Ub-target	HY5 positive regulator, represses the formation of lateral roots	(Xu et al. 2016)(Xu et al. 2018)(Job et al. 2018)
BBX32	AT3G21150	B-box type zinc finger protein 32(BBX32)	COP1 Ub-target	BBX32 is a HY5 negative regulator and suppresses blue-light dependent Pi starvation responses.	(Yeh et al. 2020)(Holtan et al. 2011)

BBX24	AT1G06040	B-box type zinc finger protein 24	COP1 Ub-target	HY5 negative regulator. BBX24 is a negative regulator of UV-B inhibition of root growth.	(Job et al. 2018)(Lyu et al. 2019)
BBX25	AT2G31380	B-box type zinc finger protein 25 , salt tolerance homolog1 (STH/BBX25)	COP1 Ub-target	BBX25 acts as a negative regulator of photomorphogenesis enhancing COP1 and suppressing HY5 functions.	(Gangappa et al. 2013b)(Gangappa et al. 2013a)
BBX4/COL3	AT2G24790	B-box type zinc finger protein 4 (CONSTANS-LIKE3)	COP1 Ub-target	BBX4/COL3 is a positive regulator of photomorphogenesis that acts downstream of COP1 and can promote lateral root development independently of COP1	(Datta et al. 2006)
GAI	AT1G14920	GRAS family transcription factor family protein (DELLA protein GAI)	COP1 Ub-target	DELLAs reduce ROS and promote flavonol accumulation in roots	(Achard et al. 2008)(Tan et al. 2019)
RGA1	AT2G01570	GRAS family transcription factor family protein (DELLA protein RGA1)	COP1 Ub-target		
RGL1	AT1G66350	GRAS family transcription factor family protein (DELLA protein RGA-like 1)	COP1 Ub-target		
RGL2	AT3G03450	GRAS family transcription factor family protein (DELLA protein RGA-like 2)	COP1 Ub-target		
RGL3	AT5G17490	GRAS family transcription factor family protein (DELLA protein RGA-like 3)	COP1 Ub-target		
GATA2	AT2G45050	GATA transcription factor 2(GATA2)	COP1 Ub-target	GATA2 is a positive regulator of photomorphogenesis and key player in the specification of the root transition domain	(Luo et al. 2010)(Jiang et al. 2017)
GBF1	AT4G36730	G-box binding factor 1(GBF1)	COP1 Ub-target	GBF1 interacts and heterodimerizes with HY5 and HYH proteins to regulate photomorphogenic growth	(Singh et al. 2012a)(Ram et al. 2014)
HY5	AT5G11260	Basic-leucine zipper (bZIP) transcription factor family protein(HY5)	COP1 Ub-target	Main photomorphogenesis regulator, induces primary root growth and represses lateral root growth under shade. Activates nitrate uptake via NRT2.1	(Oyama et al. 1997)(Burko et al. 2020a)(Zhang et al. 2017b)
HYH	AT3G17609	HY5-homolog(HYH)	COP1 Ub-target	HY5 activates HYH expression in roots and contributes to root growth under different light conditions	(Zhang et al. 2017b)
BIN2	AT4G18710	Protein kinase superfamily protein	COP1 Ub-target	Represses root growth via inhibition of BR siganling. BIN2 activates UPB1 via direct phosphorylation, which represses the expression of root peroxidases.	(Li et al. 2020)(Peng et al. 2008)
EBF1	AT2G25490	EIN3-binding F box protein 1	COP1 Ub-target	Repressor of ethylene responses and PIF3	(Binder et al. 2007; Shi et al. 2016; Pan and Shi 2017; Dong et al. 2017a)
EBF2	AT5G25350	EIN3-binding F box protein 2	COP1 Ub-target	Repressor of ethylene responses and PIF3	
GI	AT1G22770	gigantea protein (GI)	COP1 Ub-target	GI integrates circadian oscillation in roots	(Bouché et al. 2016)
FAR1	AT4G15090	FRS (FAR1 Related Sequences) transcription factor family	COP1 regulation	*FAR1* promoter main root growth and represses lateral roots	(Tang et al. 2013)

FHY3	AT3G22170	FRS (FAR1 Related Sequences) transcription factor family	COP1 regulation	FAR1 and FHY3 contribute to ABA-dependent inhibition of root elongation.	(Tang et al. 2013)
RPS6	AT4G31700	ribosomal protein S6	COP1 regulation	RPS6 acts downstream of TOR to enhance translation triggered by light. No root effect described yet.	(Chen et al. 2018)
TOR	AT1G50030	Target of Rapamycin kinase	COP1 regulation	COP1 represses TOR activity in dark-grown seedlings. TOR integrates auxin-ROP2 and glucose energy signals to activate E2Fa, leading to cell proliferation in the root. TOR phosphorylates and stabilizes PIN2 and influences the gradient distribution of PIN2 in the Arabidopsis primary root.	(Li et al. 2017)(Yuan et al. 2020)(Xiong et al. 2013)(Xiong and Sheen 2012)(Fu et al. 2021)
BRI1	AT4G39400	BRASSINOSTEROID INSENSITIVE 1, Leucine-rich receptor-like protein kinase family protein	COP1 regulation	BRI1 activity in the epidermis promotes root meristem size. BRI1 is required for root vascular cell-fate maintenance.	(Vukašinović et al. 2021)(Hacham et al. 2011)(Jaillais and Vert 2016)(Cosme et al. 2021)(Cosme et al. 2021)(Cosme et al. 2021)(Caño-Delgado et al. 2010; Ranjan et al. 2011)
ROP2	AT1G20090	RHO-related protein from plants 2. Rho GTPase family	COP1 regulation	Light promoted auxin signaling in roots activates ROP2-dependent TOR activation of translation	(Schepetilnikov et al. 2017)(Li et al. 2017)
SPA1	AT2G46340	SPA (suppressor of phyA-105) protein family(SPA1)	COP1 regulation	Photomorphogenesis repressor	(Xu et al. 2014b)(Balcerowicz et al. 2011)(Saijo et al. 2003)(Hoecker and Quail 2001; Sheerin et al. 2015a; Balcerowicz et al. 2017; Paik et al. 2019; Pham et al. 2020; Lee et al. 2021)
SPA2	AT4G11110	SPA1-related 2(SPA2)	COP1 regulation	Photomorphogenesis repressor	
SPA3	AT3G15354	SPA1-related 3(SPA3)	COP1 regulation	Photomorphogenesis repressor	
SPA4	AT1G53090	SPA1-related 4(SPA4)	COP1 regulation	Photomorphogenesis repressor	
MSBP1	At5g52240	membrane steroid binding protein 1	HY5 signaling	MSBP1 is a direct HY5/HYH target. Stimulates PIN2 cycling under gravi-stimulation.	(Yang et al. 2008)(Shi et al. 2011)
CAM7	AT3G43810	calmodulin 7(CAM7), transcription factor	HY5 signaling	CAM7 and HY5 genetically interact to control lateral root growth and ABA responses. The *cam7* mutant suppresses the *lhy5* lateral root phenotype.	(Senapati et al. 2019)(Kushwaha et al. 2008; Abbas et al. 2014)
PKL	AT2G25170	chromatin remodeling factor CHD3 (PICKLE)(PKL)	HY5 signaling	Repressor of HY5 expression. Negatively regulates auxin-mediated LR formation via ARF7/ARF19	(Jing et al. 2013)(Fukaki et al. 2006; Jing and Lin 2013)
SHW1	AT1G69935	short hypocotyl in white light1(SHW1)	HY5 signaling	SHW1 promotes COP1-mediated degradation of HY5. The *shw1* mutants display shorter main roots and suppress the gravitropic defects of *hy5* roots.	(Bhatia et al. 2008)(Srivastava et al. 2015)

TCP2	AT4G18390	TEOSINTE BRANCHED 1, cycloidea and PCF transcription factor 2(TCP2)	HY5 signaling	CRY1 interactor, positive regulator of HY5/HYH	(He et al. 2016)
PIF1	AT2G20180	bHLH transcription factor , phytochrome interacting factor 3-like 5 (PIL5/PIF1)	PIF signaling	N/A	(Shin et al. 2009a; Pham et al. 2018c; Paik et al. 2019)
PIL1/PIF2	AT2G46970	bHLH transcription factor , phytochrome interacting factor 3-like 1 (PIL1/PIF2)	PIF signaling	N/A	
PIF3	AT1G09530	bHLH transcription factor , phytochrome interacting factor 3(PIF3)	PIF signaling	PIF3 is involved in the inhibition of root growth induced by nitric oxide (NO) in light. PIF3 interacts with EIN3 in a interdependent regulatory module.	(Liu et al. 2017)(Bai et al. 2014)
PIF4	AT2G43010	bHLH transcription factor , phytochrome interacting factor 4(PIF4)	PIF signaling	PIF4 promotes Al-inhibition of primary root growth by repressing YUCCAs.	(Liu et al. 2016)
PIF5	AT3G59060	bHLH transcription factor, phytochrome interacting factor 3-like 6 (PIL6/PIF5)	PIF signaling	N/A	(Hornitschek et al. 2012; Pham et al. 2018c)
PIF6	AT3G62090	bHLH transcription factor, phytochrome interacting factor 3-like 2 (PIL2/PIF6)	PIF signaling	N/A	(Khanna et al. 2004)
PIF7	AT5G61270	bHLH transcription factor, phytochrome interacting factor 7(PIF7)	PIF signaling	N/A	(Li et al. 2012; Willige et al. 2021)
PIF8	AT4G00050	bHLH transcription factor, phytochrome interacting factor 8(PIF8)	PIF signaling	N/A	
BOP1	AT3G57130	Ankyrin repeat family protein / BTB/POZ domain-containing protein	PIF signaling	BOP1/2 control root secondary growth through activation of KNOX boundary genes and promote the expression of lignin biosynthetic genes	(Woerlen et al. 2017)(Zhang et al. 2017a)
BOP2	AT2G41370	Ankyrin repeat family protein / BTB/POZ domain-containing protein	PIF signaling		
LRB1	AT2G46260	BTB/POZ/Kelch-associated protein, Light Responsive BTB protein1 (LRB1)	PIF signaling	*lrb12* mutants display longer main roots	(Christians et al. 2012)
LRB2	AT3G61600	BTB/POZ/Kelch-associated protein, Light Responsive BTB protein2 (LRB2)	PIF signaling		

Capítulo III

- Identification of shoot light-responsive genes in *Arabidopsis* through a survey of public datasets -

Manuscrito publicado em pré-print no depositório BioRxiv e submetido à *Frontiers in Plant Science, Research Topic: Roles and Regulatory Mechanisms of ABA in Plant Development*

Cássia Fernanda Stafen, Iara Souza, Ben Hur de Oliveira, Luísa Abruzzi de Oliveira-Busatto, Rodrigo Juliani Siqueira Dalmolin, Oscar Lorenzo Sánchez, Felipe dos Santos Maraschin

https://www.biorxiv.org/content/10.1101/2022.07.24.501316v1

Identification of shoot light-responsive genes in *Arabidopsis* through a survey of public datasets

Cássia Fernanda Stafen[1], Iara Souza[2], Ben Hur de Oliveira[3], Luísa Abruzzi de Oliveira-Busatto[4], Rodrigo Juliani Siqueira Dalmolin[2], Oscar Lorenzo Sánchez[5], Felipe dos Santos Maraschin[1,6*]

[1]PPGBM - Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil

[2]Bioinformatics Multidisciplinary Environment, Universidade Federal de Natal - UFRN, Natal, RN, Brazil

[3] PPGBCM – Programa de Pós-Graduação em Biologia Celular e Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil

[4]PPG Fitotecnia –Departamento de Plantas de Lavoura, Universidade Federal do Rio Grande do Sul – UFRGS, Porto Alegre, RS, Brazil

[5]Instituto de Investigación en Agrobiotecnología (CIALE), Universidad de Salamanca, Salamanca, Spain

[6]Departamento de Botânica, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil

Abstract

Following germination, seedlings grown in light show a photomorphogenic development with open and green cotyledons and a robust root system. The light perception by the photoreceptors activate autotrophic photosynthetic metabolism to sustain growth of the whole plant. Several studies have evaluated transcriptional responses to light signals. Nevertheless, evaluating a single source experiment might bias the identificationof general, reproducible light responses. In order to identify widespread light-dependent signaling events that control early seedling photomorphogenesis we performed a survey comparing commonly regulated genes in transcriptomic public datasets derived from etiolated seedlings exposed to short light treatments. By compiling commonly regulated genes from different datasets, we obtained broadly representative regulated processes concerning general light transcriptional response. Our analysis shows that light primarly affects shoot gene expression promoting the assembly of photosynthetic machinery, signaling and redox responses. We observed that Transcriptograms allowed a better comparison among different experiments than DEseq analysis. We also identified that, transcriptional regulation of early light response is centered in the transcription factor ABA-Insensitive5 (ABI5) along with other bZIP transcription factors suggesting a mechanism by which dark expressed transcription factors guide the activation of early photomorphogenic genes.

Keywords: Abscisic acid, photomorphogenesis, deetiolation, transcriptogram, bZIP

A survey of transcriptomic datasets identifies ABA-responsive factors as regulators of photomorphogenesis in *Arabidopsis*

Cássia Fernanda Stafen[1], Iara Souza[2], Ben Hur de Oliveira[3], Luísa Abruzzi de Oliveira-Busatto[4], Rodrigo Juliani Siqueira Dalmolin[2], Inmaculada Sánchez-Vicente[5], Andrea Fuentes-Terrón[5], Oscar Lorenzo Sánchez[5], Felipe dos Santos Maraschin[1,6*]

[1]PPGBM - Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil; [2]Bioinformatics Multidisciplinary Environment, Universidade Federal de Natal - UFRN, Natal, RN, Brazil; [3]PPGBCM – Programa de Pós-Graduação em Biologia Celular e Molecular, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil; [4]PPG Fitotecnia –Departamento de Plantas de Lavoura, Universidade Federal do Rio Grande do Sul – UFRGS, Porto Alegre, RS, Brazil; [5]Department of Botany and Plant Physiology, Institute for Agribiotechnology Research (CIALE), University of Salamanca, Salamanca, Spain; [6]Departamento de Botânica, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, RS, Brazil.

* Correspondence:

Felipe dos Santos Maraschin

felipe.maraschin@ufrgs.br; Phone: +55 51 33087653; Address: Instituto de Biociências, Departamento de Botânica, Universidade Federal do Rio Grande do Sul – UFRGS. Av. Bento Gonçalves 9500. Prédio 43.423, sala 224, CEP 91501-970 Porto Alegre, RS, Brasil.

Key Words: Abscisic acid, photomorphogenesis, deetiolation, transcriptogram, bZIP.

Abstract

Following germination, seedlings grown in light show a photomorphogenic development with open and green cotyledons and a robust root system. The light perception by the photoreceptors activate autotrophic photosynthetic metabolism to sustain growth of the whole plant. Several studies have evaluated transcriptional responses to light signals. Nevertheless, evaluating a single source experiment might bias the identification of general light responses. In order to identify widespread light-dependent signaling events that control early seedling photomorphogenesis we performed a survey comparing commonly regulated genes in transcriptomic public datasets derived from etiolated seedlings exposed to short light treatments. By compiling commonly regulated genes

from different datasets, we obtained broadly representative regulated processes concerning general light transcriptional response. Our analysis shows that light primarly affects shoot gene expression promoting the assembly of photosynthetic machinery, signaling and redox responses. We also identified that transcriptional regulation of early light response is centered in the transcription factor ABA-Insensitive5 (ABI5) along with other bZIP transcription factors suggesting a mechanism by which dark expressed transcription factors guide the activation of early photomorphogenic genes.

1 Introduction

Light is one of the most important enviromental factors that controls plant growth and development. Plants have evolved multiple ways to perceive light-related changes, such as quantity, quality, period and direction, adapting to ajust their development accordingly (Mancini et al. 2016; Dong et al. 2017; Oh et al. 2019; Lacek et al. 2021). The signaling system consists of photoreceptors for blue/UV-A light (phototropins, cryptochromes and 'Zeitlupes'), red/far-red (phytochromes), and UV-B (UVR8) (Yu, 2010; Arsovski et al. 2012;Tilbrook et al. 2013; Christie et al. 2015; Galvão and Fankhauser 2015; de Wit M, Keuskamp DH, Bongers FJ 2016; Yang et al. 2017; Pham et al. 2018). Photomorphogenic development is dependent on a large transcriptional reprogramming downstream of photoreceptor signaling. Photomophogenesis is actively repressed by many regulators such as the CONSTITUTIVE PHOTOMORPHOGENIC/DE-ETIOLATED/FUSCA (COP/DET/FUS) and PHYTOCRHOME INTERACTING FACTOR (PIF) signaling modules (Chory 1993; Hellmann and Estelle 2002; Lau and Deng 2012; Xu et al. 2015). The main receptors that control photomorphogenesis are the Phytochromes (phy) and Cryptochromes (cry) that upon light activation promote degragation of PIFs and supression of COP1/SPA ubiquitin ligase complexes, allowing the accumulation of light response transcrition factors such as ELONGATED HYPOCOTYL 5 (HY5), ELONGATED HYPOCOTYL HOMOLOG (HYH), LONG AFTER FAR-RED LIGHT1 (LAF1), among others that trigger de-etiolation (Lau and Deng 2012; Xu et al. 2015; Zhong et al. 2021).

Arabidopsis seedlings display contrasting developmental phenotypes when grown under light or in the darkness. In the light, the seedlings present a photomorphogenic development with green and open cotyledons, a short hypocotyl and a long primary root) (Wei et al. 1994). In darkness, however, the skotomorphogenic development produces

seedlings with closed cotyledons and an apical hook, a long hypocotyl and a short root (Pham et al. 2018a). Under the ground, the seedling protects the apical meristem keeping closed cotyledons and stimulate hypocotyl elongation. When exposed to light, the cotyledons open, expand and start to perform photosynthesis allocating resources for root growth (Lau and Deng 2012). The shoot usually consists of the primary light responsive organ in the plant, but it also controls the developmental responses of the roots underground (Van Gelderen et al. 2018). However, the shoot-derived signals that promote root photomorphogenic growth are still under debate, such as sugars, phytohormones, the HY5 transcription factor, among others (Marchant et al. 2002; Salisbury et al. 2007; Laxmi et al. 2008; Kircher and Schopfer 2012; Regnault et al. 2015; Chen et al. 2016; Yang et al. 2020; Bhagat et al. 2021).

A large amount of transcriptomic data is available from *Arabidopsis* seedlings exposed to different light conditions. Although these datasets have been evaluated individually, a cross comparison of these data may help to find common genes involved in light perception and signaling with higher confidence. In order to explore genes and pathways involved in early shoot light responses, we aimed for integrating expression profiling studies in *Arabidopsis* performing a survey in published public transcriptomic databases from light-treated young *Arabidopsis* etiolated seedlings.

Our analysis allowed us to identify ABA-response factors as putative primary regulators of photomorphogenic gene expression linking dark-expressed transcription factors to guide the activation of early photomorphogenic genes.

2 Materials and methods

Plant materials

Arabidopsis Columbia (Col-0) was used as wild-type (WT) and the mutant *hy5* (SALK_056405C) were obtained from the European Arabidopsis Stock Centre (NASC, http://arabidopsis.info/). Seeds from *abi5-7, 35ScMyc:ABI5 (35S:ABI5)* and *pABI5:ABI5-GUS* were previously described (Albertos et al. 2015). Seeds from *35S:HY5 (35S:FLASH-HY5ox*) (Burko et al. 2020c) were kindly donated by Yogev Burko (The Salk Institute, USA). Mutants *abf1* (SALK_043079), *abf3* (SALK_075836), *and abf4* (SALK_069523) (Fernando et al. 2018) were kindly donated by Dana F. Schroeder (University of Manitoba, Canada).

Data Mining

For data collection, the NCBI GEO functional genomics repository was queried. Experiments were searched using keywords, "*Arabidopsis*", "light" AND "shoot". The microarrays selected were, GSE5617 (AtGenExpress database, http://bar.utoronto.ca/efp/cgi-bin/efpWeb.cgi) (Kilian et al. 2007); GSE29657 (Liu et al. 2012) as well as the RNA-seq GSE79576 (Sun et al., 2016). These datasets were selected because of their similar growth conditions, similar age of seedlings and wild ecotype (Col-0). Supplementary Table 1 summarizes the experimental conditions of the data sets.

Individual preprocessing and differential expression analysis of the datasets

For the microarray samples, the raw data was normalized with RMA method and expression values (Robust Multi-Array Average Expression Measure) were retrieved with affy R/Bioconductor package (Gautier et al. 2004). Differential expression analysis was performed using limma R/Bioconductor package. Genes were considered differentially expressed when p value ≤ 0.001 with FDR adjustment (Ritchie et al. 2015). For the RNA-seq databases, the raw reads were aligned and annotated to *Arabidopsis thaliana* reference genome v10 using STAR aligner (Dobin et al. 2013). Counts from aligned reads were obtained with featureCounts (Liao et al. 2014) and normalized into log-2-counts-per-million. Differential expression analysis was performed using limma R/Bioconductor package protocol for RNA-seq experiments, considering only the differentially expressed genes with p value ≤ 0.001 with FDR adjustment (Ritchie et al. 2015).

***Arabidopsis thaliana* transcriptogram**

The transcriptogram is based on an ordered gene list retreived from protein-protein association information built in such a way that the probability of two gene products to be associated exponentially decays with their distances on the list. The fold-change expression pattern compared to a control sample is plotted according to this list forming peaks and valleys indicating the gene sets that are differentially expressed.

To build the transcriptogram, protein-protein interaction data for *Arabidopsis thaliana* was obtained from the STRING v.10.5 database (Szklarczyk et al. 2017) using an associated cutoff score of 0.700. The Transcriptogramer v1.0 (Rybarczyk-Filho et al. 2011; da Silva et al. 2014) software was used for protein ordering. The Transcriptogramer package (Morais DA 2017) was applied to generate the transcriptograms of all datasets

and their treatments, these were plotted as: for each position i of the indexes of ordering in the transcriptograms, the relative expression value assigned to such position will be given by

$$Log_2\left(\frac{T_i^{tratament\ 1}}{T_i^{tratament\ 2}}\right),$$

Where Ti is the average expression of the genes encoding for proteins belonging to the 90th-windowed range. The reading counts mapped to each individual gene determined the values of gene expression. The Monte Carlo sampling process allowed the localization of significant peaks and valleys in transcriptograms, in which random sets of permutations and sorting indexes were designed and used to randomly generate transcriptograms, from which zero distributions of peaks and lengths of valleys were inferred. These null distributions served as a basis for determining critical values for statistically significant peaks and valleys ($p < 0.001$) and the number of permutations for each of the tests was established after convergence of the critical values. In order to perform this statistical analysis, internal scripts were used in the R programming environment. Functional enrichment was performed through the topGO package (Fisher test with Benjamini-Hochberg correction; Alexa and Rahnenfuhrer, 2016) and the GO annotations for the genes of the species studied were performed by the biomaRt package (Durinck et al. 2009) obtained from the ENSEMBL Plant database.

GO terms funcional enrichment

The gene enrichment analysis on the significant peaks and/or valleys of the transcriptograms and DEseq was performed by aggregation ontology for the terms of biological processes (BP) using the website agriGO (v2.0) (Tian et al. 2017). The ReViGO (Supek et al. 2011) was used for remove redundant terms, calculate and summarize the list of GO terms according to the biological process.

Transcription factor investigation

The list of DEGs and peaks/valleys at the intersection between the datasets GSE5617, GSE79576 and GSE29657 was evaluated for putative regulating transcription factors. Each of the four lists (DEseq up / down and Transcriptomic peaks/valleys) was analysed in TF2Network (http://bioinformatics.psb.ugent.be/webtools/TF2Network/) (Kulkarni et al. 2018) and the transcrption factors ranked with a Protein-DNA(PD) score ≥10% were selected for generating their interaction network with GeneMania plug-in (Mostafavi et

al. 2008) in Cytoscape software (Shannon et al. 2003).

Growth conditions for mutant phenotyping

Plants were grown on half-strength sucrose-free Murashige and Skoog medium (Murashige and Skoog 1962) supplemented with 1.5% agar (w/v; KASVI) and 0.05% MES hydrate (w/v; Sigma-Aldrich, M8250), pH 5.7, on vertically oriented square plates. Seeds were surface-sterilized and stratified at 4 °C for 2 days in complete darkness. Seedlings were grown at 21 °C ± 2 °C under completely darkness for 4 days and transferred to 1 and 4 hours of white light illumination (94 µmol m^{-2} s^{-1}, white 6500k Led lamps). For dark grown plants, the plates were covered with aluminum foil. Similarly grown seedlings were used for RNA isolation. For root and hypocotyl length measurements, seedlings were growth for 14 days in LD condition (LD - Shoot light, Dark root, as Miotto et al. 2019), and the measurements were performed at 4, 7, 10 and 14 days. Organ length was measured with ImageJ (Fiji).

Analysis by qRT-PCR

Total RNA was isolated from 4 days-old *Arabidopsis* seedlings grown as above using TRIzol™ Reagent (Thermo Fischer, #15596026). The cDNA was synthesized using M-MLV reverse transcriptase (Promega, # M5313) following the manufacturer's instructions. qRT-PCR was performed in a StepOne™ Real-Time PCR System using Platinum Taq DNA Polymerase (Thermo Fischer, # 10966) according to the manufacturer's protocol. Three independent biological samples were analyzed for each datapoint with three independent technical replicates each. The transcript levels were normalized against *ACTIN2* (AT3G18780) as a reference gene, and relative expression was calculated by the ddCt method (Livak and Schmittgen, 2008) (Supplementary table 6).

Chlorophyll quantification

Chlorophyll measurement was performed essentially as described (Holm et al. 2002). Briefly, 3-DAG seedlings harvested in darkness and after exposure to ligth for 1h, 4h, 6h, 8h and 24h were weighed, frozen in liquid nitrogen, and ground to a fine powder. Total chlorophyll was extracted with 80% acetone, and chlorophyll a and b contents were calculated using MacKinney's specific absorption coefficients in which chlorophyll a =

12.7(A663) − 2.69(A645) and chlorophyll b = 22.9(A645) − 4.48(A663). The total specific chlorophyll content is expressed as micrograms of chlorophyll per gram of seedlings.

Protochlorophyllide assay

The protochlorophyllide measurements were performed essentially as described (Job and Datta 2021). In total, 50 seedlings of were grown as above for 5-DAG in the dark (plates were covered in layers of aluminum foil). Seedlings were immediately frozen in liquid nitrogen and extracted with 90% acetone with 0.1 M NH_4OH and incubated at 4°C for 1 h. Samples were centrifuged at 14000 g for 10 min and the supernatant was collected. Fluorescence spectra was measured with excitation at 440 nm and the emission spectra was recorded from 600 nm to 750 nm.

GUS staining and microscopy analysis

Seedlings were fixed in 80% acetone for 20 minutes at -20ºC, washed 3 times in water and incubated overnight in GUS staining buffer [10 mM EDTA, 100 mM sodium phosphate (pH 7.0), 0.1% (v/v) Triton X-100, 1 mM $K_3Fe(CN)_6$, 1 mM $K_4Fe(CN)_6$, 1 mg/ml 5-bromo-4-chloro-3-indolyl-D-glucuronide] at 37 °C. Subsequently, samples were washed in water once and cleared in 70% (v/v) ethanol at room temperature before imaging.

3 Results

Transcriptogram analysis of early and late light responses

We generated a transcriptogram considering a window of 70 genes ordered according to function (Miotto et al., 2019) and later these genes form groups/clusters (Fig. 1a). After we plotted the transcriptogram with all datasets (Fig. 1b), and further separated samples of early light responses (up to 1 hour after light exposure) (Fig. 1c) and late response (4 to 6 hours of light exposure) (Fig. 1d). Individual transcriptograms for each datasets are presented in Supplementary Figure 2. When overlaid, most transcriptograms showed a similar distribution profile of peaks and valleys (Fig. 1b), although with some clear amplitude variations. Most of peaks and valleys encompass GOs terms such as “cellular nitrogen compound metabolic process”, “response to light stimulus”, “photosynthesis”, “protein transport”, “protein import into nucleus”, “glutathione metabolic process ” (Fig.

1a, b). When we compared the light response profile over time, we could observe an increase in the amplitude of significant peaks and valleys in the late responses when compared to early responses, suggesting that the general expression profiles are maintained over time and are mostly quantitatively affected by prolonged light exposure.

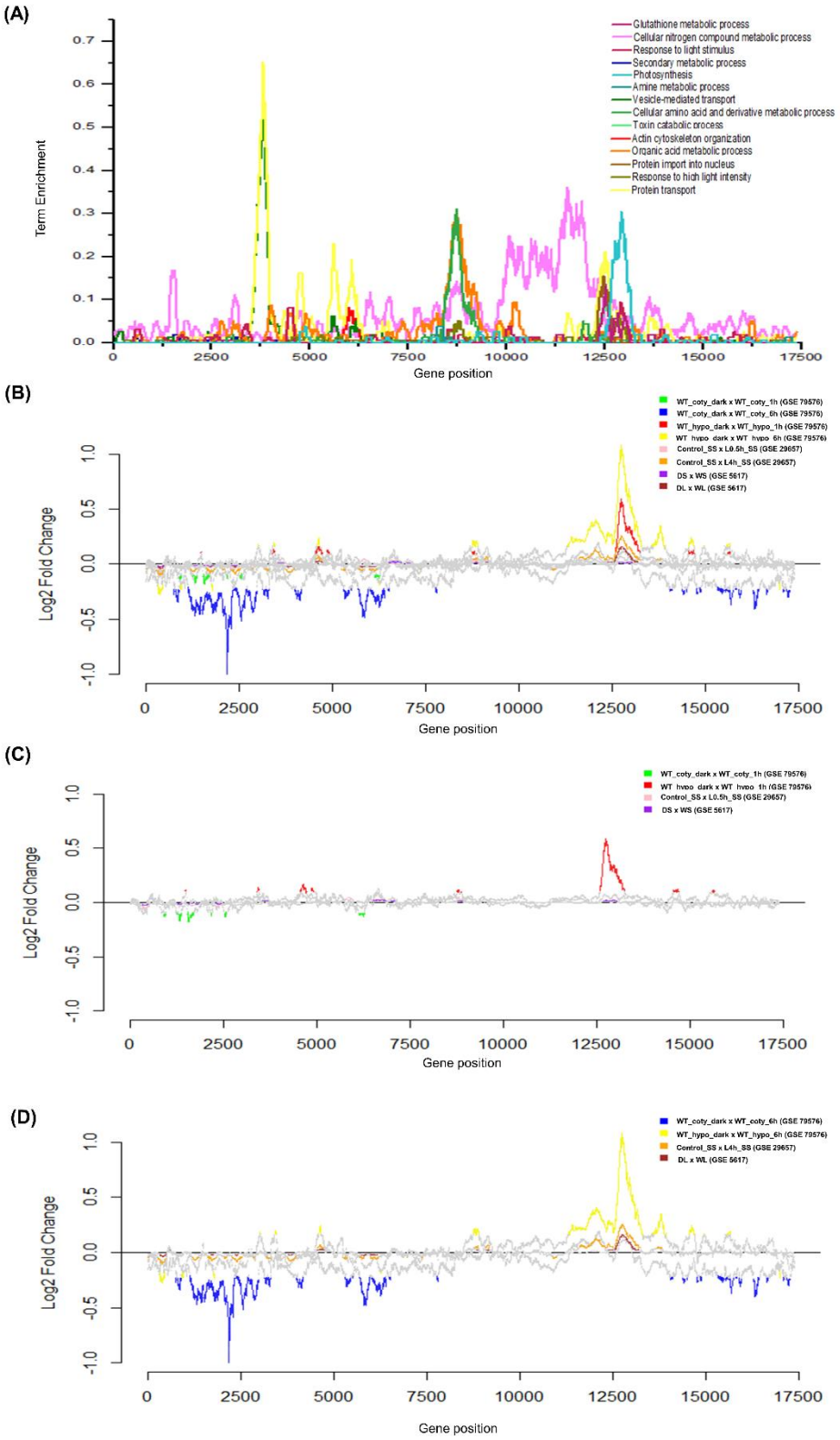

(A)
Term Enrichment
Gene position
Glutathione metabolic process
Cellular nitrogen compound metabolic process
Response to light stimulus
Secondary metabolic process
Photosynthesis
Amine metabolic process
Vesicle-mediated transport
Cellular amino acid and derivative metabolic process
Toxin catabolic process
Actin cytoskeleton organization
Organic acid metabolic process
Protein import into nucleus
Response to high light intensity
Protein transport
(B)
Log2 Fold Change
Gene position
WT_coty_dark x WT_coty_1h (GSE 79576)
WT_coty_dark x WT_coty_6h (GSE 79576)
WT_hypo_dark x WT_hypo_1h (GSE 79576)
WT_hypo_dark x WT_hypo_6h (GSE 79576)
Control_SS x L0.5h_SS (GSE 29657)
Control_SS x L4h_SS (GSE 29657)
DS x WS (GSE 5617)
DL x WL (GSE 5617)
(C)
Log2 Fold Change
Gene position
WT_coty_dark x WT_coty_1h (GSE 79576)
WT_hypo_dark x WT_hypo_1h (GSE 79576)
Control_SS x L0.5h_SS (GSE 29657)
DS x WS (GSE 5617)
(D)
Log2 Fold Change
Gene position
WT_coty_dark x WT_coty_6h (GSE 79576)
WT_hypo_dark x WT_hypo_6h (GSE 79576)
Control_SS x L4h_SS (GSE 29657)
DL x WL (GSE 5617)

Figure 1 *Arabidopsis thaliana* transcriptogram comparison among three light response datasets. **a** *Arabidopsis thaliana* transcriptogram. The x-axis relative to gene position have been divided by the total number of proteins retrieved from STRING. Projection of Gene Ontology terms is color-coded. **b** Overlay of all transcriptograms for GSE5617, GSE29657 and GSE79576 datasets, **c** early responses GSE5617 (1 h WL), GSE29657 (0.5 h WL) and GSE79576 (1 h WL, coty - cotyledons and hypo - hypocotyls) and **d** late light responses GSE5617 (4 h WL), GSE29657 (4 h WL), and GSE79576 (6 h WL, coty - cotyledons and hypo - hypocotyls). Average transcriptograms signifcant peaks (up-regulation) or valleys (down-regulation) are represented by colors. Grey lines show non-signifcant regions

Identification of common light regulated genes

In order to compare the similarity between the datasets, an intersection with the common modulated genes present in the significant peaks and valleys of all the transcriptograms as well as differentialy expressed according to DEseq was generated (Fig. 2). From the comparison of these datasets, 920 genes overlaped in significant peaks (Fig. 2a) whereas 619 genes overlapped in significant valleys (Fig. 2b). When we compared the same datasets by DESeq analysis we found an overlap of 214 up-regulated (Fig. 2c) an 456 down-regulated genes among the three datasets listed above (Fig. 2d). Based on these observations, we conclude that the two approaches are able to identify a larger set of regulated genes, allowing a broader analysis of physiological responses. In order to compare the similarity between the datasets, an intersection with the commonly modulated genes present in the significant peaks and valleys of all the transcriptograms as well as differentially expressed according to DEseq was generated (Fig. 2). From the comparison of these datasets, 920 genes overlapped in significant peaks (Fig. 2a) whereas 619 genes overlapped in significant valleys (Fig. 2b). When we compared the same datasets by DESeq analysis we found an overlap of 214 up-regulated (Fig. 2c) an 456 down-regulated genes among the three datasets listed above (Fig. 2d). Based on these observations, we conclude that the two approaches are able to identify a larger set of regulated genes, allowing a broader analysis of physiological responses.

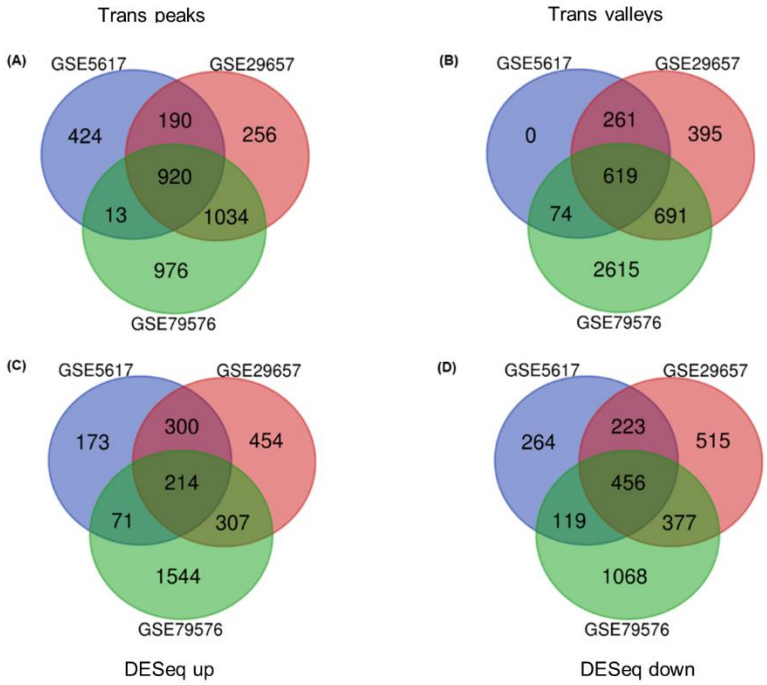


Figure 2 Intersection of commonly regulated genes in shoot light responses for **a** Transcriptome peaks, **b** Transcriptome valleys, **c** DEseq up and **d** DEseq down genes among the five datasets.

GO term enrichment in transcriptional shoot light responses

The list of significantly enriched GO terms for the genes identified as induced in the Transcriptogram peaks of the three datatsets (GSE5617, GSE29657 and GSE79576) highlights "photosynthesis" followed by "single-organism metabolic process", "oxidation-reduction process", "metabolic process", "cellular metabolic process" along with pigment and cofactor related terms (Fig. 3a), suggesting strong activation of photosynthesis and photoautotrophy. In addition, significantly overrepresented categories in valleys were related to "drug transmembrane transport", "peptidyl-proline modification", and "cellular response to auxin stimulus" among others, in agreement with the overall repression of hypocotyl growth triggered by photomorphogenesis in shoots. On the other hand Differential Expression (DESeq) upregulated genes were enriched in GO terms "carboxylic acid metabolic process", "small molecule metabolic process", "single-organism cellular process", "single-organism process" and others. The GO terms "single-organism metabolic process", "oxidation-reduction process", "cofactor metabolic process", "small molecule metabolism processes" and "photosynthesis" were the main categories down-regulated in shoot illumination (Fig. 3b). The complete list of GOs terms is listed on Supplementary Table 3. These results suggest that the two approach seems to

have a different coverage related to GO term assessment when comparing different datasets. However, this might be a consequence of the larger number of genes considered.

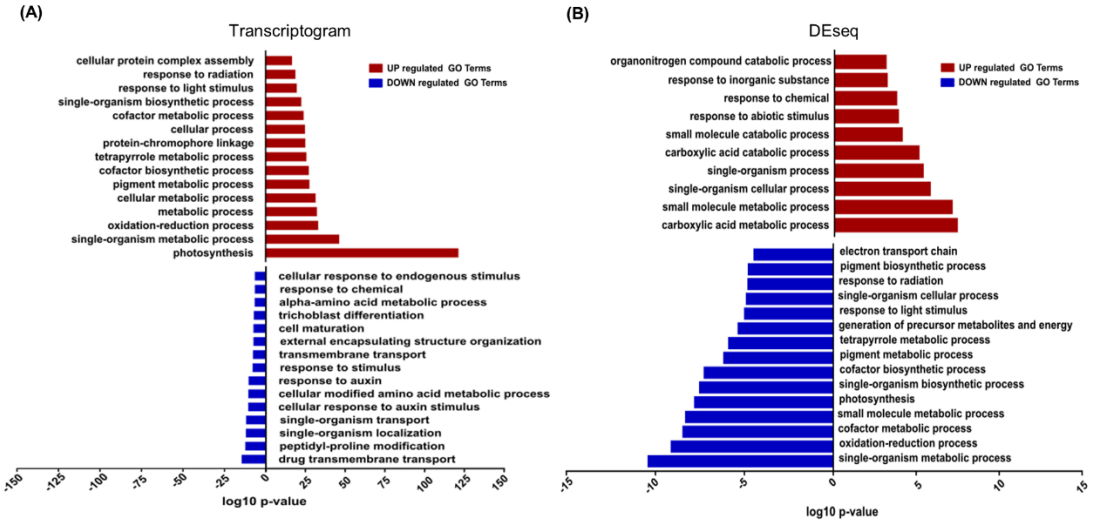


Figure 3 GO term enrichment for light responsive genes from the three datasets (GSE5617, GSE79576 and GSE29657) **a** Functional enrichment analysis of transcriptogram peaks and valleys. The top 15 enriched terms were listed. **b** Functional enrichment analysis of up and down regulated genes identified through DEseq. The top 10 up and 15 downregulated enriched terms were listed. A detailed list of the data is shown in **Supplementary Table 3.**

Association of light regulated genes with photoreceptor signaling pathways

Light perception by plant photoreceptors CRY1, CRY2, and phytochromes is the main trigger for seedling photomorphogenesis (Podolec and Ulm, 2018) which leads to PIF degradation and supression of skotomorphogenesis (Pham et al., 2018). We compared light regulated genes identified by our analysis to differentially expressed genes identified for pif1pif3pif4pif5 (pifq) (Sun et al., 2016), cry1 cry2 (He et al. 2015) an constitutively active form of phyB (YHB) (Hu et al. 2009) (Fig. 4). A detailed list of the intersections are presented in Supplementary Table 4. Interestingly, many of the genes identified by DEseq (34 DEseq up and 21 DEseq down) and the majority identified by Transcritogram (311 Peak genes and 232 Valley genes) are not listed as differentially expressed in these light signaling mutant backgrounds neither returned enriched regulators based on cis-regulatory elements by the TF2Network analysis (Kulkarni et al., 2018). However, the majority of the DEseq downregulated (DEseq down) genes (48) were affected in all three mutants (Fig. 4b). The largest single intersection happened with cry1 cry2-regulated genes regardless of the analysis

procedure (DEseq or Transcriptogram), followed by pifq and phyB affected genes. The only exception was for DEseq down, where phyB-dependent genes were more represented than pifq in the comparison. Although the larger overlap observed with the cry1 cry2 responsive genes suggests that blue light responses, mediated by cryptochromes, act as an important signal for transcriptional change in early photomorphogenesis, the pifq- and phyB-responsive genes belong in a shared signaling pathway where PIF activity is negatively regulated by active phyB (Shin et al. 2009; Leivar et al. 2009). In this context, the majority of differentially expressed genes we identified fall under phyB-PIF regulation.

The HY5 transcription factor is one of the main promoters of photomorphogenesis; its expression and protein accumulation increase in response to light and HY5 activates its expression and many downstream responsive genes, functioning as a converging hub to many light signals (Podolec and Ulm, 2018). So, we also crossed our data with the a refined list of HY5-direct targets (Burko et al., 2020). (Supplementary Figure 1, Supplementary Table 5). There was a small overlap between the genes present in Trans peaks (34), followed by DEseq down (17) and Trans valleys (3). Strikingly, there were no genes in common between the DEseq up and HY5 targets list (Supplementary Figure 1a) as one would expect in a list of light-induced genes. This suggests that, the transcriptogram comparison was more robust than DEseq in identifying common llight-responsive genes and/or, although HY5 is essential to many light responses, it does not seem to act as the main early response transcription factor to the light

stimulus, suggesting that other factors might be acting upstream or in parallel to HY5.

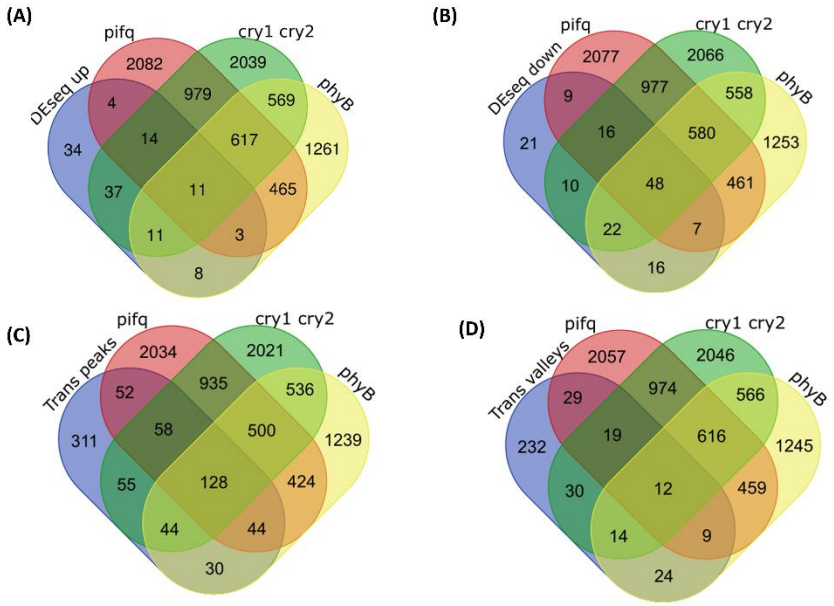


Figure 4 Intersection of common light modulated genes from three datasets (GSE5617, GSE79576 and GSE29657) identified by Differential Expression (DESeq) and Transcriptomic Analysis (Trans) overlapping with *pif1pif3pif4pif5* (*pifq*) (Sun et al., 2016), *cry1 cry2* (He et al., 2015) and phyB-YHB (Hu et al., 2009) differentially expressed genes. **a** DEseq up, **b** DEseq down, **c** Trans Peaks, **d** Trans Valleys

Light regulated gene expression networks overlap with ABA-responsive signaling

During photomorphogenic development, the earliest signaling events downstream of photoreceptor activation do not involve de novo protein synthesis. The signaling cascade involves protein stability/activity regulation through protein-protein interactions as well as targeted protein degradation by the 26S proteasome (Hellmann and Estelle 2002). So, transcriptomic analysis alone fails to identify the primary response regulators acting upstream of transcriptional control. To identify the putative cis-acting regulators of the light-responsive identified, we searched their promoter cis-elements with the TF2Network (Kulkarni et al. 2018) tool. We selected the top putative regulators based on higher Protein-DNA interaction scores and retreived their known PPI regulatory networks from both DEseq and Transcriptogram gene sets (Fig. 5). Interestingly, the ABA-response bZIP transcription factor ABI5 stood out in both networks (Fig. 5a-c) associated with

both up and down regulated genes. Besides, HY5 was present in the DEseq network, reinforcing the possible relationship of HY5 and ABI5 (Bhagat et al. 2021a). ABF1, PIF4, GBF3 and ABF4 were found as major regulators for the DEseq up and Trans peaks and Trans valleys genesets (Fig. 5c). Other putative regulator identified for the Trans valleys gene set comprise ABF3, GBF2, PIF3, PIF5, CCA1, BES1, AGL9 and AGL20. Putative regulators for the genes exclusively identified for the DEseq up gene set are EIN3, DIV2, LFY and AP3 whereas for the DEseq down, only ABI5 showed up as a putative regulator. From this analysis, stands out the abundance of the bZIP-type transcription factors GBFs (G-box binding factor 1-3), the ABFs AREB (ABA Responsive Element Binding Factors 1, 3 and 4) and ABI5 (ABA Insensitive 5) along with bHLH PIFs (PIF3, PIF4 and PIF5). This suggests that modulation of ABA responses mediated by bZIP transcription factors might be a central signaling trigger for photomorphogenesis in Arabidopsis shoots.

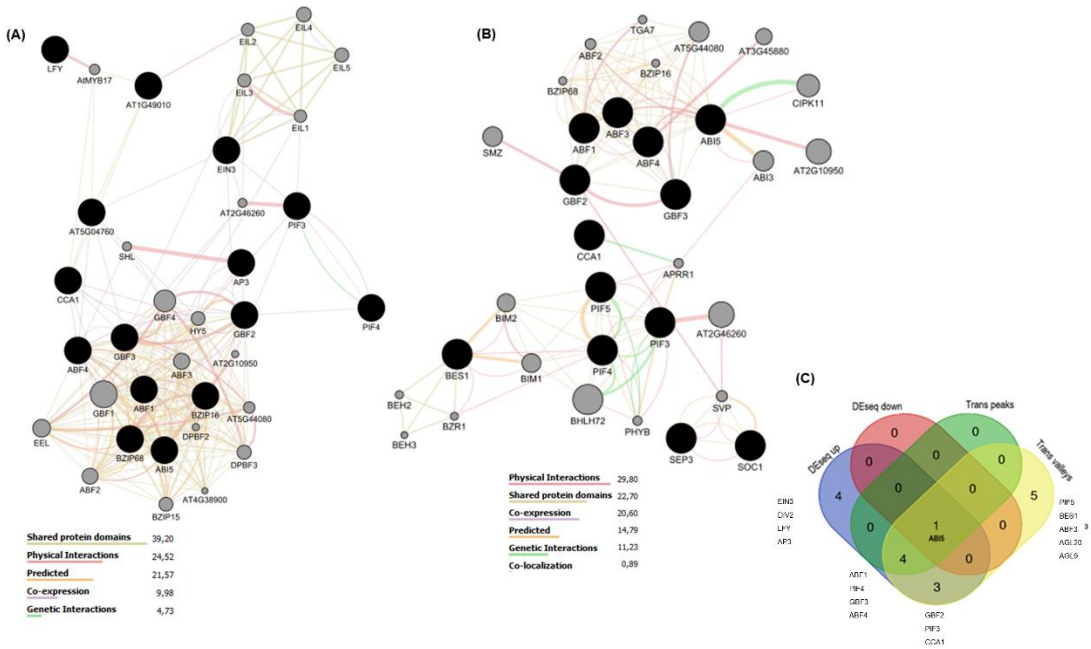


Figure 5 Putative TF networks involved in the regulation of early light responsive gene expression. **a** TF network identified for genes ideintifed by Transcriptogram and **b** Differential Expression (Deseq) analysis. Black circles are transcription factors retrieved from TF2Network and the gray circles represent connections provided by GeneMania, **c** Venn diagram of overlaping putative transcription factors identified for DESeq up and down and Transcriptogram peaks and valleys.

To validate these analysis and to investigate whether the identified transcription factors are involved in light responsiveness, we evaluated the transcriptional response of the ABI5 and HY5 genes in the following genotypes: abi5-7, abf4, hy5 and

35S:ABI5 (Supplementary Figure 4) as well Chalcone Synthase (CHS) as a HY5 target gene described as light responsive in seedlings (Zhang et al. 2011a). In the dark grown seedlings (0 h), HY5 expression was lower in abi5-7 and 35S:ABI5 when compared to WT. The 1h light-induced HY5 induction observed in the WT, abi5 and abf4 was reduced in the ABI5 overexpression line (35S:ABI5), and absent in the hy5 mutant. Interestingly, the dark (0h) expression of ABI5 was lower in the hy5 mutant , in contrast with the lower dark expression of HY5 in abi5-7 . These results indicate that HY5 and ABI5 counteract each other expression in the dark and ABI5 overexpression supresses HY5 induction. It is noticeable the significant decrease of the ABI5 expression in the 35S:ABI5 background after transition to light, suggesting that ABI5 mRNA might be post-transcriptionally regulated after exposure to light. The expression of CHS was more induced after 4 hours of light exposure in the abi5-7 mutant than in WT (Supplementary Figure 4). In the abf4 mutant, this gene was more expressed in the dark and shows less light inducibility than in WT.

As we observed that the assembly of the photosynthetic machinery was the top induced process in the trasncriptomic analysis (Fig. 3a), we decided to evaluate whether the ABA-responsive transcriptional regulators influence this transition. For that purpose, we measured the chlorophyll content during deetiolation in seedlings of WT, abi5-7, abf3, abf4 and 35S:ABI5 exposed to light over 24h (Figure 6a). Total chlorophyll content increased progressively in most genotypes. After 24h of light exposure the abi5-7, abf3 and abf4 mutants accumulated almost double the chlorophyll of wild-type suggesting a repressive role over longer light exposures. The 35S:ABI5 line had a lower content than the WT after 8-hours of light exposure, also suggesting ABI5 has a repressive role in chlorophyll accumulation. The precursor of chlorophyll, protochlorophyllide (Pchlide), is synthesised in the dark and its levels need to be tightly controlled to avoid photobleaching upon illumination. We quantified Pchlide levels in 3 DAG dark grown seedlings, where Pchlide was higher in abi5-7 and abf4, followed by abf1 and abf3 and lower in wild-type and 35S:ABI5 (Figure 6b). Transcriptional analysis of some core genes leading to protochlorophyllide accumulation (CHLH, BBX11 and HEMA1) (Job and Datta 2021) (Supplementary Figure 5) also showed that abi5-7, abf4 and 35S:ABI5 mutants have misregulated expression of chlorophyll biosynthetic genes during deetiolation, with 35S:ABI5 showing similar expression patterns as hy5. These data suggest that these ABI5 and

ABFs act in the dark repressing photochlorophyllide production.

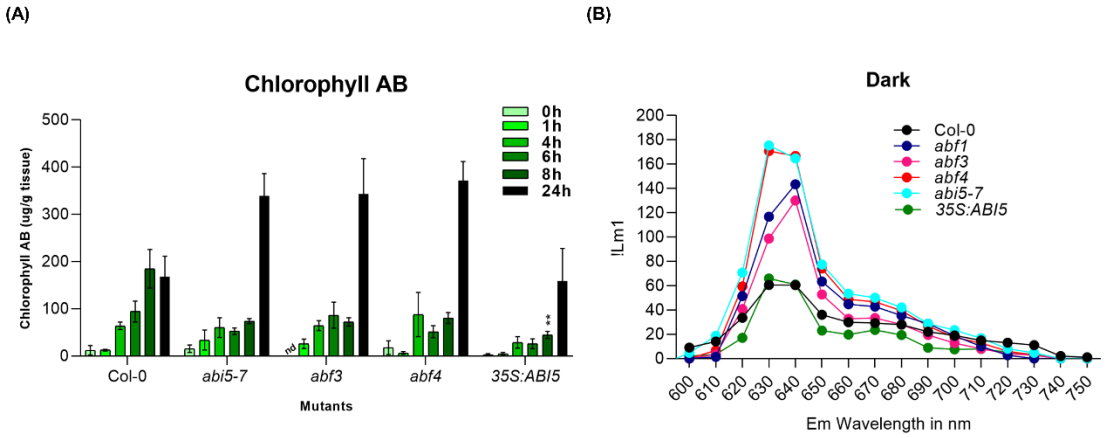


Figure 6 Chlorophyll and protochlorophyllide quantification in Abrabidopsis seedlings. **a** Total Chlorophyll A/B content in 3-DAG WT (Col-0), *abi5-7*, *abf3*, *abf4* and *35S:ABI5* seedlings grown in the dark (0h) and after exposure to white light for 1h, 4h, 6h, 8h and 24h. . Error bars indicate SE. n = 3. Statistical significance was determined by ordinary one-way ANOVA with Kruskal-Wallis post-test (**p ≤ 0.01). **b** Fluorescence emission spectra (Arbitrary Units) of acetone extracts indicating protochlorophyllide accumulation of Col-0, *abi5-7*, *abf3*, *abf4* and *35S:ABI5* seedlings, grown in the dark for 5 d.

Light controls the spatial expression of ABA response regulators

In order to evaluate the expression pattern of ABA responsive factors during deetiolation, we tested reporter constructs for pABI5:ABI5-GUS, pABI5:GUS, pABF4:GUS, 6XABRE_A:GUS. Seedlings were grown for 4 DAG in dark conditions and then exposed to 0, 1, and 4 h white light. After 4 days in the dark, ABI5:GUS staining shows that the promoter is active in most tissues. However, the ABI5p:ABI5-GUS staining is restricted to the cotyledon at first (0h) and rapidly disappears upon light exposure (1h and 4h) with the signal only remaining in the SAM showing that ABI5-GUS protein accumulation decreases in cotyledons. Interestingly, a strikingly different expression pattern was observed for the promoter GUS reporter fusions pABI5:GUS, pABF4:GUS, 6XABRE_A:GUS (Fig.7a). The ABI5 promoter is highly expressed in shoots and roots in the dark, this expression decreases specifically in roots at 1h of light exposure and increasing after 4h again. On the other hand, the pABF4:GUS and the synthetic ABA response reporter 6xABRE_A:GUS (Wu 2018) show weak cotyledon and vascular expression and a increasing root expression that is

further enhanced by light. These results suggest that the ABI5 protein abundance is repressed by light in the whole seedling during deetiolation except in the SAM. Furthermore, ABF4 and 6xABRE are transcriptionally activated by light in roots possibly to trigger root photomorphogenic development. Therefore, our results suggest that the ABA transcriptional responses are modulated by light, but ABI5 protein accumulation appears not to be quickly repressed by light in the shoot. This suggests that the shoot responses depends of the reprogramming of the ABA response to activate photomorphogenesis.

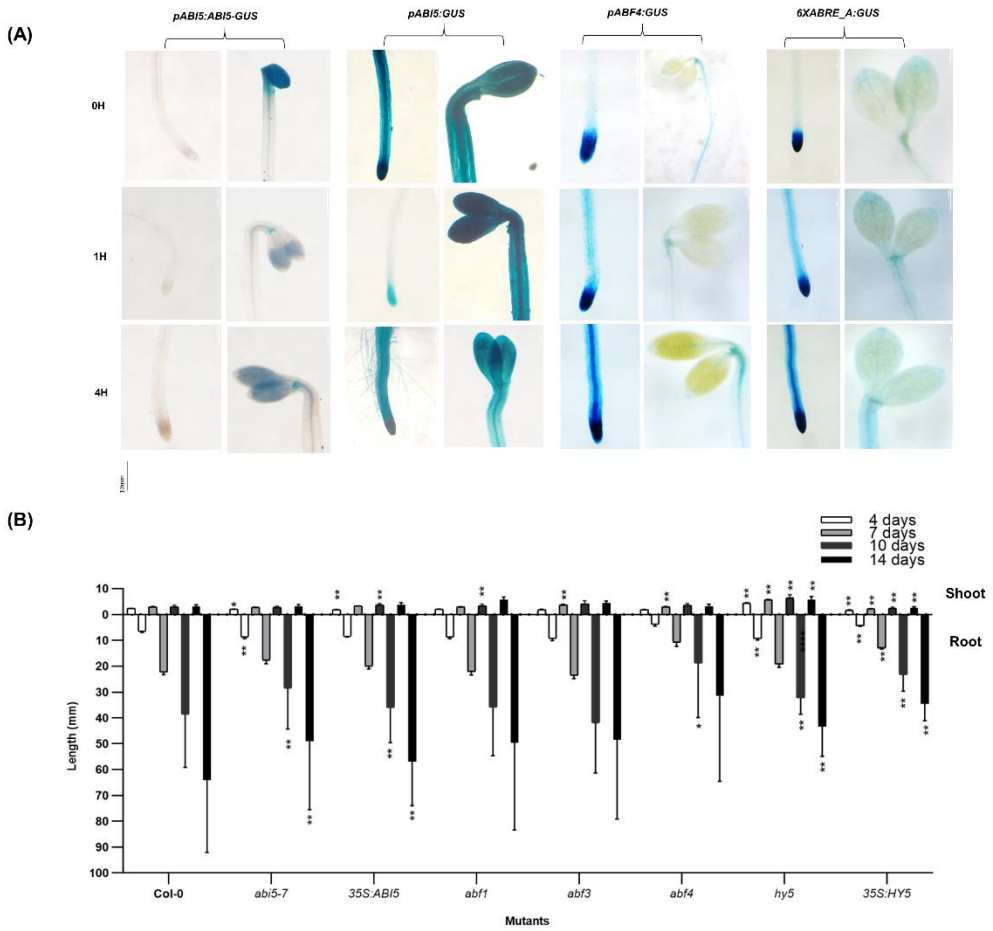


Figure 7 a β-glucuronidase assay in *pABI5:ABI5-GUS*, *pABI5:GUS*, *pABF4:GUS* and *6XABRE_A:GUS* seedling in darkness 0h and after 1h and 4h of white light exposure. Panels represent side by side the primary root and shoots of each timepoint. Scale bar= 1mm. **b** Hypocotyl and primary root lengths of single knockout and overexpression mutants ($n \geq 20$) after 4, 7, 10 and 14 days of growth. Statistical significance was determined by Kruskal–Wallis test with Dunn's -test (*$p \leq 0.05$; **$p < 0.01$). Error bars indicate SE.

ABA responsive regulators are important for seedling photomorphogenesis

In order to evaluate the role of ABA response regulators during seedling photomorphogenic development, we compared the hypocotyl and primary root length of loss-of-function and overexpression genotypes. Both abi5-7, abf4 and 35S:ABI5 showed shorter hypocotyls at 4 DAG similar to 35S:HY5 (Fig. 7b), indicating a stronger photomorphogenic response. All tested genotypes had shorter main roots than WT at 10 dag (Fig. 7b) whereas both knockout mutants abi5 and hy5 displayed comparable shorter roots (Fig. 7b). Interstingly, the localized strong cotyledon and apical hook expression of the pABI5:ABI5-GUS reporter (Fig. 8a) reflected in the early apical hook opening response of 35S:ABI5 was accelerated in comparison to WT and abi5-7 (Supplementary Figure 6) suggesting a localized promoting role for ABI5 in deetiolation. These results suggest that ABA responsive factors perform both promoting and repressive effects during seedling photomorphogenesis.

4 Discussion

A large amount of transcriptomic studies have been performed for the model species Arabidopsis thaliana. In this work, we integrated data from published transcriptomic databases to identify common regulated genes and process that comprise early shoot light responses. Gene expression profiles from five distinct datasets were examined in order to look for common regulated genes. We report an increase of amplitude of the same transcriptograms peaks and valleys in longer light exposures which suggests that gene expression patterns are sustained qualitatively during photomorphogenesis being quantitatively increased over time (Fig.1b, c). Kilian et al. (2007) (GSE5617) and Miotto et al. (2019) also reported a large number of gene sets in roots affected by shoot-illumination in transcriptogram analysis and a quantitative temporal increase in gene expression patterns in response to light treatment. Hu et al. (2009), comparing the transcriptomes of a constitutive active form of PhyB (YHB) also reported "qualitatively similar to but quantitatively greater" gene expression profiles compared to WT seedlings treated with low red light. These observations suggest that light transcriptional responses are qualitatively specific and quantitatively proportional to the light reatment. Liu et al. 2012 (GSE29657) reported that translational control is central to early photomorphogenesis responses and genes linked to biogenesis of ribosomes and translational machinery are preferentially regulated by translational control, whereas genes related to photosynthetic machinery, chlorophyll and pigments biosynthesis are preferentially regulated at the transcriptionally level. Nevertheless,

once our survey was restricted to transcriptionally regulated processes based on steady state mRNA, our results reinforce his observations. Although we could observe a large amount of similarities from the datasets evaluated, we observed an inversed pattern in the GSE79576 dataset transcript profile related to cotyledon specific samples (light blue line in Figs. 1b, d). One possibility raised by Jiao et al. (2007), is that due to the smaller vacuoles of cotyledons in comparison to hypocotyls, the observed expression patterns might be enriched for the light- induced responses of the apical hook and cotyledons. In the original publication that generated this data, Sun et al., (2016) identified a group of genes (lirSAURs) that were oppositely regulated by light in cotyledons and hypocotyls and these were related to the contrasting light effects in different organs, which may explain this pattern. This observation highlights concerns about evaluting whole seedling expression profiles for cellular processes that might have strong tissue specificities.

Being aware of the restraints imposed by transcritomic analyses, our approach focused on common regulated genes in the different datasets to identify broadly regulated genes for photomorphogenic development. A larger number differentially expressed genes appeared in the Transcriptogram analysis compared to Differential Expression. This is due to the fact that the Transciptogram method groups genes due to the "neighborhood" between them. The transcriptogram is a method that encompasses the genome to analyze genetic expression data, it calculates the average expression of a set of genes with similar functions, allowing a global view of the metabolic pathways which are coordinately regulated. It consists of an one-dimensional rearrangement of the genome based on protein-protein associations (Franceschini et al. 2012). This reordering clusters genes associated with the same pathways, allowing to globally compare if a pathway is repressed or induced (Rybarczyk-Filho et al. 2011; da Silva et al. 2014). Functional enrichment demonstrated that the categories of GOs terms identified for the DEseq gene set were not very informative (Fig. 3b) when compared to those obtained for the Transcriotogram (Fig. 3a) where terms “Photosynthesis”, “Tetrapyrrole metabolic process”, “Protein chromophore linkage” and “Pigment metabolic processes” were over-represented in the induced peaks. The GO terms of the Trans valleys indicate the repression of “Peptidyl-proline modification” which is an essential modification for the expansion of the cell wall (Zdanio et al. 2020) and “response to auxin” which is essential for hypocotyl elongation (Du et al. 2022) (Fig.

3b), are more logical than the unespected list of repressed processes we identified by DEseq terms which find “Photosynthesis” and “Pigment metabolic processes” , “Response to light stimulus” as putatively down regulated by light. Our results with the Transcriptogram tool showed enrichment terms not identified by DEseq, reinforcing the idea that different approaches to data analysis can lead to different sets of genes and processes. From our point of view, for comparison of different datasets, the Transcriptogram appears to select for more robust expression patterns, allowing better identification of core commonly regulated processes than DEseq.

Photomorphogenic responses are dependent of photoreceptor activation, mostly through the action phytochromes and cryptochromes repressing COP1 and PIFs activities. Previous works have identified transcriptomic responses that are altered in pifq, cry1cry2 and phyb(YHB) mutants, allowing us to evaluate which signaling components are required for the light signaling that regulated these datasets. We found that many light-regulated genes belong in the cry1cry2-dependent dataset, suggesting that blue light, acting through cryptochromes plays a central role as a trigger for early photomorphogenic transcriptional control. Although cryptochrome activation represses hypocotyl growth, the most represented GO categories in CRY1-regulated genes (He et al. 2015) are “Photosynthesis” and “Chloroplast organization” followed by growth related terms such as “Cell wall organization” and “Hormonal responses”, reinforcing that the establishment of the photosynthetic machinery is the main transcriptionally activated process in early photomorphogenesis. Cryptochromes also mediate blue-light dependent cell expansion in cotyledons and chloroplast development (Yu et al. 2010). This allows identification of the hypocotyl and cotyledon blue light responses which were identified in our datasets. CRY1, along with phyB, acts on repression of auxin signaling through light-induced interation with AuxIAA proteins to inhibit hypocotyl elongation (Xu et al. 2017). We found GO terms “Cellular response to auxin stimulus” and “Response to auxin” enriched in the Transcriptogram valleys of light repressed genes, which associated the suppression of auxin response downstream of photoreceptors as a central photomorphogenic response.

Phytochrome activation is also central to photomorphogenic transcriptional responses to red/far-red light (Tepperman et al. 2001; Tepperman et al. 2004; Quail 2007). Activated phytochromes modulate gene expression through direct interaction with

nuclear localized PIFs leading to their proteasomal destruction and supression of dark-induced genes (Al-Sady et al. 2006; Leivar et al. 2009; Pham 2018) as well as supression of COP1-SPA complexes by protein-protein interactions (Sheerin et al. 2015b; Zhu et al. 2015). We found the largest overlap of light modulated genes in common with pifq (Sun et al., 2016), and phyB (Hu et al. 2009) affected genes. This observation is consistent with the major role of the PhyB-PIF signaling pathway in controlling early seedling light transcriptional responses (Shin et al. 2009; Leivar et al. 2009; Zhang et al. 2013). PIFs are important repressors of light responses (Shin et al. 2009) and their light-dependent degradation is essential for the initial steps of photomorphogenesis. The pifq mutant displays a constitutive photomorphogenic phenotype in the dark (Leivar et al. 2008b), with a high expression of chlorophyll biosynthetic genes and photosynthetic apparatus proteins, similar to plants overexpressing a constitutively active form of phyB (YHB) (Hu et al. 2009).

By analyzing the transcription factors binding sites overrepresented in the promoters of the light responsive genes identified in our analysis, we were surprised not to find classical photomorphogenic activators such as HY5 or HYH (Oyama et al. 1997; Holm et al. 2002) but many to be involved with Abscisic Acid (ABA) response. The ABA-responsive A-type bZIPs (ABFs, ABI5) and G-type bZIPs (GBF2 and GBF3) were all centrally located in the PPI networks of putative TFs controlling dark-to-light transcriptional changes. Plant bZIP proteins preferentially bind to the cis-elements with a ACGT core sequence, such as G-box (CACGTG), C-box (GACGTC), Z-box (ATACGTGT), and A-box (TACGTA). The Transcriptogram network (Fig. 5b, c) also linked members of the PIF family (PIF3, PIF4 and PIF5) in a cooperative network. PIFs are activators of the ABA response, which is usually induced in the dark in cotyledons, and are degraded in light. It has been reported that much of the photomorphogenic response involves suppressing the ABA response via PIFs and phyB (Ha et al. 2018a). PIF1 interacts physically with ABI5 and other A-type bZIP transcription factors to enhance PIF1 binding to a set of target sites in vivo (Kim et al. 2016). PIF4 activates ABI5 expression in the dark (Qi et al. 2020). Part of the PIFs control of seedling growth, involves ABA signaling (Qi et al. 2020; Liang et al. 2020). The G-box binding factors (GBF1-3), also appeared largely connected to the PPI network (Fig. 5a, b, c). GBFs are ABA-responsive genes regulated by PIFs (Oh et al., 2009). GBF1 is a blue-light responsive TF acting downstream of the cryptochromes

controlling blue-light specific responses. GBF1 overexpression reduces blue-light repression on hypocotyl elongation (Mallappa et al. 2006). GBF1 is degraded in the dark by the proteasome in a COP1-independent manner, and GBF1-COP1 interaction stabilizes GBF1 in the light (Mallappa et al. 2008b). GBF1 interatcs with both HY5 and HY5 balancing their regulatory effects (Singh et al. 2012). On the other hand, GBF3 is more abundantly expressed in darkness and roots, and it can heterodimerize with other GBFs (Schindler et al. 1992). GBFs share many co-regulated genes with HY5 and HYH and change their interaction partners depending on the tissue and light. Although some are constitutively expressed (GBF1 and GBF2), their partners can change reprogramming the developmental output (Schindler et al. 1992; Kurihara et al. 2020). We suggest a scenario were, in the dark and absence of HY5, GBFs control a set of dark-response genes and, upon illumination, GBFs can physically interact with HY5 which accumulates and displaces GBFs to different promoters activating photomorphogenesis (Singh et al. 2012).

ABA INSENSITIVE 5 (ABI5) was the only common transcription factor putatively regulating up- and down-regulated sets of genes (Fig. 6a, b, c). In this same Research Topic edition, (Bulgakov and Koren 2022) reviewed the centrality of ABI5 in light signaling networks based on protein-interactios. Our work reinforces their observations by linking ABI5 and ABA responsive genes to control seedling photomorphogenesis gene expression. ABI5 is a positive regulator of ABA signaling, expressed in cotyledons, hypocotyls, and roots of young seedlings, it is involved in postgermination developmental arrest, repression of germination and early seedling development (Collin et al. 2021). From our results from young seedlings using ABI5 reporter lines (Fig. 7a), we observed that transcription from the ABI5 promoter is high in all tissues but ABI5-GUS protein abundance was very light sensitive. We saw little light effect to repress transcription from the ABI5 promoter (ABI5p:GUS line) in cotyledons at 1h and 4h light treatments. In Supplementary Figure 4B transcriptional analysis of ABI5 shows that the light treatment reduces mRNA abundance only after 4h in Col-0. However, we found very interesting that in the 35S:ABI5 line (with a constitutive promoter) a significant reduction of mRNA abundance was observed for ABI5, which in an accordance with the reduction observed in the ABI5p:ABI5-GUS signal (Fig. 7a) suggests also there might be a light induced post-transcriptional control of ABI5 mRNA abundance and/or a repression of ABI5 translation.

ABI5 regulates genes both during seed development, germination and post germination growth (Skubacz et al. 2016) and enhances the binding of PIF1 to target promoters to inhibit seed germination (Cheng et al. 2014; Kim et al. 2016). Several previous studies have identified factors that promote photochlorophilide accumulation in the dark as pif1 and pif3 mutants have higher levels of photochlorophilide (Job and Datta 2021). Our studies show that ABI5, ABF3 and ABF4 can act as potential repressors, since their mutants showed a higher levels of photochlorophilide in the dark compared to wild type (Figure 6b).

ABI5 is positively regulated by HY5 (Chen et al. 2008) and also promotes its own expression which represents an integration light and ABA signaling process (Xu et al. 2014a; Jing and Lin 2020). It has been identified that HY5 and ABI5 interact and integrate light and ABA responses, indicating that ABI5 can act as a negative regulator in photomorphogenesis and HY5 acts as a positive regulator of ABA signaling (Bhagat et al. 2021). The overexpression of ABI5 inhibits hypocotyl elongation under blue, red, or far-red light in Col-0 (Chen et al. 2008; Xu et al. 2014), which places ABI5 as a component of photomorphogenic responses. Based on our observations that many of early light transcriptional responses might depend on ABA response factors which are already present in the dark grown seedling, we propose a model where light signaling repurposes part of this available transcriptional machinery to activate the early responsive genes upon PIF inactivation and later on, the stabilization of positive regulators of light responses (e.g. HY5, HYH, LAF1, GBFs, among others) takes over to sustain photomorphogenic growth (Fig.8). This effect might occur by direct interaction with ABA-responsive bZIPs, as HY5 and ABI5 have recently been found to physically interact (Bhagat et al. 2021). Other recently study demostrated that, COP1 modulates ABA signaling during seedling growth in dark conditions by regulating ABA-induced ABI5 accumulation, suggesting that plants adjust their signaling machinery to the ABA according to luminosity in which they find themselves (Du et al. 2022). In summary, through a survey of transcriptomic datasets, the transcriptogram method allowed us to identify common light regulated processes central to early seedling photomorphogenesis and propose a novel transitory transcription cascade for deetiolation dependent on ABA-responsive bZIP trancription factors guiding photomorphogenic development.

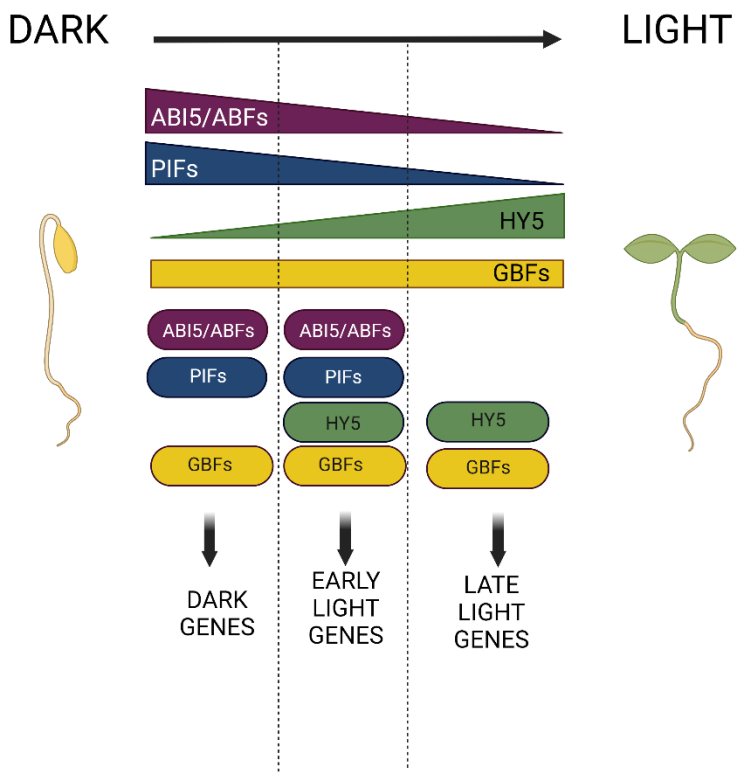


Figure 8 Proposed working model for the activation of early photomorphogenesis. PIFs, ABI5/ABFs and GBFs regulate the expression of skotomorphogenic genes the dark (Dark Genes) where PIFs and ABI5/ABFs act cooperatively to regulate ABA responses. ABI5 and PIFs protein abundance is progressively reduced after exposure to light whereas HY5 abundance increases. During the induction of early light responsive genes, the decaying transcription factors ABI5/ABFs and PIFs interact and cooperate with light responsive regulators GBFs and HY5 to initiate photopmorphogenesis (Early Light Genes). GBFs are continuosly expressed. After prolonged light exposure ABI5/ABFs and PIFs are degraded and positive photomorphogenic regulators overtake transcriptional control (Late Light Genes). Figure created in Biorender.

6 Author contributions CFS, IS-V and AF-T - performed experiments; CFS analyzed the data and wrote the manuscript. RJSD and IS—processed the sequencing raw data. BHO and LA—helped with the transcriptogram analysis. OLS and FSM—conceived, supervised the study and wrote and edited the manuscript. All the contributors read and approved the final

7 Acknowledgements We thank Dr. Fernanda Lazzarotto for the critical reviewing of the manuscript. This study was financed in part by Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) Finance Code

88881.068110/2014-01 (to FSM) and by grants PID2020-119731RB-I00 from the Ministerio de Ciencia e Innovación (MCIN/AEI), SA137P20 from Junta de Castilla y León and Escalera de Excelencia CLU-2018-04 co-funded by the P.O. FEDER of Castilla y León 2014–2020 Spain (to O.L.).

8 References

Alexa A, Rahnenfuhrer J (2016). topGO: Enrichment Analysis for Gene Ontology. R package version 2.28.0.

Abbas N, Maurya JP, Senapati D, Gangappa SN and Chattopadhyaya S (2014) Arabidopsis CAM7 and HY5 physically interact and directly bind to the HY5 promoter to regulate its expression and thereby promote photomorphogenesis. Plant Cell 26:1036–1052. doi: 10.1105/tpc.113.122515

Achard P, Liao L, Jiang C, Desnos T, Bartlett J, Fu X and Harberd NP (2007) DELLAs contribute to plant photomorphogenesis. Plant Physiol 143:1163–1172. doi: 10.1104/pp.106.092254

Achard P, Renou J-P, Berthomé R, Harberd NP and Genschik P (2008) Plant DELLAs Restrain Growth and Promote Survival of Adversity by Reducing the Levels of Reactive Oxygen Species. Curr Biol 18:656–660. doi: 10.1016/J.CUB.2008.04.034

Agurla S, Gahir S, Munemasa S, Murata Y, Raghavendra AS, Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I et al. (2020) Light and abscisic acid coordinately regulate greening of seedlings. Plant Physiol 183:1281–1294. doi: 10.1104/pp.20.00503

Al-Sady B, Ni W, Kircher S, Schäfer E and Quail PH (2006) Photoactivated Phytochrome Induces Rapid PIF3 Phosphorylation Prior to Proteasome-Mediated Degradation. Mol Cell 23:439–446. doi: 10.1016/j.molcel.2006.06.011

Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I, Nambara E and Lorenzo O (2015) S-nitrosylation triggers ABI5 degradation to promote seed germination and seedling growth. Nat Commun 6:1–10. doi: 10.1038/ncomms9669

Ali F, Qanmber G, Li F and Wang Z (2022) Updated role of ABA in seed maturation, dormancy, and germination. J Adv Res 35:199–214. doi: 10.1016/J.JARE.2021.03.011

An F, Zhang X, Zhu Z, Ji Y, He W, Jiang Z, Li M and Guo H (2012) Coordinated regulation of apical hook development by gibberellins and ethylene in etiolated Arabidopsis seedlings. Cell Res 2012 225 22:915–927. doi: 10.1038/cr.2012.29

Ang Lay Hong and Deng Xing Wang (1994) Regulatory hierarchy of photomorphogenic loci: Allele-specific and light-dependent interaction between the HY5 and COP1 loci. Plant Cell 6:613–628. doi: 10.1105/tpc.6.5.613

Ang LH, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A and Deng XW (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. Mol Cell 1:213–222. doi: 10.1016/S1097-2765(00)80022-2

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012a)

Photomorphogenesis. Arab B 10:e0147. doi: 10.1199/tab.0147

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012b) Photomorphogenesis Photomorphogenesis. Society. doi: 10.1199/tab.0147

Bai MY, Shang JX, Oh E, Fan M, Bai Y, Zentella R, Sun TP and Wang ZY (2012) Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. Nat Cell Biol 14:810–817. doi: 10.1038/ncb2546

Bai S, Yao T, Li M, Guo X, Zhang Y, Zhu S and He Y (2014) PIF3 Is Involved in the Primary Root Growth Inhibition of Arabidopsis Induced by Nitric Oxide in the Light. Mol Plant 7:616–625. doi: 10.1093/MP/SST142

Balcerowicz M, Fittinghoff K, Wirthmueller L, Maier A, Fackendahl P, Fiene G, Koncz C and Hoecker U (2011) Light exposure of Arabidopsis seedlings causes rapid de-stabilization as well as selective post-translational inactivation of the repressor of photomorphogenesis SPA2. Plant J 65:712–723. doi: 10.1111/J.1365-313X.2010.04456.X

Balcerowicz M, Kerner K, Schenkel C and Hoecker U (2017) SPA proteins affect the subcellular localization of COP1 in the COP1/SPA ubiquitin ligase complex during photomorphogenesis. Plant Physiol 174:1314–1321. doi: 10.1104/pp.17.00488

Banerjee A and Roychoudhury A (2017) Abscisic-acid-dependent basic leucine zipper (bZIP) transcription factors in plant abiotic stress. Protoplasma 254:3–16. doi: 10.1007/S00709-015-0920-4/FIGURES/1

Bao F, Shen J, Brady SR, Muday GK, Asami T and Yang Z (2004) Brassinosteroids interact with auxin to promote lateral root development in arabidopsis. Plant Physiol 134:1624–1631. doi: 10.1104/pp.103.036897

Bhagat PK, Verma D, Sharma D and Sinha AK (2021a) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z/FIGURES/6

Bhagat PK, Verma D, Sharma D and Sinha AK (2021b) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z

Bhalerao RP, Eklo J, Ljung K, Marchant A, Bennett M and Sandberg È (2002a) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. 29:

Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett M and Sandberg G (2002b) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. Plant J 29:325–332. doi: 10.1046/j.0960-7412.2001.01217.x

Bhatia S, Gangappa SN, Kuswaha R, Kundu S and Chattopadhyay S (2008) Short Hypocotyl in White Light1, a serine-arginine-aspartate-rich protein in Arabidopsis, acts as a negative regulator of photomorphogenic growth. Plant Physiol 147:169–178. doi: 10.1104/pp.108.118174

Bhatnagar A, Singh S, Khurana JP and Burman N (2020) HY5-COP1: the central module of light signaling pathway. J Plant Biochem Biotechnol 29:590–610. doi: 10.1007/s13562-020-00623-3

Binder BM, Walker JM, Gagne JM, Emborg TJ, Hemmann G, Bleecker AB and

Vierstra RD (2007) The Arabidopsis EIN3 Binding F-Box Proteins EBF1 and EBF2 Have Distinct but Overlapping Roles in Ethylene Signaling. Plant Cell 19:509–523. doi: 10.1105/TPC.106.048140

Binenbaum J, Weinstain R and Shani E (2018) Gibberellin Localization and Transport in Plants. Trends Plant Sci 23:410–421. doi: 10.1016/J.TPLANTS.2018.02.005

Bouché F, D'Aloia M, Tocquin P, Lobet G, Detry N and Périlleux C (2016) Integrating roots into a whole plant network of flowering time genes in Arabidopsis thaliana. Sci Reports 2016 61 6:1–12. doi: 10.1038/srep29042

Brumos J, Robles LM, Yun J, Vu TC, Jackson S, Alonso JM and Stepanova Correspondence AN (2018) Local Auxin Biosynthesis Is a Key Regulator of Plant Development. Dev Cell 47:306–318. doi: 10.1016/j.devcel.2018.09.022

Brunetti C, Sebastiani F and Tattini M (2019) Review: ABA, flavonols, and the evolvability of land plants. Plant Sci 280:448–454. doi: 10.1016/j.plantsci.2018.12.010

Buer CS, Muday GK and Djordjevic MA (2007) Flavonoids are differentially taken up and transported long distances in Arabidopsis. Plant Physiol 145:478–490. doi: 10.1104/pp.107.101824

Bulgakov VP and Koren OG (2022) Basic Protein Modules Combining Abscisic Acid and Light Signaling in Arabidopsis. Front Plant Sci 12:2986. doi: 10.3389/FPLS.2021.808960/BIBTEX

Burko Y, Gaillochet C, Seluzicki A, Chory J and Busch W (2020a) Local HY5 Activity Mediates Hypocotyl Growth and Shoot-to-Root Communication. Plant Commun 1:100078. doi: 10.1016/j.xplc.2020.100078

Burko Y, Seluzicki A, Zander M, Pedmale U V., Ecker JR and Chory J (2020b) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/TPC.19.00772

Burko Y, Seluzicki A, Zander M, Pedmale U V, Ecker JR and Chory J (2020c) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/tpc.19.00772

Cabrera J, Conesa CM and Pozo JC (2022) May the dark be with roots: a perspective on how root illumination may bias in vitro research on plant–environment interactions. New Phytol 233:1988–1997. doi: 10.1111/nph.17936

Canamero RC, Bakrim N, Bouly J-P, Garay A, Dudkin EE, Habricot Y and Ahmad M (2006) Cryptochrome photoreceptors cry1 and cry2 antagonistically regulate primary root elongation in Arabidopsis thaliana. Planta 2006 2245 224:995–1003. doi: 10.1007/S00425-006-0280-6

Cañibano E, Bourbousse C, García-León M, Garnelo Gómez B, Wolff L, García-Baudino C, Lozano-Durán R, Barneche F, Rubio V and Fonseca S (2021) DET1-mediated COP1 regulation avoids HY5 activity over second-site gene targets to tune plant photomorphogenesis. Mol Plant 14:963–982. doi: 10.1016/j.molp.2021.03.009

Caño-Delgado A, Lee J-Y and Demura T (2010) Regulatory Mechanisms for Specification and Patterning of Plant Vascular Tissues. Annu Rev Cell Dev Biol 26:605–637. doi: 10.1146/annurev-cellbio-100109-104107

Carella P, Merl-Pham J, Wilson DC, Dey S, Hauck SM, Vlot AC and Cameron RK (2016) Comparative Proteomics Analysis of Phloem Exudates Collected during the Induction of Systemic Acquired Resistance. Plant Physiol 171:1495. doi: 10.1104/PP.16.00269

Chaiwanon J, Wang W, Zhu J-Y, Oh E and Wang Z-Y (2016) Information Integration and Communication in Plant Growth Regulation. Cell 164:1257–1268. doi: 10.1016/j.cell.2016.01.044

Chaiwanon J and Wang ZY (2015) Spatiotemporal brassinosteroid signaling and antagonism with auxin pattern stem cell dynamics in Arabidopsis roots. Curr Biol 25:1031–1042. doi: 10.1016/j.cub.2015.02.046

Chamovitz D a, Wei N, Osterlund MT, von Arnim a G, Staub JM, Matsui M and Deng XW (1996) The COP9 complex, a novel multisubunit nuclear regulator involved in light control of a plant developmental switch. Cell 86:115–21.

Chen G-H, Liu M-J, Xiong Y, Sheen J and Wu S-H (2018) TOR and RPS6 transmit light signals to enhance protein translation in deetiolating Arabidopsis seedlings. Proc Natl Acad Sci 115:12823–12828. doi: 10.1073/pnas.1809526115

Chen H, Huang X, Gusmaroli G, Terzaghi W, Lau OS, Yanagawa Y, Zhang Y, Li J, Lee JH, Zhu D et al. (2010) Arabidopsis CULLIN4-damaged DNA binding protein 1 interacts with CONSTITUTIVELY PHOTOMORPHOGENIC1-SUPPRESSOR OF PHYA complexes to regulate photomorphogenesis and flowering time. Plant Cell 22:108–123. doi: 10.1105/tpc.109.065490

Chen H, Zhang J, Neff MM, Hong S-WW, Zhang H, Deng X-WW, Xiong L and Korea S (2008a) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen H, Zhang J, Neff MM, Hong SW, Zhang H, Deng XW and Xiong L (2008b) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen Q, Dai X, De-Paoli H, Cheng Y, Takebayashi Y, Kasahara H, Kamiya Y and Zhao Y (2014) Auxin overproduction in shoots cannot rescue auxin deficiencies in arabidopsis roots. Plant Cell Physiol 55:1072–1079. doi: 10.1093/pcp/pcu039

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016a) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016b) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Cheng ZJ, Zhao XY, Shao XX, Wang F, Zhou C, Liu YG, Zhang Y and Zhang XS (2014) Abscisic acid regulates early seed development in arabidopsis by ABI5-Mediated transcription of SHORT HYPOCOTYL UNDER BLUE1. Plant Cell 26:1053–1068. doi: 10.1105/tpc.113.121566

Chory J (1993) Out of darkness: mutants reveal pathways controlling light-regulated development in plants. Trends Genet 9:167–172. doi: 10.1016/0168-9525(93)90163-

C

Christians MJ, Gingerich DJ, Hua Z, Lauer TD and Vierstra RD (2012) The Light-Response BTB1 and BTB2 Proteins Assemble Nuclear Ubiquitin Ligases That Modify Phytochrome B and D Signaling in Arabidopsis. Plant Physiol 160:118–134. doi: 10.1104/pp.112.199109

Christie JM, Blackwood L, Petersen J and Sullivan S (2015) Plant Flavoprotein Photoreceptors. Plant Cell Physiol 56:401–413. doi: 10.1093/pcp/pcu196

Collin A, Daszkowska-Golec A and Szarejko I (2021) Updates on the Role of ABSCISIC ACID INSENSITIVE 5 (ABI5) and ABSCISIC ACID-RESPONSIVE ELEMENT BINDING FACTORs (ABFs) in ABA Signaling in Different Developmental Stages in Plants. Cells 2021, Vol 10, Page 1996 10:1996. doi: 10.3390/CELLS10081996

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C et al. (2007) FT protein movement contributes to long-distance signaling in floral induction of Arabidopsis. Science 316:1030–1033. doi: 10.1126/SCIENCE.1141752

Correll MJ and Kiss JZ (2005a) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Correll MJ and Kiss JZ (2005b) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Cosme M, Fernández I, Declerck S, van der Heijden MGA and Pieterse CMJ (2021) A coumarin exudation pathway mitigates arbuscular mycorrhizal incompatibility in Arabidopsis thaliana. Plant Mol Biol 1:3. doi: 10.1007/s11103-021-01143-x

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011a) Root-localized phytochrome chromophore synthesis is required for photoregulation of root elongation and impacts root sensitivity to jasmonic acid in Arabidopsis. Plant Physiol 157:1138–50. doi: 10.1104/pp.111.184689

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011b) Root-Localized Phytochrome Chromophore Synthesis Is Required for Photoregulation of Root Elongation and Impacts Root Sensitivity to Jasmonic Acid in Arabidopsis. Plant Physiol 157:1138–1150. doi: 10.1104/pp.111.184689

da Silva SR, Perrone GC, Dinis JM and de Almeida RM (2014a) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics 15:1181. doi: 10.1186/1471-2164-15-1181

da Silva SRM, Perrone GC, Dinis JM and de Almeida RMC (2014b) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics. doi: 10.1186/1471-2164-15-1181

Datta S, Hettiarachchi GHCM, Deng X-W and Holm M (2006) Arabidopsis CONSTANS-LIKE3 Is a Positive Regulator of Red Light Signaling and Root Growth. Plant Cell 18:70–84. doi: 10.1105/TPC.105.038182

de Lucas M, Davière J-M, Rodríguez-Falcón M, Pontin M, Iglesias-Pedraz JM, Lorrain S, Fankhauser C, Blázquez MA, Titarenko E and Prat S (2008) A molecular framework for light and gibberellin control of cell elongation. Nature 451:480–484. doi: 10.1038/nature06520

de Wit M, Keuskamp DH, Bongers FJ et al. (2016) Integration of Phytochrome and Cryptochrome Signals Determines Plant Growth during Competition for Light. Curr Biol 26:3320–3326. doi: 10.1016/j.cub.2016.10.031

De Wit M, Galvão VC and Fankhauser C (2016) Light-Mediated Hormonal Regulation of Plant Growth and Development. Annu Rev Plant Biol 67:513–537. doi: 10.1146/annurev-arplant-043015-112252

Deng X-WX -W and Quail PH (1992) Genetic and phenotypic characterization of cop1 mutants of Arabidopsis thaliana. Plant J 2:83–95. doi: 10.1111/j.1365-313X.1992.00083.x

Deng XW, Caspar T and Quail PH (1991) cop1: a regulatory locus involved in light-controlled development and gene expression in Arabidopsis. Genes Dev 5:1172–1182. doi: 10.1101/GAD.5.7.1172

Dobin A, Davis CA, Schlesinger F, Drenkow J, Zaleski C, Jha S, Batut P, Chaisson M and Gingeras TR (2013) Sequence analysis STAR: ultrafast universal RNA-seq aligner. 29:15–21. doi: 10.1093/bioinformatics/bts635

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017a) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017b) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Tang D, Gao Z, Yu R, Li K, He H, Terzaghi W, Deng XW and Chen H (2014) Arabidopsis DE-ETIOLATED1 Represses Photomorphogenesis by Positively Regulating Phytochrome-Interacting Factors in the Dark. Plant Cell 26:3630–3645. doi: 10.1105/tpc.114.130666

Du M, Daher FB, Liu Y, Steward A, Tillmann M, Zhang X, Wong JH, Ren H, Cohen JD, Li C et al. (2022) Biphasic control of cell expansion by auxin coordinates etiolated seedling development. Sci Adv 8:1570. doi: 10.1126/SCIADV.ABJ1570/SUPPL_FILE/SCIADV.ABJ1570_MOVIES_S1_TO_S8.ZIP

Duan L, Pérez-Ruiz JM, Cejudo FJ and Dinneny JR (2021) Characterization of CYCLOPHILLIN38 shows that a photosynthesis-derived systemic signal controls lateral root emergence. Plant Physiol 185:503–518. doi: 10.1093/PLPHYS/KIAA032

Durinck S, Spellman PT, Birney E and Huber W (2009) Mapping identifiers for the integration of genomic datasets with the R/ Bioconductor package biomaRt. Nat Protoc 4:1184–1191. doi: 10.1038/nprot.2009.97

Dyachok J, Zhu L, Liao F, He J, Huq E and Blancaflor EB (2011) SCAR Mediates Light-Induced Root Elongation in Arabidopsis through Photoreceptors and Proteasomes. Plant Cell 23:3610–3626. doi: 10.1105/tpc.111.088823

Feng S, Martinez C, Gusmaroli G, Wang Y, Zhou J, Wang F, Chen L, Yu L, Iglesias-Pedraz JM, Kircher S et al. (2008) Coordinated regulation of Arabidopsis thaliana development by light and gibberellins. Nature 451:475–479. doi: 10.1038/nature06448

Fernández-Milmanda GL and Ballaré CL (2021) Shade Avoidance: Expanding the

Color and Hormone Palette. Trends Plant Sci 26:509–523. doi: 10.1016/j.tplants.2020.12.006

Fernando VCD, Al Khateeb W, Belmonte MF and Schroeder DF (2018) Role of Arabidopsis ABF1/3/4 during det1 germination in salt and osmotic stress conditions. Plant Mol Biol 97:149–163. doi: 10.1007/S11103-018-0729-6/FIGURES/10

Forde BG (2002) Local and long-range signaling pathways regulating plant responses to nitrate. Annu Rev Plant Biol 53:203–224. doi: 10.1146/annurev.arplant.53.100301.135256

Franceschini A, Szklarczyk D, Frankild S, Kuhn M, Simonovic M, Roth A, Lin J, Minguez P, Bork P, von Mering C et al. (2012) STRING v9.1: protein-protein interaction networks, with increased coverage and integration. Nucleic Acids Res 41:D808–D815. doi: 10.1093/nar/gks1094

Fu L, Liu Y, Qin G, Wu P, Zi H, Xu Z, Zhao X, Wang Y, Li Y, Yang S et al. (2021) The TOR–EIN2 axis mediates nuclear signalling to modulate plant growth. Nature 591:288–292. doi: 10.1038/s41586-021-03310-y

Fu X and Harberd NP (2003) Auxin promotes Arabidopsis root growth by modulating gibberellin response. Nature 421:740–743. doi: 10.1038/nature01387

Fukaki H, Taniguchi N and Tasaka M (2006) PICKLE is required for SOLITARY-ROOT/IAA14-mediated repression of ARF7 and ARF19 activity during Arabidopsis lateral root initiation. Plant J 48:380–389. doi: 10.1111/J.1365-313X.2006.02882.X

Gaillochet C, Burko Y, Platre MP, Zhang L, Simura J, Willige BC, Kumar SV, Ljung K, Chory J and Busch W (2020) HY5 and phytochrome activity modulate shoot to root coordination during thermomorphogenesis. Development. doi: 10.1242/dev.192625

Galen C, Rabenold JJ and Liscum E (2007) Functional ecology of a blue light photoreceptor: effects of phototropin-1 on root growth enhance drought tolerance in Arabidopsis thaliana. New Phytol 173:91–99. doi: 10.1111/J.1469-8137.2006.01893.X

Galvã VC and Fankhauser C (2015) Sensing the light environment in plants: photoreceptors and early signaling steps. Curr Opin Neurobiol 34:46–53. doi: 10.1016/j.conb.2015.01.013

Gangappa SN, Crocco CD, Johansson H, Datta S, Hettiarachchi C, Holm M and Botto JF (2013a) The Arabidopsis B-BOX Protein BBX25 Interacts with HY5, Negatively Regulating BBX22 Expression to Suppress Seedling Photomorphogenesis. Plant Cell 25:1243–1257. doi: 10.1105/TPC.113.109751

Gangappa SN, Holm M and Botto JF (2013b) Molecular interactions of BBX24 and BBX25 with HYH, HY5 HOMOLOG, to modulate Arabidopsis seedling development. Plant Signal Behav. doi: 10.4161/psb.25208

Gao YQ, Bu LH, Han ML, Wang YL, Li ZY, Liu HT and Chao DY (2021) Long-distance blue light signalling regulates phosphate deficiency-induced primary root growth inhibition. Mol Plant 14:1539–1553. doi: 10.1016/j.molp.2021.06.002

García-González J, Lacek J, Weckwerth W and Retzer K (2021) Exogenous carbon source supplementation counteracts root and hypocotyl growth limitations under increased cotyledon shading, with glucose and sucrose differentially modulating

growth curves. Plant Signal Behav. doi: 10.1080/15592324.2021.1969818

Gautier L, Cope L, Bolstad BM and Irizarry RA (2004) affy-analysis of Affymetrix GeneChip data at the probe level. BIOINFORMATICS 20:307–315. doi: 10.1093/bioinformatics/btg405

Ge S, He L, Jin L, Xia X, Li L, Ahammed GJ, Qi Z, Yu J and Zhou Y (2022) Light-dependent activation of HY5 promotes mycorrhizal symbiosis in tomato by systemically regulating strigolactone biosynthesis. New Phytol 233:1900–1914. doi: 10.1111/nph.17883

Gil K-E, Ha J-H and Park C-M (2018) Abscisic acid-mediated phytochrome B signaling promotes primary root growth in Arabidopsis. Plant Signal Behav 13:e1473684. doi: 10.1080/15592324.2018.1473684

Gommers CMM and Monte E (2018) Seedling Establishment: A Dimmer Switch-Regulated Process between Dark and Light Signaling. Plant Physiol 176:1061–1074. doi: 10.1104/pp.17.01460

Grunewald W, De Smet I, Lewis DR, Löfke C, Jansen L, Goeminne G, Vanden Bossche R, Karimi M, De Rybel B, Vanholme B et al. (2012) Transcription factor WRKY23 assists auxin distribution patterns during Arabidopsis root development through local control on flavonol biosynthesis. Proc Natl Acad Sci U S A 109:1554–9. doi: 10.1073/pnas.1121134109

Guo Z, Xu J, Wang Y, Hu C, Shi K, Zhou J, Xia X, Zhou Y, Foyer CH and Yu J (2021) The phyB-dependent induction of HY5 promotes iron uptake by systemically activating FER expression. EMBO Rep 22:e51944. doi: 10.15252/embr.202051944

Ha J-HH, Kim J-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-HJ-IIJH and Park C-MM (2018a) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant J 94:790–798. doi: 10.1111/tpj.13902

Ha J-HH, Kim J-IJ-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-IJ-HJ-IIJH and Park C-MM (2018b) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant J 94:790–798. doi: 10.1111/tpj.13902

Hacham Y, Holland N, Butterfield C, Ubeda-Tomas S, Bennett MJ, Chory J and Savaldi-Goldstein S (2011) Brassinosteroid perception in the epidermis controls root meristem size. Development 138:839–848. doi: 10.1242/DEV.061804

Ham B-K and Lucas WJ (2017a) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Ham B-K and Lucas WJ (2017b) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Hamon-josse M, Villaecija-aguilar JA, Ljung K and Leyser O (2021) KAI2 regulates seedling development by mediating light- induced remodelling of auxin transport. bioRxiv 2021.05.06.443001. doi: 10.1101/2021.05.06.443001

Hamon-Josse M, Villaécija-Aguilar JA, Ljung K, Leyser O, Gutjahr C and Bennett T (2022) KAI2 regulates seedling development by mediating light-induced remodelling

of auxin transport. New Phytol 235:126–140. doi: 10.1111/NPH.18110

Han X, Huang X and Deng XW (2020) The Photomorphogenic Central Repressor COP1: Conservation and Functional Diversification during Evolution. Plant Commun 1:100044. doi: 10.1016/j.xplc.2020.100044

Hannapel DJ, Sharma P and Lin T (2013) Phloem-mobile messengerRNAs and root development. Front Plant Sci 4:257. doi: 10.3389/FPLS.2013.00257/BIBTEX

Harkey AF, Watkins JM, Olex AL, DiNapoli KT, Lewis DR, Fetrow JS, Binder BM and Muday GK (2018) Identification of Transcriptional and Receptor Networks That Control Root Responses to Ethylene. Plant Physiol 176:2095–2118. doi: 10.1104/PP.17.00907

Hartmann L, Drewe-Boß P, Wießner T, Wagner G, Geue S, Lee H-C, Obermüller DM, Kahles A, Behr J, Sinz FH et al. (2016) Alternative Splicing Substantially Diversifies the Transcriptome during Early Photomorphogenesis and Correlates with the Energy Availability in Arabidopsis. Plant Cell 28:2715–2734. doi: 10.1105/tpc.16.00508

He S-B, Wang W-X, Zhang J-Y, Xu F, Lian H-L, Li L and Yang H-Q (2015a) The CNT1 Domain of Arabidopsis CRY1 Alone Is Sufficient to Mediate Blue Light Inhibition of Hypocotyl Elongation. Mol Plant 8:822–825. doi: 10.1016/J.MOLP.2015.02.008

He SB, Wang WX, Zhang JY, Xu F, Lian HL, Li L and Yang HQ (2015b) The CNT1 domain of arabidopsis CRY1 alone is sufficient to mediate blue light inhibition of hypocotyl elongation. Mol Plant 8:822–825. doi: 10.1016/j.molp.2015.02.008

He Z, Zhao X, Kong F, Zuo Z and Liu X (2016) TCP2 positively regulates HY5/HYH and photomorphogenesis in Arabidopsis. J Exp Bot 67:775–785. doi: 10.1093/JXB/ERV495

Hellmann H and Estelle M (2002a) Plant development: regulation by protein degradation. Science 297:793–7. doi: 10.1126/science.1072831

Hellmann H and Estelle M (2002b) Plant development: Regulation by protein degradation. Science (80-) 297:793–797. doi: 10.1126/science.1072831

Heo J-O, Chang KS, Kim IA, Lee M-H, Lee SA, Song S-K, Lee MM and Lim J (2011) Funneling of gibberellin signaling by the GRAS transcription regulator SCARECROW-LIKE 3 in the Arabidopsis root. Proc Natl Acad Sci 108:2166–2171. doi: 10.1073/pnas.1012215108

Hoecker U and Quail PH (2001) The Phytochrome A-specific Signaling Intermediate SPA1 Interacts Directly with COP1, a Constitutive Repressor of Light Signaling inArabidopsis. J Biol Chem 276:38173–38178. doi: 10.1074/jbc.M103140200

Hoecker U, Tepperman JM and Quail PH (1999) SPA1, a WD-Repeat Protein Specific to Phytochrome A Signal Transduction. Science (80-) 284:496–499. doi: 10.1126/science.284.5413.496

Holm M, Ma LG, Qu LJ and Deng XW (2002) Two interacting bZIP proteins are direct targets of COP1-mediated control of light-dependent gene expression in Arabidopsis. Genes Dev 16:1247–1259. doi: 10.1101/gad.969702

Holtan HE, Bandong S, Marion CM, Adam L, Tiwari S, Shen Y, Maloof JN, Maszle DR, Ohto M, Preuss S et al. (2011) BBX32, an Arabidopsis B-Box Protein, Functions

in Light Signaling by Suppressing HY5-Regulated Gene Expression and Interacting with STH2/BBX21. Plant Physiol 156:2109–2123. doi: 10.1104/PP.111.177139

Hornitschek P, Kohnen M V., Lorrain S, Rougemont J, Ljung K, López-Vidriero I, Franco-Zorrilla JM, Solano R, Trevisan M, Pradervand S et al. (2012) Phytochrome interacting factors 4 and 5 control seedling growth in changing light conditions by directly controlling auxin signaling. Plant J 71:699–711. doi: 10.1111/j.1365-313X.2012.05033.x

Hu W, Su Y-S and Lagarias JC (2009a) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant • 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009b) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009c) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Humplík JF, Bergougnoux V and Van Volkenburgh E (2017) To Stimulate or Inhibit? That Is the Question for the Function of Abscisic Acid. Trends Plant Sci 22:830–841. doi: 10.1016/j.tplants.2017.07.009

Jaillais Y and Vert G (2016) Brassinosteroid signaling and BRI1 dynamics went underground. Curr Opin Plant Biol 33:92–100. doi: 10.1016/J.PBI.2016.06.014

Jeong J and Choi G (2013) Phytochrome-interacting factors have both shared and distinct biological roles. Mol Cells 35:371–380. doi: 10.1007/s10059-013-0135-5

Jeong J, Kim K, Kim ME, Kim HG, Heo GS, Park OK, Park Y Il, Choi G and Oh E (2016) Phytochrome and ethylene signaling integration in Arabidopsis occurs via the transcriptional regulation of genes co-targeted by PIFs and EIN3. Front Plant Sci 7:1055. doi: 10.3389/fpls.2016.01055

Jiang K, Yung V, Chiba T and Feldman LJ (2017) Longitudinal patterning in roots: a GATA2–auxin interaction underlies and maintains the root transition domain. Planta 2017 2474 247:831–843. doi: 10.1007/S00425-017-2831-4

Jiao Y, Lau OS and Deng XW (2007a) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jiao Y, Lau OS and Deng XW (2007b) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jing Y and Lin R (2013) Plant Signaling & Behavior PICKLE is a repressor in seedling de-etiolation pathway. doi: 10.4161/psb.25026

Jing Y and Lin R (2020) Transcriptional regulatory network of the light signaling pathways. New Phytol 227:683–697. doi: 10.1111/nph.16602

Jing Y, Zhang D, Wang X, Tang W, Wang W, Huai J, Xu G, Chen D, Li Y and Lin R (2013) Arabidopsis chromatin remodeling factor PICKLE interacts with transcription factor HY5 to regulate hypocotyl cell elongation. Plant Cell 25:242–256. doi: 10.1105/tpc.112.105742

Job N and Datta S (2021) PIF3/HY5 module regulates BBX11 to suppress

protochlorophyllide levels in dark and promote photomorphogenesis in light. New Phytol 230:190–204. doi: 10.1111/nph.17149

Job N, Yadukrishnan P, Bursch K, Datta S and Johansson H (2018) Two B-Box Proteins Regulate Photomorphogenesis by Oppositely Modulating HY5 through their Diverse C-Terminal Domains. Plant Physiol 176:2963–2976. doi: 10.1104/PP.17.00856

Khanna R, Huq E, Kikis EA, Al-Sady B, Lanzatella C and Quail PH (2004) A novel molecular recognition motif necessary for targeting photoactivated phytochrome signaling to specific basic helix-loop-helix transcription factors. Plant Cell 16:3033–3044. doi: 10.1105/tpc.104.025643

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J and Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363. doi: 10.1111/j.1365-313X.2007.03052.x

Kim B, Jeong YJ, Corvalán C, Fujioka S, Cho S, Park T and Choe S (2014) Darkness and gulliver2/phyB mutation decrease the abundance of phosphorylated BZR1 to activate brassinosteroid signaling in Arabidopsis. Plant J 77:737–747. doi: 10.1111/tpj.12423

Kim J, Kang H, Park J, Kim W, Yoo J, Lee N, Kim J, Yoon T-Y and Choi G (2016) PIF1-Interacting Transcription Factors and Their Binding Sequence Elements Determine the in Vivo Targeting Sites of PIF1. doi: 10.1105/tpc.16.00125

Kircher S and Schopfer P (2012) Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. Proc Natl Acad Sci U S A 109:11217–11221. doi: 10.1073/pnas.1203746109

Kircher S and Schopfer P Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. doi: 10.1073/pnas.1203746109

Ko D and Helariutta Y (2017) Shoot–Root Communication in Flowering Plants. Curr Biol 27:R973–R978. doi: 10.1016/j.cub.2017.06.054

Kondhare KR, Patil NS and Banerjee AK (2021) A historical overview of long-distance signalling in plants. J Exp Bot 72:4218–4236. doi: 10.1093/JXB/ERAB048

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010a) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/j.devcel.2010.05.008

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010b) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/J.DEVCEL.2010.05.008

Kulkarni SR, Vaneechoutte D, de Velde J Van and Vandepoele K (2018) TF2Network: predicting transcription factor regulators and gene regulatory networks in Arabidopsis using publicly available binding site information. Nucleic Acids Res.

Kumar P, Montgomery CE and Kiss JZ (2008) The role of phytochrome C in gravitropism and phototropism in Arabidopsis thaliana. Funct Plant Biol 35:298–305. doi: 10.1071/FP08013

Kumari S, Yadav S, Patra D, Singh S, Sarkar AK and Panigrahi KCS (2019) Uncovering the molecular signature underlying the light intensity-dependent root development in Arabidopsis thaliana. BMC Genomics 20:1–23. doi: 10.1186/s12864-019-5933-5

Kurata T and Yamamoto KT (1997) Light-stimulated root elongation in Arabidopsis thaliana. J Plant Physiol 151:346–351. doi: 10.1016/S0176-1617(97)80263-5

Kurihara Y, Makita Y, Shimohira H and Matsui M (2020) Time-Course Transcriptome Study Reveals Mode of bZIP Transcription Factors on Light Exposure in Arabidopsis. Int J Mol Sci 21:1993. doi: 10.3390/ijms21061993

Kushwaha R, Singh A and Chattopadhyay S (2008) Calmodulin7 Plays an Important Role as Transcriptional Regulator in Arabidopsis Seedling Development. Plant Cell 20:1747–1759. doi: 10.1105/TPC.107.057612

Kwok SF, Piekos B, Miśera S and Deng XW (1996) A complement of ten essential and pleiotropic arabidopsis COP/DET/FUS genes is necessary for repression of photomorphogenesis in darkness. Plant Physiol 110:731–742. doi: 10.1104/pp.110.3.731

Lacek J, García-González J, Weckwerth W and Retzer K (2021a) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 22:12784. doi: 10.3390/ijms222312784

Lacek J, García-González J, Weckwerth W and Retzer K (2021b) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 2021, Vol 22, Page 12784 22:12784. doi: 10.3390/IJMS222312784

Lau K, Podolec R, Chappuis R, Ulm R and Hothorn M (2019) Plant photoreceptors and their signaling components compete for COP1 binding via VP peptide motifs. EMBO J 38:e102140. doi: 10.15252/embj.2019102140

Lau OS and Deng XW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci 17:584–593. doi: 10.1016/J.TPLANTS.2012.05.004

Lau OS, Huang X, Charron J-B, Lee J-H, Li G and Deng XW (2011) Interaction of Arabidopsis DET1 with CCA1 and LHY in mediating transcriptional repression in the plant circadian clock. Mol Cell 43:703. doi: 10.1016/J.MOLCEL.2011.07.013

Laxmi A, Pan J, Morsy M and Chen R (2008a) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Laxmi A, Pan J, Morsy M and Chen R (2008b) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Leasure CD, Tong H, Yuen G, Hou X, Sun X and He ZH (2009) Root UV-B sensitive2 acts with root UV-B sensitive1 in a root ultraviolet B-sensing pathway. Plant Physiol 150:1902–1915. doi: 10.1104/pp.109.139253

Lee H-J, Ha J-H, Kim S-G, Choi H-K, Kim ZH, Han Y-J, Kim J-I, Oh Y, Fragoso V,

Shin K et al. (2016a) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal 9:1–9. doi: 10.1126/scisignal.aaf6530

Lee HJ, Ha JH, Kim SG, Choi HK, Kim ZH, Han YJ, Kim J Il, Oh Y, Fragoso V, Shin K et al. (2016b) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal. doi: 10.1126/SCISIGNAL.AAF6530

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017a) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/j.tplants.2017.06.009

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017b) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/J.TPLANTS.2017.06.009

Lee S, Wang W and Huq E (2021) Spatial regulation of thermomorphogenesis by HY5 and PIF4 in Arabidopsis. Nat Commun 2021 121 12:1–12. doi: 10.1038/s41467-021-24018-7

Leivar P and Monte E (2014) PIFs: Systems Integrators in Plant Development. Plant Cell 26:56–78. doi: 10.1105/TPC.113.120857

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008a) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi: 10.1016/j.cub.2008.10.058

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008b) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi: 10.1016/J.CUB.2008.10.058

Leivar P and Quail PH (2011) PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci 16:19–28. doi: 10.1016/j.tplants.2010.08.003

Leivar P, Tepperman JM, Monte E, Calderon RH, Liu TL and Quail PH (2009) Definition of early transcriptional circuitry involved in light-induced reversal of PIF-imposed repression of photomorphogenesis in young Arabidopsis seedlings. Plant Cell 21:3535–3553. doi: 10.1105/tpc.109.070672

Lejay L, Wirth J, Pervent M, Cross JMF, Tillard P and Gojon A (2008) Oxidative pentose phosphate pathway-dependent sugar sensing as a mechanism for regulation of root ion transporters by photosynthesis. Plant Physiol 146:2036–2053. doi: 10.1104/pp.107.114710

Li L, Ljung K, Breton G, Schmitz RJ, Pruneda-Paz J, Cowing-Zitron C, Cole BJ, Ivans LJ, Pedmale U V, Jung HS et al. (2012) Linking photoreceptor excitation to changes in plant architecture. Genes Dev 26:785–790. doi: 10.1101/gad.187849.112

Li L and Sheen J (2016) Dynamic and diverse sugar signaling. Curr Opin Plant Biol 33:116–125. doi: 10.1016/j.pbi.2016.06.018

Li L, Xu J, Xu ZH and Xue HW (2005) Brassinosteroids stimulate plant tropisms through modulation of polar auxin transport in Brassica and Arabidopsis. Plant Cell 17:2738–2753. doi: 10.1105/tpc.105.034397

Li S, Yamada M, Han X, Ohler U and Benfey PN (2016) High-Resolution Expression Map of the Arabidopsis Root Reveals Alternative Splicing and lincRNA Regulation. Dev Cell 39:508–522. doi: 10.1016/j.devcel.2016.10.012

Li T, Lei W, He R, Tang X, Han J, Zou L, Yin Y, Lin H and Zhang D (2020) Brassinosteroids regulate root meristem development by mediating BIN2-UPB1 module in Arabidopsis. PLOS Genet 16:e1008883. doi: 10.1371/JOURNAL.PGEN.1008883

Li X, Cai W, Liu Y, Li H, Fu L, Liu Z, Xu L, Liu H, Xu T and Xiong Y (2017) Differential TOR activation and cell proliferation in Arabidopsis root and shoot apexes. Proc Natl Acad Sci 114:2765–2770. doi: 10.1073/pnas.1618782114

Li Y, Ende W Van den and Rolland F (2014) Sucrose Induction of Anthocyanin Biosynthesis Is Mediated by DELLA. Mol Plant 7:570–572. doi: 10.1093/MP/SST161

Liang S, Gao X, Wang Y, Zhang H, Yin K, Chen S, Zhang M and Zhao R (2020) Phytochrome-interacting factors regulate seedling growth through ABA signaling. Biochem Biophys Res Commun 526:1100–1105. doi: 10.1016/j.bbrc.2020.04.011

Liao Y, Smyth GK and Shi W (2014) featureCounts: an efficient general purpose program for assigning sequence reads to genomic features. Bioinformatics 30:923–930. doi: 10.1093/bioinformatics/btt656

Lilley JLS, Gee CW, Sairanen I, Ljung K and Nemhauser JL (2012) An endogenous carbon-sensing pathway Triggers increased auxin flux and hypocotyl elongation. Plant Physiol 160:2261–2270. doi: 10.1104/pp.112.205575

Liu G, Gao S, Tian H, Wu W, Robert HS and Ding Z (2016) Local Transcriptional Control of YUCCA Regulates Auxin Promoted Root-Growth Inhibition in Response to Aluminium Stress in Arabidopsis. PLOS Genet 12:e1006360. doi: 10.1371/journal.pgen.1006360

Liu M-J, Wu S-H, Chen H-M and Wu S-H (2012) Widespread translational control contributes to the regulation of Arabidopsis photomorphogenesis. Mol Syst Biol 8:566. doi: 10.1038/msb.2011.97

Liu TY, Chang CY and Chiou TJ (2009) The long-distance signaling of mineral macronutrients. Curr Opin Plant Biol 12:312–319. doi: 10.1016/j.pbi.2009.04.004

Liu X, Liu R, Li Y, Shen X, Zhong S and Shi H (2017) EIN3 and PIF3 form an interdependent module that represses chloroplast development in buried seedlings. Plant Cell 29:3051–3067. doi: 10.1105/tpc.17.00508

Ljung K, Bhalerao RP and Sandberg G (2001) Sites and homeostatic control of auxin biosynthesis in Arabidopsis during vegetative growth. Plant J 28:465–474. doi: 10.1046/j.1365-313X.2001.01173.x

Ljung K, Hull AK, Celenza J, Yamada M, Estelle M, Normanly J and Sandberg G (2005) Sites and regulation of auxin biosynthesis in arabidopsis roots. Plant Cell 17:1090–1104. doi: 10.1105/tpc.104.029272

Ljung K, Nemhauser JL and Perata P (2015) New mechanistic links between sugar and hormone signalling networks. Curr Opin Plant Biol 25:130–137. doi: 10.1016/j.pbi.2015.05.022

Luo X-M, Lin W-H, Zhu S, Zhu J-Y, Sun Y, Fan X-Y, Cheng M, Hao Y, Oh E, Tian M et al. (2010) Integration of Light- and Brassinosteroid-Signaling Pathways by a GATA Transcription Factor in Arabidopsis. Dev Cell 19:872–883. doi: 10.1016/J.DEVCEL.2010.10.023

Lyu G, Li D, Li S and Hu H (2019) STO and GA negatively regulate UV-B-induced Arabidopsis root growth inhibition. Plant Signal Behav. doi: 10.1080/15592324.2019.1675471

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008a) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008b) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Yadav V, Negi P and Chattopadhyay S (2006) A basic leucine zipper transcription factor, G-box-binding factor 1, regulates blue light-mediated photomorphogenic growth in Arabidopsis. J Biol Chem 281:22190–22199. doi: 10.1074/jbc.M601172200

Mancini E, Sanchez SE, Romanowski A, Schlaen RG, Sanchez-Lamas M, Cerdán PD and Yanovsky MJ (2016) Acute Effects of Light on Alternative Splicing in Light-Grown Plants. Photochem Photobiol 92:126–133. doi: 10.1111/php.12550

Marchant A, Bhalerao R, Casimiro I, Eklöf J, Casero PJ, Bennett M and Sandberg G (2002) AUX1 promotes lateral root formation by facilitating indole-3-acetic acid distribution between sink and source tissues in the Arabidopsis seedling. Plant Cell 14:589–597. doi: 10.1105/tpc.010354

Matsubayashi Y (2014) Posttranslationally Modified Small-Peptide Signals in Plants. http://dx.doi.org/101146/annurev-arplant-050312-120122 65:385–413. doi: 10.1146/ANNUREV-ARPLANT-050312-120122

McAdam SAM, Brodribb TJ and Ross JJ (2016a) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McAdam SAM, Brodribb TJ and Ross JJ (2016b) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McNellis TW, von Arnim AG, Araki T, Komeda Y, Misera S and Deng X-W (1994) Genetic and Molecular Analysis of an Allelic Series of cop1 Mutants Suggests Functional Roles for the Multiple Protein Domains. Plant Cell 6:487. doi: 10.2307/3869929

Meng LS, Wei ZQ, Cao XY, Tong C, Lv MJ, Yu F and Loake GJ (2020) Cytosolic invertase-mediated root growth is feedback regulated by a glucose-dependent signaling loop. Plant Physiol 184:895–908. doi: 10.1104/pp.20.00778

Metsalu T and Vilo J (2015) ClustVis: A web tool for visualizing clustering of multivariate data using Principal Component Analysis and heatmap. Nucleic Acids Res 43:W566–W570. doi: 10.1093/nar/gkv468

Miotto YE, da Costa CT, Offringa R, Kleine-Vehn J and Maraschin F dos S (2021)

Effects of Light Intensity on Root Development in a D-Root Growth System. Front Plant Sci 12:1–9. doi: 10.3389/fpls.2021.778382

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019a) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019b) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Mo M, Yokawa K, Wan Y and Baluska F (2015a) How and why do root apices sense light under the soil surface? Front Plant Sci 6:1–8. doi: 10.3389/fpls.2015.00775

Mo M, Yokawa K, Wan Y and Baluška F (2015b) How and why do root apices sense light under the soil surface? Front Plant Sci 6:775. doi: 10.3389/fpls.2015.00775

Möglich A, Yang X, Ayers RA and Moffat K (2010) Structure and function of plant photoreceptors. Annu Rev Plant Biol 61:21–47. doi: 10.1146/annurev-arplant-042809-112259

Molas ML, Kiss JZ and Correll MJ (2006) Gene profiling of the red light signalling pathways in roots. J Exp Bot 57:3217–3229. doi: 10.1093/jxb/erl086

Moni A, Lee A-Y, Briggs WR and Han I-S (2015) The blue light receptor Phototropin 1 suppresses lateral root growth by controlling cell elongation. Plant Biol 17:34–40. doi: 10.1111/PLB.12187

Morais DA DR (2017) Bioconductor - transcriptogramer. In: Morais DA, Dalmolin RJ (2017). Transcr. Transcr. Anal. based Transcr. doi 10.18129/B9.bioc.transcriptogramer, R Packag. https://bioconductor.org/packages/release/bioc/html/transcriptogramer.html. Accessed 12 Dec 2018

Mostafavi S, Ray D, Warde-Farley D, Grouios C and Morris Q (2008) GeneMANIA: A real-time multiple association network integration algorithm for predicting gene function. Genome Biol 9:S4. doi: 10.1186/gb-2008-9-s1-s4

Murashige T and Skoog F (1962) A Revised Medium for Rapid Growth and Bio Assays with Tobacco Tissue Cultures. Physiol Plant 15:473–497. doi: 10.1111/J.1399-3054.1962.TB08052.X

Ni M, Tepperman JM and Quail PH (1998a) PIF3, a phytochrome-interacting factor necessary for normal photoinduced signal transduction, is a novel basic helix-loop-helix protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Ni M, Tepperman JM and Quail PH (1998b) PIF3, a Phytochrome-Interacting Factor Necessary for Normal Photoinduced Signal Transduction, Is a Novel Basic Helix-Loop-Helix Protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Notaguchi M, Wolf S and Lucas WJ (2012) Phloem-Mobile Aux/IAA Transcripts Target to the Root Tip and Modify Root ArchitectureF. J Integr Plant Biol 54:760–772. doi: 10.1111/J.1744-7909.2012.01155.X

Novák J, Černý M, Pavlů J, Zemánková J, Skalák J, Plačková L and Brzobohatý B

(2014) Roles of proteome dynamics and cytokinin signaling in root to hypocotyl ratio changes induced by shading roots of arabidopsis seedlings. Plant Cell Physiol 56:1006–1018. doi: 10.1093/pcp/pcv026

Oh E, Kang H, Yamaguchi S, Park J, Lee D, Kamiya Y and Choi G (2009) Genome-wide analysis of genes targeted by PHYTOCHROME INTERACTING FACTOR 3-LIKE5 during seed germination in arabidopsis. Plant Cell 21:403–419. doi: 10.1105/tpc.108.064691

Oh E, Seo PJ and Kim J (2018) Signaling Peptides and Receptors Coordinating Plant Root Development. Trends Plant Sci 23:337–351. doi: 10.1016/J.TPLANTS.2017.12.007/ATTACHMENT/BD6CC66E-2342-46C7-8AA9-996959725A60/MMC2.PDF

Oh J, Park E, Song K, Bae G and Choi G (2019) PHYTOCHROME INTERACTING FACTOR 8 Inhibits Phytochrome A-mediated Far-red Light Responses in Arabidopsis. Plant Cell Adv Publ. doi: 10.1105/tpc.19.00515

Osterlund MT and Deng XW (1998) Multiple photoreceptors mediate the light-induced reduction of GUS-COP1 from Arabidopsis hypocotyl nuclei. Plant J 16:201–208. doi: 10.1046/j.1365-313X.1998.00290.x

Osterlund MT, Hardtke CS, Ning W and Deng XW (2000) Targeted destabilization of HY5 during light-regulated development of Arabidopsis. Nature 405:462–466. doi: 10.1038/35013076

Oyama T, Shimura Y and Okada K (1997) The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus- induced development of root and hypocotyl. Genes Dev 11:2983–2995. doi: 10.1101/gad.11.22.2983

Pacín M, Legris M and Casal JJ (2014) Rapid decline in nuclear COSTITUTIVE PHOTOMORPHOGENESIS1 abundance anticipates the stabilization of its target ELONGATED HYPOCOTYL5 in the light. Plant Physiol 164:1134–1138. doi: 10.1104/pp.113.234245

Paik I, Chen F, Ngoc Pham V, Zhu L, Kim J Il and Huq E (2019) A phyB-PIF1-SPA1 kinase regulatory complex promotes photomorphogenesis in Arabidopsis. Nat Commun 10:1–17. doi: 10.1038/s41467-019-12110-y

Pan Y and Shi H (2017) Stabilizing the Transcription Factors by E3 Ligase COP1. Trends Plant Sci 22:999–1001. doi: 10.1016/j.tplants.2017.09.012

Park BS, Eo HJ, Jang I-C, Kang H-G, Song JT and Seo HS (2010) Ubiquitination of LHY by SINAT5 regulates flowering time and is inhibited by DET1. Biochem Biophys Res Commun 398:242–246. doi: 10.1016/j.bbrc.2010.06.067

Peng P, Yan Z, Zhu Y and Li J (2008) Regulation of the Arabidopsis GSK3-like Kinase BRASSINOSTEROID-INSENSITIVE 2 through Proteasome-Mediated Protein Degradation. Mol Plant 1:338–346. doi: 10.1093/MP/SSN001

Petersson S V., Johansson AI, Kowalczyk M, Makoveychuk A, Wang JY, Moritz T, Grebe M, Benfey PN, Sandberg G and Ljung K (2009) An Auxin Gradient and Maximum in the Arabidopsis Root Apex Shown by High-Resolution Cell-Specific Analysis of IAA Distribution and Synthesis. Plant Cell 21:1659–1668. doi: 10.1105/tpc.109.066480

Pham VN, Kathare PK and Huq E (2018a) Phytochromes and phytochrome interacting

factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Kathare PK and Huq E (2018b) Phytochromes and phytochrome interacting factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Paik I, Hoecker U and Huq E (2020) Genomic evidence reveals SPA-regulated developmental and metabolic pathways in dark-grown Arabidopsis seedlings. Physiol Plant 169:380–396. doi: 10.1111/PPL.13095

Pham VN, Xu X and Huq E (2018c) Molecular bases for the constitutive photomorphogenic phenotypes in Arabidopsis. Development. doi: 10.1242/dev.169870

Podolec R and Ulm R (2018a) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Podolec R and Ulm R (2018b) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Ponnu J and Hoecker U (2021a) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/FPLS.2021.662793/BIBTEX

Ponnu J and Hoecker U (2021b) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/fpls.2021.662793

Ponnu J, Riedel T, Penner E, Schrader A and Hoecker U (2019) Cryptochrome 2 competes with COP1 substrates to repress COP1 ubiquitin ligase activity during Arabidopsis photomorphogenesis. Proc Natl Acad Sci U S A 116:27133–27141. doi: 10.1073/PNAS.1909181116/-/DCSUPPLEMENTAL

Prát T, Hajný J, Grunewald W, Vasileva M, Molnár G, Tejos R, Schmid M, Sauer M and Friml J (2018) WRKY23 is a component of the transcriptional network mediating auxin feedback on PIN polarity. PLOS Genet 14:e1007177. doi: 10.1371/journal.pgen.1007177

Qi L, Liu S, Li C, Fu J, Jing Y, Cheng J, Li H, Zhang D, Wang X, Dong X et al. (2020) PHYTOCHROME-INTERACTING FACTORS Interact with the ABA Receptors PYL8 and PYL9 to Orchestrate ABA Signaling in Darkness. Mol Plant 13:414–430. doi: 10.1016/j.molp.2020.02.001

Qu Y, Liu S, Bao W, Xue X, Ma Z, Yokawa K, Baluška F and Wan Y (2017) Expression of root genes in Arabidopsis seedlings grown by standard and improved growing methods. Int J Mol Sci 18:951. doi: 10.3390/ijms18050951

Quail PH (2007) Phytochrome-regulated Gene Expression. J Integr Plant Biol. doi: 10.1111/j.1672-9072.2007.00422.x

Ram H, Priya P, Jain M and Chattopadhyay S (2014) Genome-wide DNA binding of GBF1 is modulated by its heterodimerizing protein partners, HY5 and HYH. Mol Plant 7:448–451. doi: 10.1093/mp/sst143

Ranjan A, Fiene G, Fackendahl P and Hoecker U (2011) The Arabidopsis repressor of light signaling SPA1 acts in the phloem to regulate seedling de-etiolation, leaf expansion and flowering time. Development 138:1851–1862. doi: 10.1242/dev.061036

Regnault T, Davière J-M, Wild M, Sakvarelidze-Achard L, Heintz D, Carrera Bergua E, Lopez Diaz I, Gong F, Hedden P and Achard P (2015) The gibberellin precursor GA_{12}acts as a long-distance growth signal in <italic>Arabidopsis</italic>. doi: 10.1038/NPLANTS.2015.73

Ritchie ME, Phipson B, Wu D, Hu Y, Law CW, Shi W and Smyth GK (2015) limma powers differential expression analyses for RNA-sequencing and microarray studies. Nucleic Acids Res. doi: 10.1093/nar/gkv007

Rolland F, Moore B and Sheen J (2002) Sugar sensing and signaling in plants. Plant Cell 14 Suppl:S185-205. doi: 10.1105/TPC.010455

Rosado D, Ackermann A, Spassibojko O, Rossi M and Pedmale U V (2021) WRKY transcription factors and ethylene signaling modify root growth during the shade-avoidance response. Plant Physiol. doi: 10.1093/PLPHYS/KIAB493

Rybarczyk-Filho JL, Castro MAA, Dalmolin RJS, Moreira JCF, Brunnet LG and de Almeida RMC (2011) Towards a genome-wide transcriptogram: the Saccharomyces cerevisiae case. Nucleic Acids Res 39:3005–16. doi: 10.1093/nar/gkq1269

Saijo Y, Sullivan J a, Wang H, Yang J, Shen Y, Rubio V, Ma L, Hoecker U and Deng XW (2003) The COP1-SPA1 interaction defines a critical step in phytochrome A-mediated regulation of HY5 activity. Genes Dev 17:2642–7. doi: 10.1101/gad.1122903

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013a) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013b) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sakaguchi J, Matsushita T and Watanabe Y (2019) DWARF4 accumulation in root tips is enhanced via blue light perception by cryptochromes. Plant Cell Environ 42:1615–1629. doi: 10.1111/pce.13510

Sakaguchi J and Watanabe Y (2017a) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakaguchi J and Watanabe Y (2017b) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakamoto K and Briggs WR (2002) Cellular and Subcellular Localization of Phototropin 1. Plant Cell 14:1723–1735. doi: 10.1105/TPC.003293

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K and Yamaguchi-Shinozaki K (2006) Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. Plant Cell 18:1292–1309. doi: 10.1105/tpc.105.035881

Sakuraba Y, Kanno S, Mabuchi A, Monda K, Iba K and Yanagisawa S (2018) A phytochrome-B-mediated regulatory mechanism of phosphorus acquisition. Nat Plants 4:1089–1101. doi: 10.1038/s41477-018-0294-7

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007a) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007b) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Sanchez SE, Rugnone ML and Kay SA (2020) Light Perception: A Matter of Time. Mol Plant 13(3):363–385. doi: 10.1016/j.molp.2020.02.006

Sassi M, Lu Y, Zhang Y, Wang J, Dhonukshe P, Blilou I, Dai M, Li J, Gong X, Jaillais Y et al. (2012) COP1 mediates the coordination of root and shoot growth by light through modulation of PIN1- and PIN2-dependent auxin transport in Arabidopsis. Development 139:3402–3412. doi: 10.1242/dev.078212

Schepetilnikov M, Makarian J, Srour O, Geldreich A, Yang Z, Chicher J, Hammann P and Ryabova LA (2017) GTPase ROP2 binds and promotes activation of target of rapamycin TOR in response to auxin. EMBO J 36:886–903. doi: 10.15252/embj.201694816

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992a) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992b) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Senapati D, Kushwaha R, Dutta S, Maurya JP, Biswas S, Gangappa SN and Chattopadhyay S (2019) COP1 regulates the stability of CAM7 to promote photomorphogenic growth. Plant Direct 3:1–14. doi: 10.1002/pld3.144

Seo HS, Yang J, Ishikawa M and Bolle C (2003) LAF1 ubiquitination by COP1 controls photomorphogenesis and is stimulated by SPA1. Nature 8:995–999. doi: 10.1038/nature01751.1.

Shaikhali J, Norén L, De Dios Barajas-López J, Srivastava V, König J, Sauer UH, Wingsle G, Dietz KJ and Strand Å (2012) Redox-mediated mechanisms regulate DNA binding activity of the G-group of basic region leucine zipper (bZIP) transcription factors in Arabidopsis. J Biol Chem 287:27510–27525. doi: 10.1074/jbc.M112.361394

Shani E, Weinstain R, Zhang Y, Castillejo C, Kaiserli E, Chory J, Tsien RY and Estelle M (2013) Gibberellins accumulate in the elongating endodermal cells of Arabidopsis root. Proc Natl Acad Sci U S A 110:4834–4839. doi: 10.1073/pnas.1300436110

Shannon P, Markiel A, Ozier O, Baliga NS, Wang JT, Ramage D, Amin N, Schwikowski B and Ideker T (2003) Cytoscape: A software Environment for integrated models of biomolecular interaction networks. Genome Res 13:2498–2504. doi: 10.1101/gr.1239303

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015a) Light-activated

phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant Cell 27:189–201. doi: 10.1105/tpc.114.134775

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015b) Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant Cell 27:189–201. doi: 10.1105/tpc.114.134775

Shi H, Liu R, Xue C, Shen X, Wei N, Deng XW and Zhong S (2016) Seedlings Transduce the Depth and Mechanical Pressure of Covering Soil Using COP1 and Ethylene to Regulate EBF1/EBF2 for Soil Emergence. Curr Biol 26:139–149. doi: 10.1016/J.CUB.2015.11.053

Shi QM, Yang X, Song L and Xue HW (2011) Arabidopsis MSBP1 is activated by HY5 and HYH and is involved in photomorphogenesis and brassinosteroid sensitivity regulation. Mol Plant 4:1092–1104. doi: 10.1093/mp/ssr049

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009a) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009b) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Silva-Navas J, Moreno-Risueno MA, Manzano C, Pallero-Baena M, Navarro-Neila S, Téllez-Robledo B, Garcia-Mina JM, Baigorri R, Gallego FJ and Del Pozo JC (2015) D-Root: A system for cultivating plants with the roots in darkness or under different light conditions. Plant J 84:244–255. doi: 10.1111/tpj.12998

Silva-Navas J, Moreno-Risueno MA, Manzano C, Téllez-Robledo B, Navarro-Neila S, Carrasco V, Pollmann S, Gallego FJ and Del Pozo JC (2016) Flavonols mediate root phototropism and growth through regulation of proliferation-to-differentiation transition. Plant Cell 28:1372–1387. doi: 10.1105/tpc.15.00857

Singh A, Ram H, Abbas N and Chattopadhyay S (2012a) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Singh A, Ram H, Abbas N and Chattopadhyay S (2012b) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Skubacz A, Daszkowska-Golec A and Szarejko I (2016) The role and regulation of ABI5 (ABA-insensitive 5) in plant development, abiotic stress responses and phytohormone crosstalk. Front Plant Sci 7:1–18. doi: 10.3389/fpls.2016.01884

Spaninks K, van Lieshout J, van Ieperen W and Offringa R (2020) Regulation of Early Plant Development by Red and Blue Light: A Comparative Analysis Between Arabidopsis thaliana and Solanum lycopersicum. Front Plant Sci. doi: 10.3389/fpls.2020.599982

Spiegelman Z, Ham BK, Zhang Z, Toal TW, Brady SM, Zheng Y, Fei Z, Lucas WJ and Wolf S (2015) A tomato phloem-mobile protein regulates the shoot-to-root ratio by mediating the auxin response in distant organs. Plant J 83:853–863. doi: 10.1111/TPJ.12932

Srivastava AK, Senapati D, Srivastava A, Chakraborty M, Gangappa SN and Chattopadhyay S (2015) Short Hypocotyl in White Light1 Interacts with Elongated Hypocotyl5 (HY5) and Constitutive Photomorphogenic1 (COP1) and Promotes COP1-Mediated Degradation of HY5 during Arabidopsis Seedling Development. Plant Physiol 169:2922–2934. doi: 10.1104/PP.15.01184

Stewart JL, Maloof JN and Nemhauser JL (2011) PIF Genes Mediate the Effect of Sucrose on Seedling Growth Dynamics. PLoS One 6:e19894. doi: 10.1371/JOURNAL.PONE.0019894

Stracke R, Favory JJ, Gruber H, Bartelniewoehner L, Bartels S, Binkert M, Funk M, Weisshaar B and Ulm R (2010) The Arabidopsis bZIP transcription factor HY5 regulates expression of the PFG1/MYB12 gene in response to light and ultraviolet-B radiation. Plant, Cell Environ 33:88–103. doi: 10.1111/j.1365-3040.2009.02061.x

Sun N, Wang J, Gao Z, Dong J, He H, Terzaghi W, Wei N, Deng XW and Chen H (2016) Arabidopsis SAURs are critical for differential light regulation of the development of various organs. Proc Natl Acad Sci U S A 113:6071–6. doi: 10.1073/pnas.1604782113

Supek F, Bošnjak M, Škunca N and Šmuc T (2011) REVIGO Summarizes and Visualizes Long Lists of Gene Ontology Terms. PLoS One 6:e21800. doi: 10.1371/journal.pone.0021800

Swarup K, Benková E, Swarup R, Casimiro I, Péret B, Yang Y, Parry G, Nielsen E, De Smet I, Vanneste S et al. (2008) The auxin influx carrier LAX3 promotes lateral root emergence. Nat Cell Biol 10:946–954. doi: 10.1038/ncb1754

Szklarczyk D, Morris JH, Cook H, Kuhn M, Wyder S, Simonovic M, Santos A, Doncheva NT, Roth A, Bork P et al. (2017) The STRING database in 2017: quality-controlled protein-protein association networks, made broadly accessible. Nucleic Acids Res 45:D362–D368. doi: 10.1093/nar/gkw937

Tabata R, Sumida K, Yoshii T, Ohyama K, Shinohara H and Matsubayashi Y (2014) Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. Science 346:343–346. doi: 10.1126/SCIENCE.1257800

Tan H, Man C, Xie Y, Yan J, Chu J and Huang J (2019) A Crucial Role of GA-Regulated Flavonol Biosynthesis in Root Growth of Arabidopsis. Mol Plant 12:521–537. doi: 10.1016/j.molp.2018.12.021

Tang W, Ji Q, Huang Y, Jiang Z, Bao M, Wang H and Lin R (2013) FAR-RED ELONGATED HYPOCOTYL3 and FAR-RED IMPAIRED RESPONSE1 Transcription Factors Integrate Light and Abscisic Acid Signaling in Arabidopsis 1[C][W][OPEN]. doi: 10.1104/pp.113.224386

Tepperman JM, Hudson ME, Khanna R, Zhu T, Chang SH, Wang X and Quail PH (2004) Expression profiling of phyB mutant demonstrates substantial contribution of other phytochromes to red-light-regulated gene expression during seedling de-etiolation. Plant J 38:725–739. doi: 10.1111/j.1365-313X.2004.02084.x

Tepperman JM, Zhu T, Chang H-S, Wang X and Quail PH (2001) Multiple transcription-factor genes are early targets of phytochrome A signaling. Proc Natl Acad Sci 98:9437–9442. doi: 10.1073/pnas.161300998

Thieme CJ, Rojas-Triana M, Stecyk E, Schudoma C, Zhang W, Yang L, Minãmbres M, Walther D, Schulze WX, Paz-Ares J et al. (2015) Endogenous Arabidopsis messenger RNAs transported to distant tissues. Nat Plants 2015 14 1:1–9. doi: 10.1038/nplants.2015.25

Tian T, Liu Y, Yan H, You Q, Yi X, Du Z, Xu W and Su Z (2017) agriGO v2.0: a GO analysis toolkit for the agricultural community, 2017 update. Nucleic Acids Res 45:W122–W129. doi: 10.1093/nar/gkx382

Tilbrook K, Arongaus AB, Binkert M, Heijde M, Yin R and Ulm R (2013) The UVR8 UV-B Photoreceptor: Perception, Signaling and Response. Arab B 11:e0164. doi: 10.1199/tab.0164

Tong H, Leasure CD, Hou X, Yuen G, Briggs W and He ZH (2008) Role of root UV-B sensing in Arabidopsis early seedling development. Proc Natl Acad Sci U S A 105:21039–21044. doi: 10.1073/pnas.0809942106

Ubeda-Tomás S, Federici F, Casimiro I, Beemster GTS, Bhalerao R, Swarup R, Doerner P, Haseloff J and Bennett MJ (2009) Gibberellin Signaling in the Endodermis Controls Arabidopsis Root Meristem Size. Curr Biol 19:1194–1199. doi: 10.1016/j.cub.2009.06.023

Ubeda-Tomás S, Swarup R, Coates J, Swarup K, Laplaze L, Beemster GTS, Hedden P, Bhalerao R and Bennett MJ (2008) Root growth in Arabidopsis requires gibberellin/DELLA signalling in the endodermis. Nat Cell Biol 10:625–628. doi: 10.1038/ncb1726

Unterholzner SJ, Rozhon W, Papacek M, Ciomas J, Lange T, Kugler KG, Mayer KF, Sieberer T and Poppenberger B (2015) Brassinosteroids are master regulators of gibberellin biosynthesis in Arabidopsis. Plant Cell 27:2261–2272. doi: 10.1105/tpc.15.00433

van Gelderen K, Kang C, Paalman R, Keuskamp D, Hayes S and Pierik R (2018a) Far-red light detection in the shoot regulates lateral root development through the HY5 transcription factor. Plant Cell 30:101–116. doi: 10.1105/tpc.17.00771

van Gelderen K, Kang C and Pierik R (2018b) Light Signaling, Root Development, and Plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Van Gelderen K, Kang C and Pierik R (2018) Light signaling, root development, and plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Vaseva II, Qudeimat E, Potuschak T, Du Y, Genschik P, Vandenbussche F and Van Der Straeten D (2018) The plant hormone ethylene restricts Arabidopsis growth via the epidermis. Proc Natl Acad Sci 115:E4130–E4139. doi: 10.1073/pnas.1717649115

von Arnim AG and Deng X-W (1994) Light inactivation of arabidopsis photomorphogenic repressor COP1 involves a cell-specific regulation of its nucleocytoplasmic partitioning. Cell 79:1035–1045. doi: 10.1016/0092-8674(94)90034-5

Vukašinović N, Wang Y, Vanhoutte I, Fendrych M, Guo B, Kvasnica M, Jiroutová P, Oklestkova J, Strnad M and Russinova E (2021) Local brassinosteroid biosynthesis

enables optimal root growth. Nat Plants 7:619–632. doi: 10.1038/s41477-021-00917-x

Wan Y, Jasik J, Wang L, Hao H, Volkmann D, Menzel D, Mancuso S, Baluška F and Lin J (2012) The signal transducer NPH3 integrates the phototropin1 photosensor with PIN2-based polar auxin transport in Arabidopsis root phototropism. Plant Cell 24:551–565. doi: 10.1105/tpc.111.094284

Wan Y, Yokawa K and Baluška F (2019) Arabidopsis Roots and Light: Complex Interactions. Mol Plant 12:1428–1430. doi: 10.1016/j.molp.2019.10.001

Wan YL, Eisinger W, Ehrhardt D, Kubitscheck U, Baluska F and Briggs W (2008) The subcellular localization and blue-light-induced movement of phototropin 1-GFP in etiolated seedlings of Arabidopsis thaliana. Mol Plant 1:103–117. doi: 10.1093/mp/ssm011

Wang W, Chen Q, Botella JR and Guo S (2019) Beyond light: Insights into the role of constitutively photomorphogenic1 in plant hormonal signaling. Front Plant Sci 10:557. doi: 10.3389/FPLS.2019.00557/BIBTEX

Wang W, Paik I, Kim J, Hou X, Sung S and Huq E (2021) Direct phosphorylation of HY5 by SPA kinases to regulate photomorphogenesis in Arabidopsis. New Phytol 230:2311–2326. doi: 10.1111/nph.17332

Wei N, Kwok SF, von Arnim AG, Lee A, McNellis TW, Piekos B, Deng XW, Deng XW and Chen H (1994) Arabidopsis COP8, COP10, and COP11 Genes Are Involved in Repression of Photomorphogenic Development in Darkness. PLANT CELL ONLINE 6:629–643. doi: 10.1105/tpc.6.5.629

Wieczorek K, Golecki B, Gerdes L, Heinen P, Szakasits D, Durachko DM, Cosgrove DJ, Kreil DP, Puzio PS, Bohlmann H et al. (2006) Expansins are involved in the formation of nematode-induced syncytia in roots of Arabidopsis thaliana. Plant J 48:98–112. doi: 10.1111/J.1365-313X.2006.02856.X

Willige BC, Zander M, Yoo CY, Phan A, Garza RM, Trigg SA, He Y, Nery JR, Chen H, Chen M et al. (2021) PHYTOCHROME-INTERACTING FACTORs trigger environmentally responsive chromatin dynamics in plants. Nat Genet 53:955–961. doi: 10.1038/s41588-021-00882-3

Wilson K, Long D, Swinburne J and Coupland G (1996) A Dissociation insertion causes a semidominant mutation that increases expression of TINY, an arabidopsis gene related to APETALA2. Plant Cell 8:659–671. doi: 10.1105/tpc.8.4.659

Woerlen N, Allam G, Popescu A, Corrigan L, Pautot V and Hepworth SR (2017) Repression of BLADE-ON-PETIOLE genes by KNOX homeodomain protein BREVIPEDICELLUS is essential for differentiation of secondary xylem in Arabidopsis root. Planta 2017 2456 245:1079–1090. doi: 10.1007/S00425-017-2663-2

Wu Y, Shi L, Li L, Fu L, Liu Y, Xiong Y and Sheen J (2019) Integration of nutrient, energy, light, and hormone signalling via TOR in plants. J Exp Bot 70:2227–2238. doi: 10.1093/jxb/erz028

Xie Z, Nolan T, Jiang H, Tang B, Zhang M, Li Z and Yin Y (2019) The AP2/ERF transcription factor TINY modulates brassinosteroid-regulated plant growth and drought responses in arabidopsis. Plant Cell 31:1788–1806. doi:

10.1105/tpc.18.00918

Xiong Y, McCormack M, Li L, Hall Q, Xiang C and Sheen J (2013) Glucose–TOR signalling reprograms the transcriptome and activates meristems. Nature 496:181–186. doi: 10.1038/nature12030

Xiong Y and Sheen J (2012) Rapamycin and glucose-target of rapamycin (TOR) protein signaling in plants. J Biol Chem 287:2836–2842. doi: 10.1074/jbc.M111.300749

Xu D, Jiang Y, Li J, Holm M and Deng XW (2018) The B-Box Domain Protein BBX21 Promotes Photomorphogenesis. Plant Physiol 176:2365–2375. doi: 10.1104/PP.17.01305

Xu D, Jiang Y, Li J, Lin F, Holm M and Deng XW (2016) BBX21, an Arabidopsis B-box protein, directly activates HY5 and is targeted by COP1 for 26S proteasome-mediated degradation. Proc Natl Acad Sci 113:7655–7660. doi: 10.1073/PNAS.1607687113

Xu D, Li J, Gangappa SN, Hettiarachchi C, Lin F, Andersson MX, Jiang Y, Deng XW and Holm M (2014a) Convergence of Light and ABA Signaling on the ABI5 Promoter. PLoS Genet 10:e1004197. doi: 10.1371/journal.pgen.1004197

Xu P, Chen H, Li T, Xu F, Mao Z, Cao X, Miao L, Du S, Hua J, Zhao J et al. Blue light-dependent interactions of CRY1 with GID1 and DELLA proteins regulate gibberellin signaling and photomorphogenesis in Arabidopsis. doi: 10.1093/plcell/koab124

Xu W, Ding G, Yokawa K, Baluška F, Li QF, Liu Y, Shi W, Liang J and Zhang J (2013) An improved agar-plate method for studying root growth and response of Arabidopsis thaliana. Sci Rep 3:1–7. doi: 10.1038/srep01273

Xu X, Kathare PK, Pham VN, Bu Q, Nguyen A and Huq E (2017) Reciprocal proteasome-mediated degradation of PIFs and HFR1 underlies photomorphogenic development in Arabidopsis. Dev 144:1831–1840. doi: 10.1242/dev.146936

Xu X, Paik I, Zhu L, Bu Q, Huang X, Deng XW and Huq E (2014b) PHYTOCHROME INTERACTING FACTOR1 enhances the E3 ligase activity of CONSTITUTIVE PHOTOMORPHOGENIC1 to synergistically repress photomorphogenesis in Arabidopsis. Plant Cell 26:1992–2006. doi: 10.1105/tpc.114.125591

Xu X, Paik I, Zhu L and Huq E (2015a) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. Trends Plant Sci 20:641–650. doi: 10.1016/j.tplants.2015.06.010

Xu X, Paik I, Zhu L and Huq E (2015b) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. doi: 10.1016/j.tplants.2015.06.010

Yadukrishnan P and Datta S (2021) Light and abscisic acid interplay in early seedling development. New Phytol 229:763–769. doi: 10.1111/NPH.16963

Yadukrishnan P, Rahul PV and Datta S (2020a) HY5 Suppresses, Rather Than Promotes, Abscisic Acid-Mediated Inhibition of Postgermination Seedling Development. Plant Physiol 184:574–578. doi: 10.1104/pp.20.00783

Yadukrishnan P, Rahul PV, Ravindran N, Bursch K, Johansson H and Datta S (2020b)

CONSTITUTIVELY PHOTOMORPHOGENIC1 promotes ABA-mediated inhibition of post-germination seedling establishment. Plant J 103:481–496. doi: 10.1111/tpj.14844

Yang M, Li C, Cai Z, Hu Y, Nolan T, Yu F, Yin Y, Xie Q, Tang G and Wang X (2017a) SINAT E3 Ligases Control the Light-Mediated Stability of the Brassinosteroid-Activated Transcription Factor BES1 in Arabidopsis. Dev Cell 41:47. doi: 10.1016/J.DEVCEL.2017.03.014

Yang X, Song L and Xue H-W (2008) Membrane Steroid Binding Protein 1 (MSBP1) Stimulates Tropism by Regulating Vesicle Trafficking and Auxin Redistribution. Mol Plant 1:1077–1087. doi: 10.1093/MP/SSN071

Yang Y and Liu H (2020) Coordinated Shoot and Root Responses to Light Signaling in Arabidopsis. Plant Commun 1:100026. doi: 10.1016/j.xplc.2020.100026

Yang Y, Zhang L, Chen P, Liang T, Li X and Liu H (2020) UV-B photoreceptor UVR8 interacts with MYB73/MYB77 to regulate auxin responses and lateral root development. EMBO J. doi: 10.15252/embj.2019101928

Yang Z, Liu B, Su J, Liao J, Lin C and Oka Y (2017b) Cryptochromes Orchestrate Transcription Regulation of Diverse Blue Light Responses in Plants. Photochem Photobiol 93:112–127. doi: 10.1111/php.12663

Yeh C-M, Kobayashi K, Fujii S, Fukaki H, Mitsuda N and Ohme-Takagi M (2020) Blue Light Regulates Phosphate Deficiency-Dependent Primary Root Growth Inhibition in Arabidopsis. Front Plant Sci 0:1803. doi: 10.3389/FPLS.2019.01803

Yokawa K, Fasano R, Kagenishi T and BaluÅ¡ka F (2014) Light as stress factor to plant roots â€“ case of root halotropism. Front Plant Sci 5:1–9. doi: 10.3389/fpls.2014.00718

Yokawa K, Kagenishi T and Baluška F (2013) Root photomorphogenesis in laboratory-maintained Arabidopsis seedlings. Trends Plant Sci 18:117–119. doi: 10.1016/j.tplants.2013.01.002

Yokawa K, Kagenishi T, Kawano T, Mancuso S and Baluška F (2011) Illumination of arabidopsis roots induces immediate burst of ROS production. Plant Signal Behav 6:1460–1464. doi: 10.4161/psb.6.10.18165

Yu X, Liu H, Klejnot J and Lin C (2010) The Cryptochrome Blue Light Receptors. Arab B 8:e0135. doi: 10.1199/tab.0135

Yuan X, Xu P, Yu Y and Xiong Y (2020) Glucose-TOR signaling regulates PIN2 stability to orchestrate auxin gradient and cell expansion in Arabidopsis root. Proc Natl Acad Sci U S A 117:32223–32225. doi: 10.1073/pnas.2015400117

Zdanio M, Boron AK, Balcerowicz D, Schoenaers S, Markakis MN, Mouille G, Pintelon I, Suslov D, Gonneau M, Höfte H et al. (2020) The Proline-Rich Family Protein EXTENSIN33 Is Required for Etiolated Arabidopsis thaliana Hypocotyl Growth. Plant Cell Physiol 61:1191–1203. doi: 10.1093/PCP/PCAA049

Zeng J, Wang Q, Lin J, Deng K, Zhao X, Tang D and Liu X Arabidopsis cryptochrome-1 restrains lateral roots growth by inhibiting auxin transport. JI Plant Physiol 167:670–673. doi: 10.1016/j.jplph.2009.12.003

Zhang B, Holmlund M, Lorrain S, Norberg M, Bakó LS, Fankhauser C and Nilsson O

(2017a) BLADE-ON-PETIOLE proteins act in an E3 ubiquitin ligase complex to regulate PHYTOCHROME INTERACTING FACTOR 4 abundance. Elife. doi: 10.7554/eLife.26759

Zhang H, He H, Wang X, Wang X, Yang X, Li L and Deng XW (2011a) Genome-wide mapping of the HY5-mediated genenetworks in Arabidopsis that involve both transcriptional and post-transcriptional regulation. Plant J 65:346–358. doi: 10.1111/J.1365-313X.2010.04426.X

Zhang Y, Li C, Zhang J, Wang J, Yang J, Lv Y, Yang N, Liu J, Wang X, Palfalvi G et al. (2017b) Dissection of HY5/HYH expression in Arabidopsis reveals a root-autonomous HY5-mediated photomorphogenic pathway. PLoS One 12:e0180449. doi: 10.1371/journal.pone.0180449

Zhang Y, Wang C, Xu H, Shi X, Zhen W, Hu Z, Huang J, Zheng Y, Huang P, Zhang KX et al. (2019) HY5 Contributes to Light-Regulated Root System Architecture Under a Root-Covered Culture System. Front Plant Sci 10:1490. doi: 10.3389/FPLS.2019.01490/BIBTEX

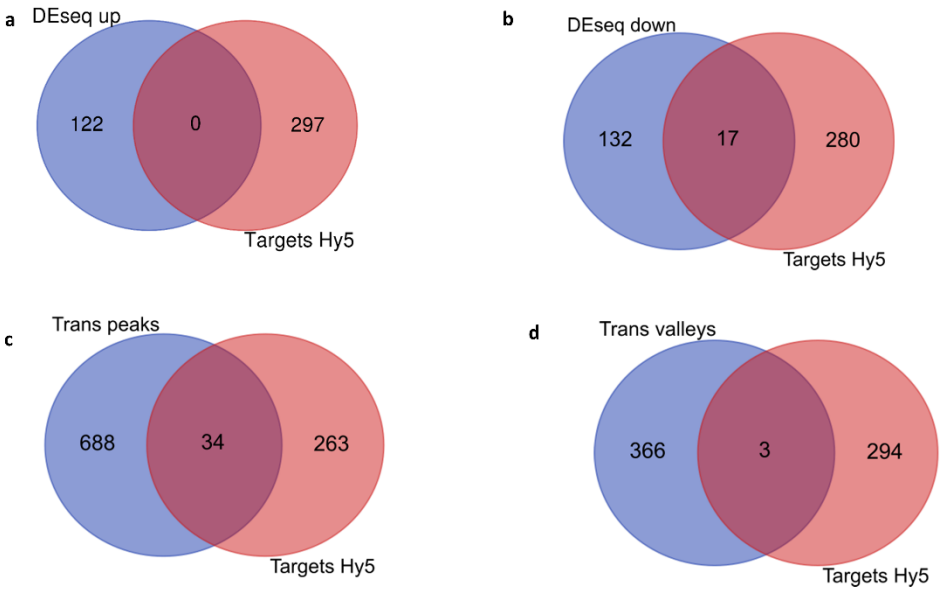
Zhang Z, Zhu J-Y, Roh J, Marchive C, Kim S-K, Meyer C, Sun Y, Wang W and Wang Z-Y (2016) TOR Signaling Promotes Accumulation of BZR1 to Balance Growth with Carbon Availability in Arabidopsis. Curr Biol 26:1854–1860. doi: 10.1016/j.cub.2016.05.005

Zhang ZL, Ogawa M, Fleet CM, Zentella R, Hu J, Heo JO, Lim J, Kamiya Y, Yamaguchi S and Sun TP (2011b) SCARECROW-LIKE 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in Arabidopsis. Proc Natl Acad Sci U S A 108:2160–2165. doi: 10.1073/pnas.1012232108

Zhong M, Zeng B, Tang D, Yang J, Qu L, Yan J, Wang X, Li X, Liu X and Zhao X (2021) The blue light receptor CRY1 interacts with GID1 and DELLA proteins to repress GA signaling during photomorphogenesis in Arabidopsis. Mol Plant 14:1328–1342. doi: 10.1016/J.MOLP.2021.05.011

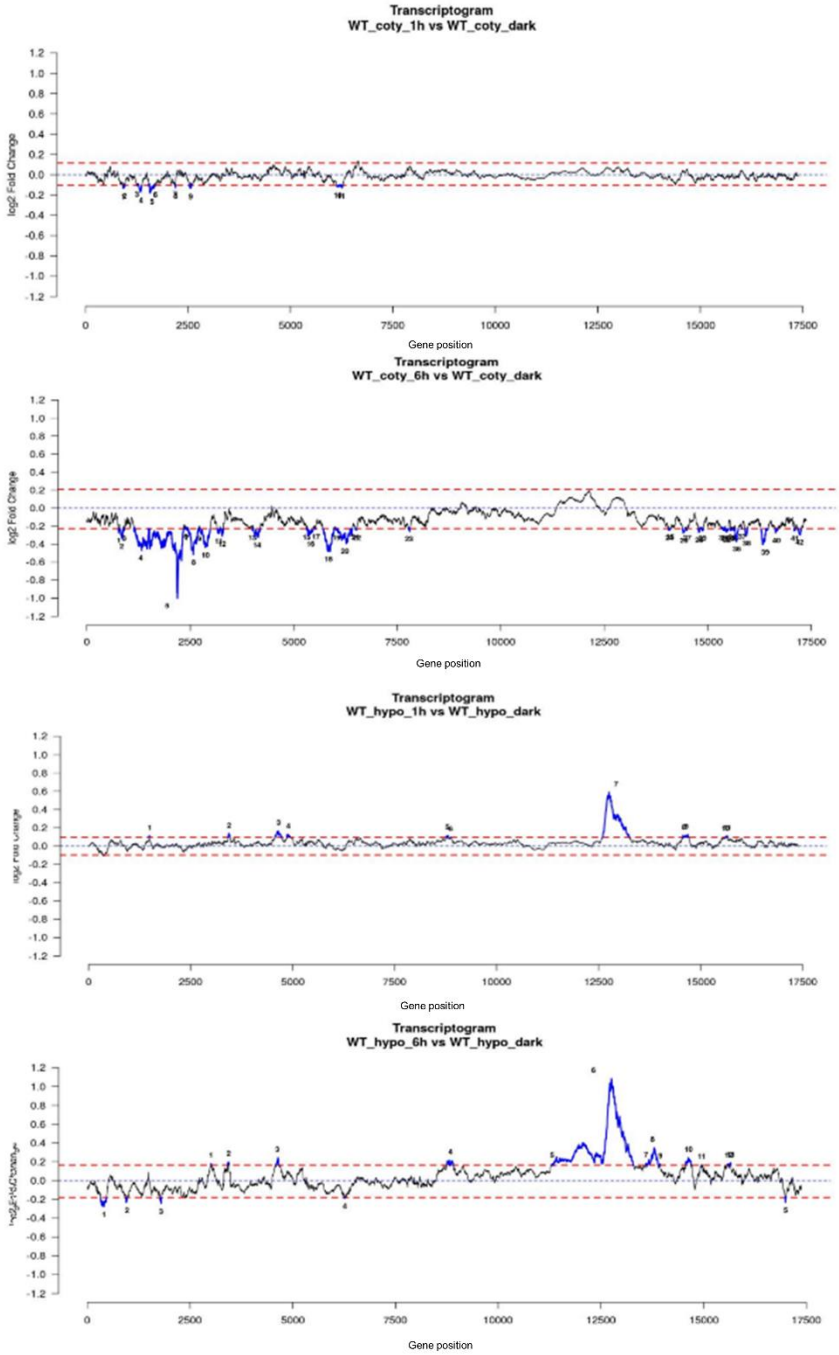
Zhu L, Bu Q, Xu X, Paik I, Huang X, Hoecker U, Deng XW and Huq E (2015) CUL4 forms an E3 ligase with COP1 and SPA to promote light-induced degradation of PIF1. Nat Commun 6:1–10. doi: 10.1038/ncomms8245

Supplementary material

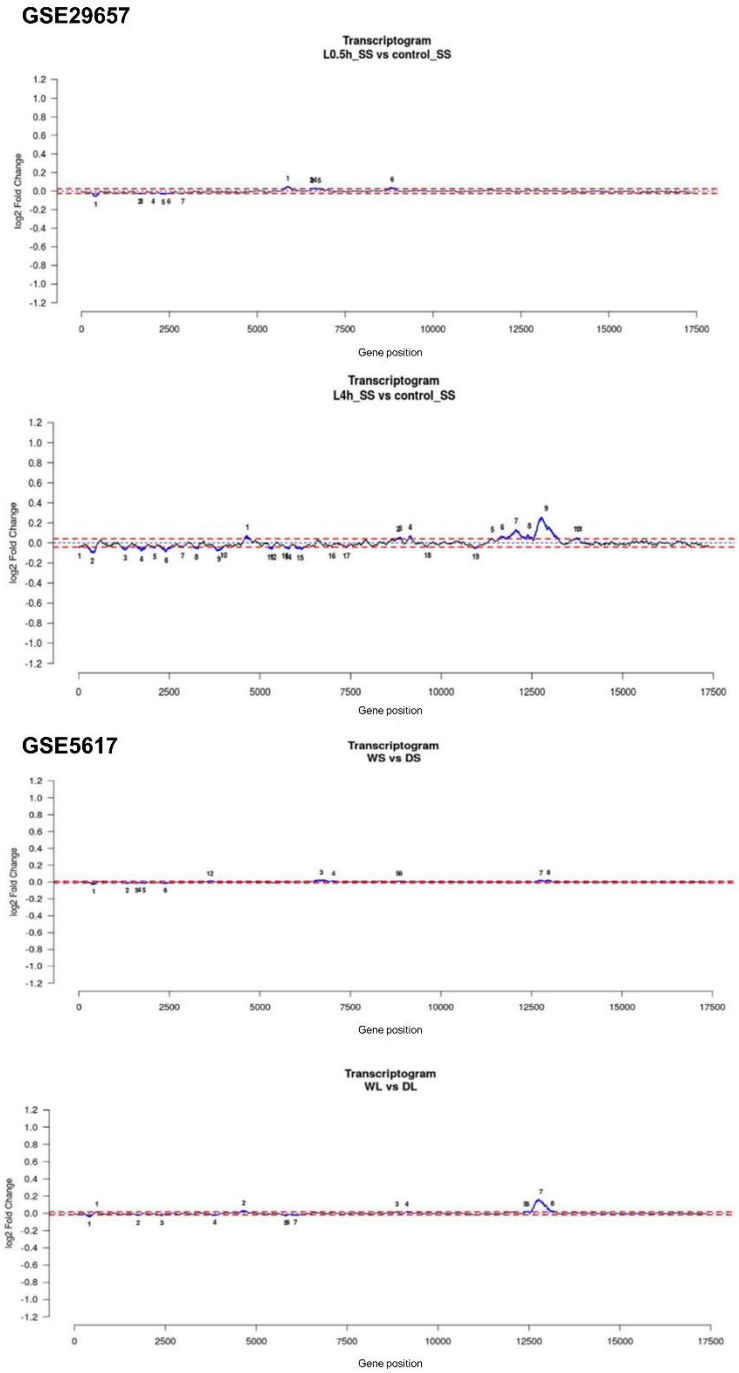


Supplementary Figure 1 Venn diagram of genes from Differential Expression (DESeq) **a** up, **b** down and Transcriptomic Analysis (Trans) **c** peaks, **d** valleys, from three datasets (GSE5617, GSE79576 and GSE29657) of light modulated genes and HY5 target genes (Burko et al., 2020)

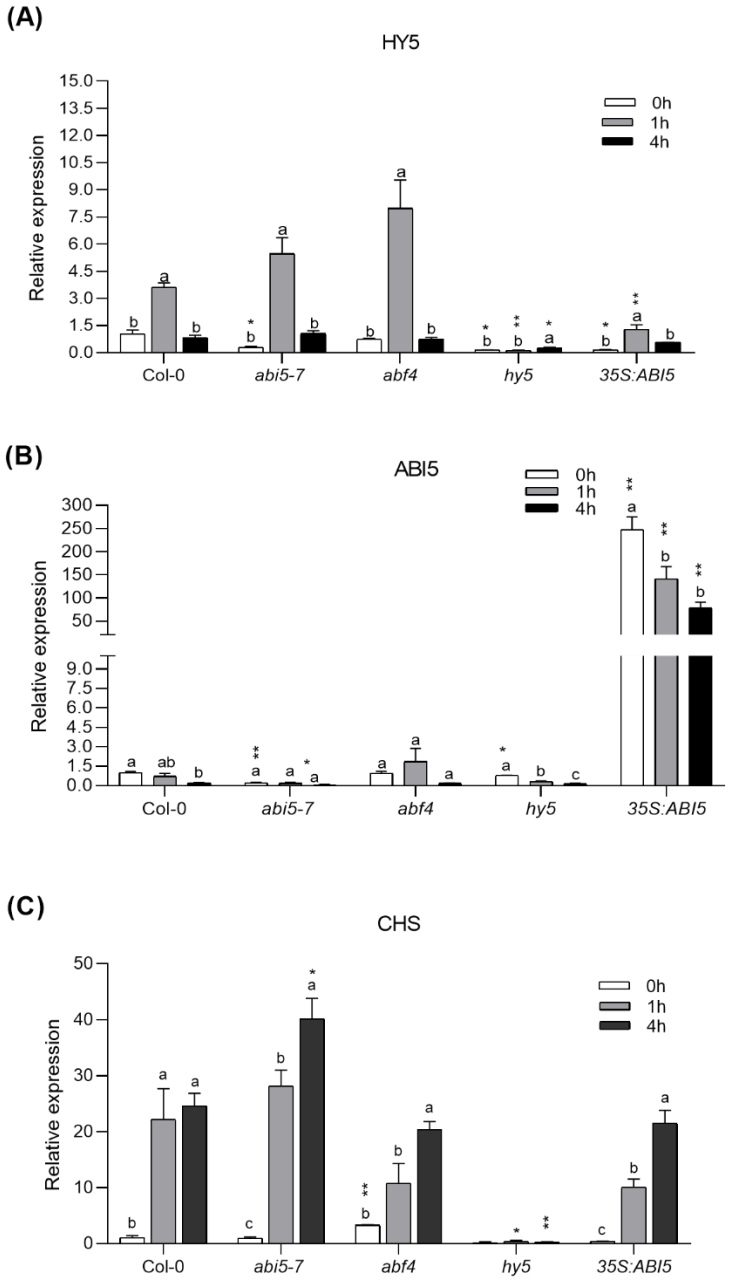
GSE79576



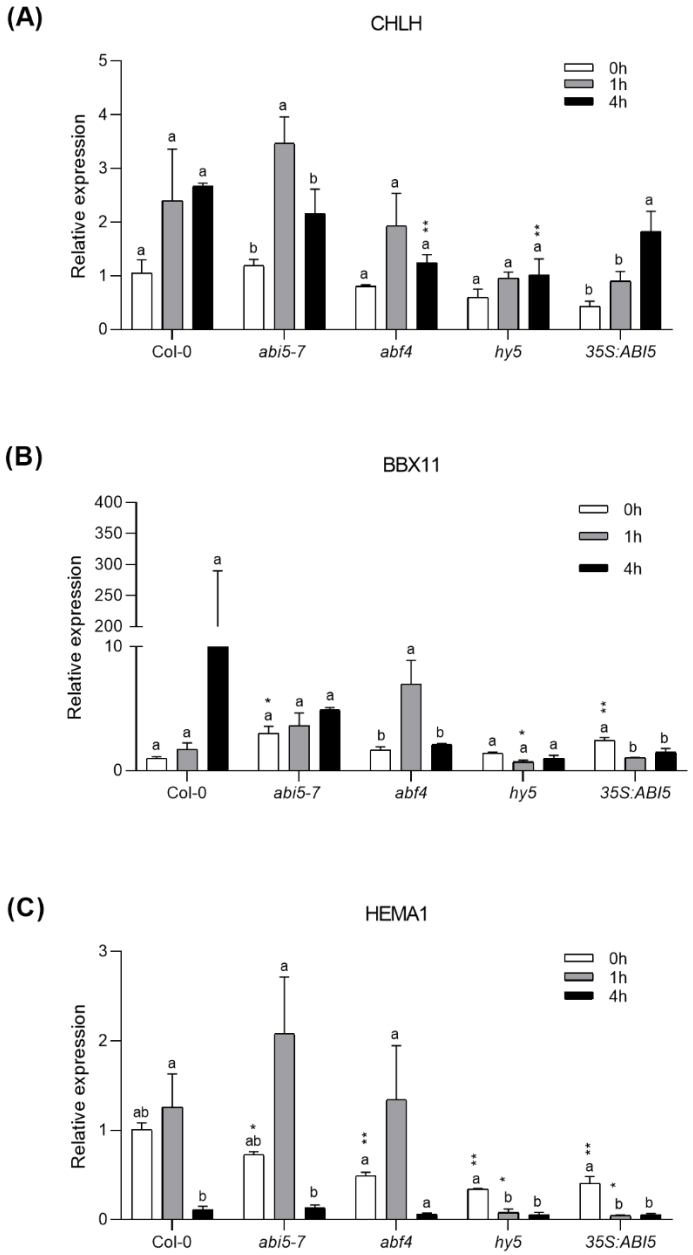
Supplementary Figure 2 *Arabidopsis thaliana* transcriptogram of dataset GSE79576. The x-axis relative to gene position have been divided by the total number of proteins retrieved from STRING. Average transcriptograms for r=90, signifcant peaks (up-regulation) or valleys (down-regulation) are colored in blue. Grey lines show non-signifcant regions.



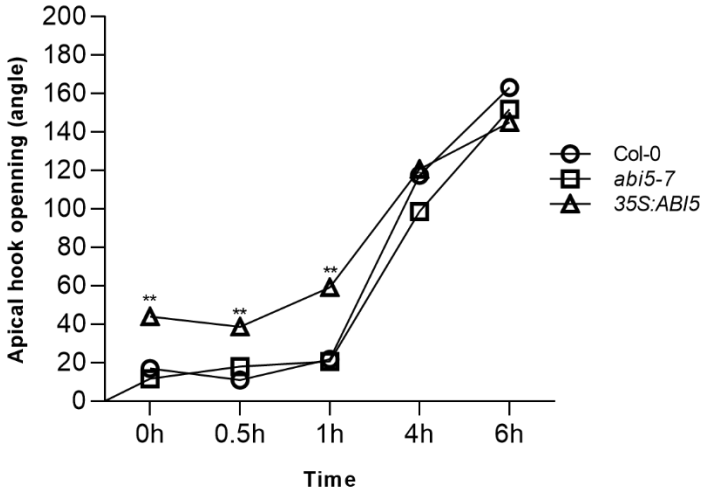
Supplementary Figure 3 *Arabidopsis thaliana* transcriptogram of dataset GSE29657 and GSE5917. The x-axis relative to gene position have been divided by the total number of proteins retrieved from STRING. Average transcriptograms for r=90, signifcant peaks (up-regulation) or valleys (down-regulation) are colored in blue. Grey lines show non-signifcant regions.



Supplementary Figure 4 RT-qPCR analysis of gene expression in light treated seedlings. **a** HY5, **b** ABI5, **c** CHS. Four-day old dark grown seedlings (0 h) were exposed to white light for 1 (1h) and 4 hours (4h). Statistical significance was determined by ordinary one-way ANOVA with Tukey´s post-test (letters represent the statistical significance between the time within the genotype) and the means were compared by unpaired test t (asterisks denote differentially expressed genes with $*p \leq 0.05$; $**p \leq 0.01$) in the same light condition against the wild-type genotype. Error bars indicate SE.



Supplementary Figure 5 RT-qPCR analysis of gene expression of chlorophyll related genes in seedlings. **a** *CHLH*, **b** *BBX11*, **c** *HEMA1*. Four-day old dark grown seedlings (0 h) were exposed to white light for 1 (1h) and 4 hours (4h). Statistical significance was determined by ordinary one-way ANOVA with Tukey´s post-test (letters represent the statistical significance between the time within the genotype) and the means were compared by unpaired test t (asterisks denote differentially expressed genes with *p ≤ 0.05; **p ≤ 0.01) in the same light condition against the wild-type genotype. Error bars indicate SE.



Supplementary Figure 6 Apical hook opening response of WT (Col-0), *abi5-7* and *35S:ABI5*. Four-day old dark grown seedlings (0 h) were exposed to white light for 0.5h, 1h, 4h and 6h. Statistical significance was determined by Shapiro-Wilk normality test and Kruskal-Wallis post-test (**p < 0.01).

Supplementary tables available in:

https://www.biorxiv.org/content/10.1101/2022.07.24.501316v1.supplementary-material

Supplementary Table 1. Datasets used in this work

Supplementary Table 2 Differentially expressed genes and genes present in peaks or valleys of transcriptogram, in common between the three datasets (GSE79576, GSE28657 and GSE5617) in their conditions.

Supplementary Table 3 Functional enrichment analysis of list of genes present in DEseq up or down and peaks or valleys from three datasets select (GSE5617, GSE79576 and GSE29657). Bold terms were those plotted Fig. 3.

Supplementary Table 4 Differentially expressed genes and genes present in peaks or valleys of transcriptogram, in common between the three datasets (GSE79576, GSE28657 and GSE5617), with expression value in datasets associated the *pifq* (Sun et al., 2016), *cry1 cry2* (He et al., 2015) and phyB-YHB (Hu et al. 2009).

Supplementary Table 5 Differentially expressed genes in common between the three datasets (GSE79576, GSE28657 and GSE5617) compared to HY5 targets (Burko *et al.*, 2020).

Supplementary Table 6 RT-qPCR primers. List of RT-qPCR primers used for gene expression analysis of Figure 7.

Capítulo IV

- Screening of putative mobile transcription factors controlling seedling photomorphogenesis-

Introduction

Seedlings show contrasting developmental phenotypes when grown in light or darkness. In light, seedlings show a photomorphogenic pattern of development with green, open cotyledons, a short hypocotyl and a long root. In the dark, however, skotomorphogenic development produces seedlings with closed cotyledons and apical hook, a long hypocotyl, and a short root. This survival strategy allows the seedling to invest in the elongation of the hypocotyl and to protect the shoot apical meristem while it is buried. Once the seedling emerges from the soil, it opens its cotyledons, begins to perform photosynthesis and develops leaves that start to allocate resources for root growth (Lau and Deng 2012). The light-dependent signaling cascade that induces root growth from the shoot is still unknown. Potential signaling molecules may be the sugars produced in the shoot (Rolland et al. 2002) but auxins may also play an essential role. It has been shown that shoot-derived auxin is necessary for emergence of lateral root primordia and therefore for root development (Bhalerao et al. 2002a).

In plants, several macromolecules, including non-coding RNAs, mRNAs and proteins act as important long-distance signals, regulating physiological and morphological processes such as transitions to flowering, growth and stress responses (Ham and Lucas 2017a). Therefore, it is plausible that macromolecules such as proteins and RNAs act as mobile signals activated in the shoot capable of inducing root growth.

Several studies have identified some molecules with a crucial role in activating root growth, such as auxins and sucrose. Auxins are involved in several processes of plant development. They are synthesized in young shoots and transported polarly towards the roots. Some studies have shown that the spatio-temporal division of auxin synthesis during early seedling development involves a differential contribution of auxin produced in the cotyledons and subsequent to the activation of its synthesis at the root apex (Bhalerao et al. 2002a). Activation of auxin synthesis at the root apex is essential for maintaining root growth. The majority of signals from the shoot capable of inducing root growth remain unknown.

Transcriptomic studies have identified several mobile RNAs (mRNAs and miRNAs) translocated between root and shoot in Arabidopsis, some even bidirectionally (Thieme et al. 2015). Thus, a wide possibility of regulatory effects triggered by these molecules can be unraveled through the functional analysis of their

gene products. Recently, it was demonstrated that the transcription factor HY5, one of the main activators of photomorphogenesis, is translocated from leaves to roots where it induces its own expression and promoters the expression of nitrate transporter genes in response to elevated C/N ratios (Chen et al. 2016b).

Light can penetrate root tissues underground through a stem light-pipe mechanism (Lee et al. 2016) that activates root-expressed phytochrome B (phyB) and induces local HY5 stabilization, promoting root growth and root gravitropism. Despite having a central role in photomorphogenesis in both shoots and roots, the transcription factor HY5 does not explain all light-triggered events in root growth.

Proteins and RNAs have been identified as mobile signals in the phloem acting in the communication between leaves and stem meristems, as in the case of the flowering promoter protein FT (Corbesier et al. 2007) as well as signals exchanged between leaves and roots to trigger growth (Hannapel et al. 2013; Spiegelman et al. 2015) SAR (Carella et al. 2016) nitrogen uptake (Tabata et al. 2014) among others (Ham and Lucas 2017). Although some signaling molecules have already been identified as important long-distance signals, few transcription factors were identified as mobile signals in the communication between shoots and roots.

Our research group performed an RNAseq experiment comparing 4- and 7-day-old plant roots that were grown with shoot-illumination only or completely in the dark. Numerous genes and cellular processes differentially expressed in roots were identified in this experiment (Miotto et al., 2019), however, the long distance singals that modulate this vast transcriptional reprogramming remain to be identified.

Considering that numerous transcriptomic databases on Arabidopsis are publicly available, we can compare the genes regulated by light in the shoots with our root data directly to select for putative long-distance acting candidate genes. Therefore, this chapter aims to identify candidate genes encoding transcription factors that potentially regulate the photomorphogenic response of roots acting in the communication between shoots and roots.

Materials and methods

Screening of public datasets

We dedicated our search in public transcriptome depositories for samples of young Arabidopsis seedlings. We searched the Gene Expression Omnibus Database (GEO) database with keywords: *Arabidopsis thaliana*, *light*, *shoot* and selected among the retrieved results samples from seedlings of 4 days of age. The raw data from microarray experiments were selected through accession codes GSE5617 (Kilian et al. 2007), GSE28297 (Leivar et al. 2012), GSE29657 (Liu et al. 2012); and Expression Atlas Database through accession code E-MEXP-1784 (Zhang et al. 2008). All microarray datasets considered here used the same platform (Affymetrix Arabidopsis ATH1 Genome Array – ATH1-121501). RNA-seq data from shoots (hypocotyl and cotyledons) exposed to light were downloaded from Sequence Read Archive database under accession code SRP072300, GEO code GSE79576 (Sun et al. 2016) (Table 1).

Table I Datasets used in the meta-analysis.

Dataset	Plant part	Exposure conditions	Technology	Reference
GSE5617	Seedlings	Seedlings were kept for 4 days in dark. Then, were exposed to 1 hour and 4 hours of white light. Exposed seedlings were compared to non-exposed controls.	Microarray	Kilian et al. 2007
GSE29657	Shoot	Seedlings were kept for 4 days in dark. Then, were exposed to 30 minutes and 4 hours of white light. Exposed shoot was compared to non-exposed controls.	Microarray	Liu et al. 2012
GSE28297	Seedlings	Seedlings were grown in 2 and 3 days of white light exposure.	Microarray	Leivar et al. 2012
E-MEXP-1784	Seedlings	Seedlings were kept for 4 days in dark. Then, seedlings were exposed to 1 hour of blue light and compared to non-exposed controls.	Microarray	Zhang et al. 2008
GSE79576	Shoot	Seedlings were kept for 4 days in dark. Then, were exposed to 1 hour and 6 hours of white light. Exposed hypocotyls and cotyledons separately were compared to non-exposed controls.	RNA-seq	Sun et al. 2016

Individual preprocessing and differential expression analysis of the datasets

For the microarray samples, the raw data was normalized with RMA method and expression values (Robust Multi-Array Average Expression Measure) were

retrieved with affy R/Bioconductor package (Gautier et al. 2004). Differential expression analysis was performed using limma R/Bioconductor package. Genes were considered differentially expressed when p value ≤ 0.001 with FDR adjustment (Ritchie et al. 2015). For the RNA-seq databases, the raw reads were aligned and annotated to Arabidopsis thaliana reference genome v10 (versão 10 do genoma de Arabidopsis Thaliana no TAIR) using STAR aligner (Dobin et al. 2013). Counts from aligned reads were obtained with featureCounts program (Liao et al. 2014) and normalized into log-2-counts-per-million. Differential expression analysis was performed using limma R/Bioconductor package protocol for RNA-seq experiments, considering only the differentially expressed genes with p value ≤ 0.001 with FDR adjustment (Ritchie et al. 2015).

Selection of candidate genes and filtering

Light regulated genes common to the five public datasets were selected. Then, this list was filtered in some databases, as Plant Transcription Factor Database (Banerjee and Roychoudhury 2017), a list of identified mobile mRNAs (Thieme et al. 2015), PlaMoM (database compiling plant mobile macromolecules), and light-regulated genes in roots (Miotto et al. 2019) - although this is not an excluding factor, and in addition to information of the Gene Description and Biological Process (Figure 1).

Plant material and growth conditions

Arabidopsis Col-0 was used as wild-type (WT), and all the mutants used are listed in Table II. Seeds were surface-sterilized and stratified at 4 °C for 2 days in complete darkness. Seedlings were grown at 21 °C ± 2 °C under LD condition (LD - Shoot light, Dark root, as Miotto et al. 2019) or D (completely darkness) for 7 days-old and exposure white light illumination (94 µmol m−2 s−1). Plants were grown on half-strength sucrose-free Murashige and Skoog media supplemented with 1.5% agar (w/v; KASVI) and 0.05% MES hydrate (w/v; Sigma-Aldrich, M8250), pH 5.7, on vertically oriented square plates in LD (dark roots) or D grown plants (complete darkness). Similarly grown seedlings were used for RNA isolation. For root and hypocotyl length measurements, seedlings were growth in LD condition (LD - Shoot light, Dark root, as Miotto et al. 2019), and the measurements were performed at 7 and 14 days. Organ length was measured with ImageJ (Fiji) and plotted into graphs in

GraphPad Prism 8. For nitrate experiment, seedlings were grown at 21 °C ± 2 °C under L condition (68 µmol m−2 s−1) for 8 and 12 days in MS media without KNO_3, 0.2mM KNO_3 and 1mM KNO_3 (Krouk et al. 2010a).

DNA isolation and genotyping

DNA extraction and PCR were performed as described in Miotto et al. (2019). Primer sequences can be found in the Supplementary Table 1. Single T-DNA insertion knockout lines were requested from ABRC and the presence of the mutation was confirmed by PCR.

Results

Aiming to identify among light regulated genes common to the selected transcriptomic databases, we crossed the common light regulated transcripts coding for transcription factors to those of root regulated genes (Miotto et al., 2019). After all filtering steps, 20 genes were selected as putative candidates for light regulated transcription factors and mobile mRNAs (Figure 1, Table II and Table III).

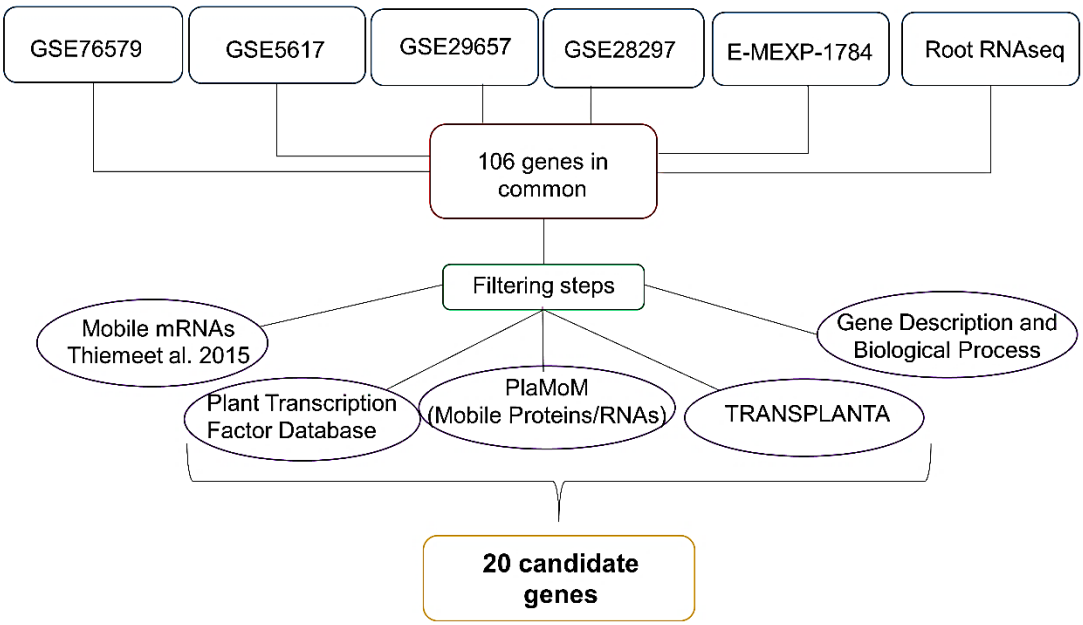


Figure 1 - Flowchart of candidate gene selection steps.

Table II List of *Arabidopsis thaliana* genes in common between the six datasets.

Gene ID	Name	Description
AT1G67810	SUFE2	SufE-like protein 2, chloroplastic
AT4G25580	AT4G25580	At4g25580/M7J2_50
AT1G44446	CAO	CH1
AT4G14130	XTH15	Xyloglucan endotransglucosylase/hydrolase protein 15
AT1G26270	PI4KG5	Phosphatidylinositol 4-kinase gamma 5
AT4G36930	SPT	SPT
AT1G31850	AT1G31850	Probable methyltransferase PMT20
AT5G17050	UGT78D2	Glycosyltransferase (Fragment)
AT5G25810	TINY	Tny
AT5G24850	CRYD	Cryptochrome DASH, chloroplastic/mitochondrial
AT5G66650	AT5G66650	Calcium uniporter protein 3, mitochondrial
AT5G57660	COL5	Zinc finger protein CONSTANS-LIKE 5
AT5G48880	KAT5	PKT2
AT5G44110	ABCI21	ABC transporter I family member 21
AT5G37550	AT5G37550	At5g37550
AT5G23730	RUP2	WD repeat-containing protein RUP2
AT5G18650	MIEL1	MIEL1
AT5G13930	CHS	Chalcone synthase family protein
AT5G13630	CHLH	Magnesium-chelatase subunit ChlH, chloroplastic
AT5G13650	AT5G13650	Elongation factor family protein
AT5G09590	HSP70-10	Heat shock 70 kDa protein 10, mitochondrial
AT5G08640	FLS1	Flavonol synthase/flavanone 3-hydroxylase
AT5G05270	CHI3	Probable chalcone--flavonone isomerase 3
AT5G05100	AT5G05100	Single-stranded nucleic acid binding R3H protein
AT5G02270	ATNAP9	Non-intrinsic ABC protein 9
AT3G60140	BGLU30	Beta-glucosidase 30
AT3G56290	AT3G56290	Potassium transporter
AT3G54770	ARP1	Probable RNA-binding protein ARP1
AT3G48350	CEP3	KDEL-tailed cysteine endopeptidase CEP3
AT3G45300	IVD	Isovaleryl-CoA dehydrogenase, mitochondrial
AT4G36040	ATJ11	At4g36040
AT4G34830	MRL1	Pentatricopeptide repeat-containing protein MRL1, chloroplastic
AT4G33010	GLDP1	Glycine cleavage system P protein
AT4G32770	VTE1	Tocopherol cyclase, chloroplastic
AT4G30290	XTH19	Xyloglucan endotransglucosylase/hydrolase
AT4G29590	AT4G29590	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
AT4G28250	EXPB3	EXPB3
AT4G27520	ENODL2	Early nodulin-like protein 2
AT4G27560	UGT79B2	UDP-glycosyltransferase 79B2

AT4G26400	AT4G26400	AT4G26400 protein
AT4G17840	AT4G17840	At4g17840
AT4G11570	PYRP2	5-amino-6-(5-phospho-D-ribitylamino)uracil phosphatase, chloroplastic
AT4G02920	AT4G02920	Uncharacterized protein At4g02920
AT4G02290	AtGH9B13	Endoglucanase 17
AT1G16720	HCF173	high chlorophyll fluorescence phenotype 173 [Source:TAIR
AT2G33250	AT2G33250	At2g33250/F25I18.1
AT1G34000	OHP2	OHP2
AT1G18060	AT1G18060	AT1g18060/T10F20.23
AT3G12610	DRT100	DRT100
AT3G12320	LNK3	LNK3
AT1G69526	AT1G69526	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
AT1G55020	LOX1	Linoleate 9S-lipoxygenase 1
AT3G27170	CLC-B	CLC-B
AT3G23990	CPN60	Chaperonin CPN60, mitochondrial
AT3G23810	SAHH2	Adenosylhomocysteinase
AT3G23510	AT3G23510	Cyclopropane-fatty-acyl-phospholipid synthase
AT3G23530	AT3G23530	AT3g23510/MEE5_5
AT3G26570	PHT2	ORF02, PHOSPHATE TRANSPORTER 2;1, low affinity phosphate transporter
AT3G20340	AT3G20340	At3g20340
AT3G27380	SDH2-1	Succinate dehydrogenase [ubiquinone] iron-sulfur subunit 1, mitochondrial
AT3G21560	UGT84A2	UGT84A2
AT3G21690	DTX40	Protein DETOXIFICATION 40
AT3G22840	ELIP1	ELIP1
AT3G15500	NAC055	NAC3
AT3G02730	TRXF1	TRXF1
AT3G02830	ZFN1	Zinc finger CCCH domain-containing protein 33
AT3G08030	AT3G08030	F17A17.37 protein
AT5G04130	GYRBM	DNA gyrase subunit B, mitochondrial
AT3G10270	GYRB1	DNA gyrase subunit B
AT3G07770	HSP90-6	Heat shock protein 90-6, mitochondrial
AT1G52870	AT1G52870	At1g52870/F14G24_14
AT1G70560	TAA1	L-tryptophan--pyruvate aminotransferase 1
AT1G10960	FD1	Ferredoxin-1, chloroplastic
AT2G43400	ETFQO	Electron transfer flavoprotein-ubiquinone oxidoreductase, mitochondrial
AT1G55960	AT1G55960	Polyketide cyclase/dehydrase and lipid transport superfamily protein
AT1G05840	AT1G05840	Eukaryotic aspartyl protease family protein
AT1G53090	SPA4	SPA4
AT1G07700	AT1G07700	Thioredoxin superfamily protein [Source:TAIR

AT1G49660	CXE5	Probable carboxylesterase 5
AT1G33110	DTX21	Protein DETOXIFICATION
AT1G30530	UGT78D1	Glycosyltransferase (Fragment)
AT1G65060	4CL3	4-coumarate--CoA ligase 3
AT1G21680	AT1G21680	DPP6 N-terminal domain-like protein
AT1G28570	AT1G28570	GDSL esterase/lipase At1g28570
AT1G54100	ALDH7B4	ALDH7B4
AT2G16500	ADC1	Arginine decarboxylase 1
AT2G42570	TBL39	Protein trichome birefringence-like 39
AT2G16430	PAP10	Purple acid phosphatase
AT2G36900	MEMB11	Membrin
AT2G21880	RABG2	RAB7A
AT2G36290	AT2G36290	Alpha/beta-Hydrolases superfamily protein
AT2G42870	PAR1	Transcription factor PAR1
AT1G60270	BGLU6	Putative beta-glucosidase 6
AT1G09570	PHYA	phytochrome A [Source:TAIR
AT2G15970	COR413PM1	WCOR413-like protein
AT2G05620	PGR5	Protein PROTON GRADIENT REGULATION 5, chloroplastic
AT2G25530	AT2G25530	AFG1-like ATPase family protein
AT2G37330	ALS3	ALS3
AT2G35260	AT2G35260	At2g35260/T4C15.7
AT2G46260	AT2G46260	BTB/POZ domain-containing protein At2g46260
AT2G46140	AT2G46140	Desiccation-related protein At2g46140
AT2G25900	ATCTH	Zinc finger CCCH domain-containing protein 23
AT2G34460	AT2G34460	Uncharacterized protein At2g34460, chloroplastic
AT2G38230	PDX11	Pyridoxal 5'-phosphate synthase subunit PDX1.1
AT2G40000	HSPRO2	Nematode resistance protein-like HSPRO2
AT2G30570	PSBW	PSBW

All tested seedlings grown in LD condition showed normal photomorphogenesis as well as normal etiolation in complete darkness (D condition) (Figure 2). However, we observed significant deviations from the WT in *bbx4* and *ccd4* that showed longer shoots in LD and *ccd1* that displayed longer shoots in the dark (Figure 2a). The mutant *jaz9* displayed longer roots in darkness and longer shoots in LD. Interestingly, *penta1* presented longer shoots and roots in LD condition (Figure 2b) while mutants *expb3, gk064h04, salk011787, salk202632, tny* and *nap* had longer primary roots in darkness (Figure 2c-d). These results suggest that these genes may influence shoot and root growth in response to light.

Table III List of *Arabidopsis thaliana* candidate genes and respective mutants requested from ABRC.

Gene ID	Name	Germplasm
AT3G15500	NAC055	SALK_014331
AT5G57660	COL5	SALK_096361
AT2G24790	ATCOL3, BBX4, COL3, CONSTANS-LIKE 3	SALKSEQ_60825.1/ cs926382
AT1G69490	NAP	SALK_005010
AT5G04410	ANAC078, NAC2, NAC78, NTL11	SALK_025098
AT4G28250	ATEXPB3, EXPB3	SALK_124760
AT5G25810	TINY, TNY	SALK_206788
AT2G31790	unknown	SALK_202632
AT5G11790	NDL2	SALK_013645
AT4G19170	CCD4	SALK_097984
AT2G14878	unknown	SALK_030214
AT1G46554	unknown	SALK_011787
AT4G39675	unknown	SALK_111156
AT5G24880	unknown	GK064H04
AT3G23810	SAHH2	GK139A1201 / cs314094
AT4G36930	SPATULA, SPT	WISCDSLOX466B7
AT1G30530	UGT78D1	SAIL_568_F08
AT1G70700	JAZ9/TIFY7	SALK_004872
AT3G02830	PENTA 1, PNT1, ZFN1	GABI_676A09 / cs374793
AT3G63520	CCD1	SAIL 390 C01/ cs878019

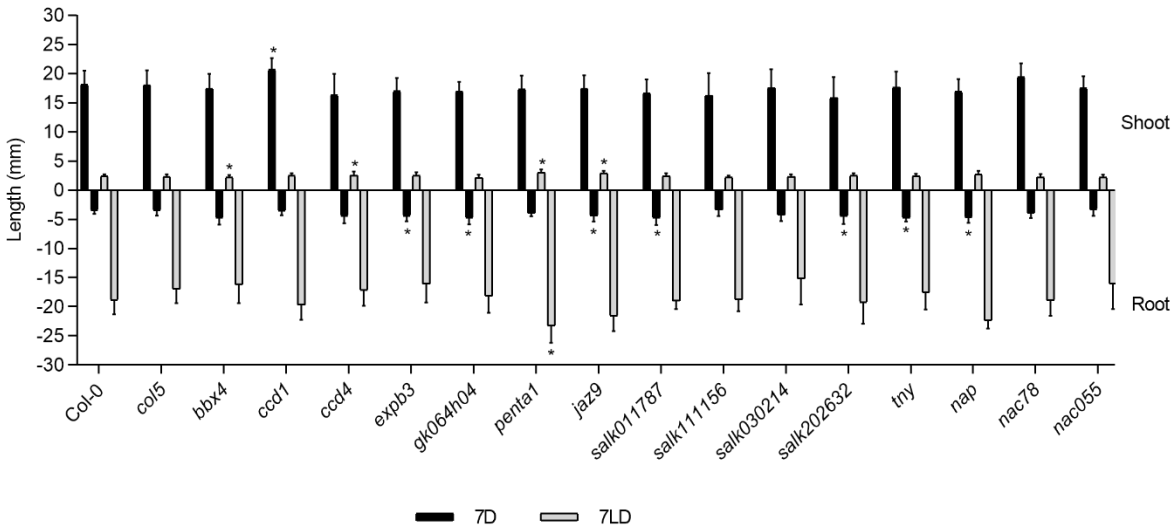


Figure 2 Shoot and primary root growth lengths of single knockout mutants (n≥ 15). Statistical significance was determined by Kruskal-Wallis test with Dunn's post-test (* p≤ 0.05). Error bars indicate SD.

Seedlings were further grown in LD and the number of lateral roots was quantified after 14 DAG. Some mutants showed a higher number of lateral roots when

compared to the wild type, such as *tny*, *salk011787* and *gk064h04* (Figure 3). These results possible suggest that these genes, specially *AT1G46554* (*salk011787)*, act as repressors of lateral root development in response to shoot light.

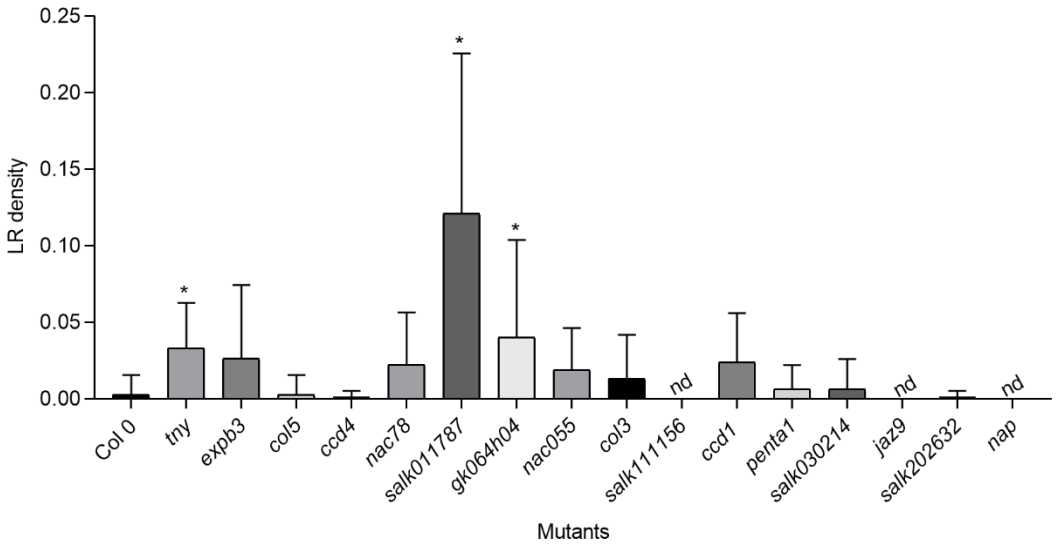
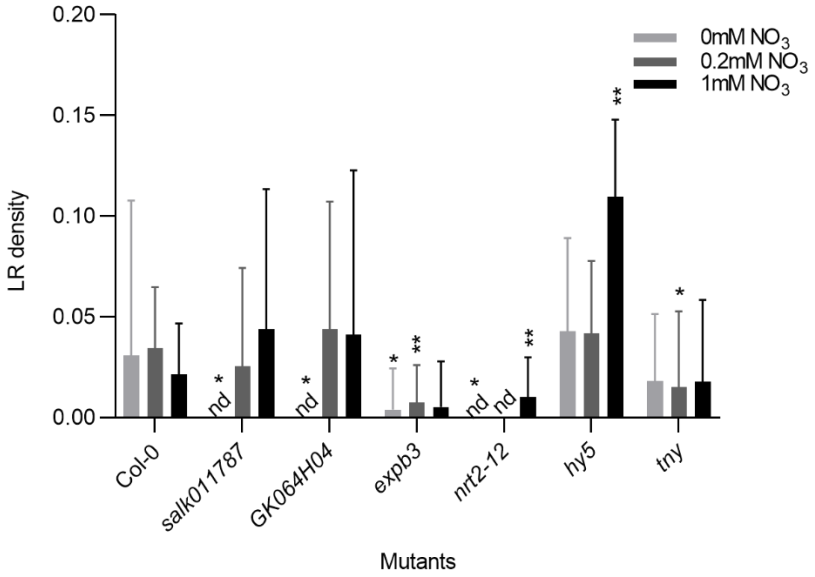


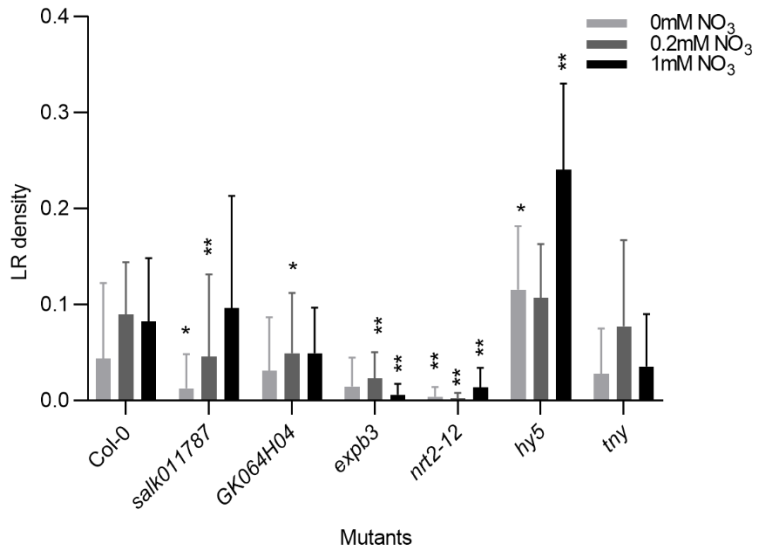
Figure 3. Lateral root density of single knockout mutants at 14 days in LD condition (n≥ 15). Statistical significance was determined by Kruskal-Wallis test with Dunn's post-test (* p≤ 0.05). Error bars indicate SD.

Low nitrate concentrations stimulate lateral root formation whereas high nitrate represses lateral root growth (Bulgakov and Koren 2022), so we decided to carry out another experiment only with the mutants that showed significant differences in lateral root growth. Seedlings were grown as Krouk et al. 2010 in medium without N, 0.2 mM or 1 mM KNO_3 Evaluations were performed at 8 and 12 DAG. At 8 DAG, *hy5* mutants showed a higher amount of LR when compared to Col-0 in 1 mM KNO_3. On the other hand, *tny* showed less LR in 0.2 mM of NO_3 (Figure 4a). In the absence of NO_3, mutants *salk011787*, *GK06H04*, *exp3*, *nrt2-12* all showed a strong reduction of LR compared to the WT. Interestingly, *salk011787* displayed much longer LRs than the WT in 0,2 mM and 1 mM KNO_3 which suggests a repressive role for the gene *AT1G46554* both for LR emergence and growth in response to NO_3. LR was restored in higher (1mM NO_3) concentrations for all genotypes at 8 DAG but *exp3* and *nrt2-12* did not increase LRs at 12 DAG. These two genotypes behaved similarly in all NO_3 concentrations and timepoints tested, suggesting they might operate in a similar pathway.

(A)


0mM NO3
0.2mM NO3
1mM NO3
LR density
0.20
0.15
0.10
0.05
0.00
nd
nd
nd
Col-0
salk011787
GK064H04
expb3
nrt2-12
hy5
tny
Mutants

(B)


0mM NO3
0.2mM NO3
1mM NO3
LR density
0.4
0.3
0.2
0.1
0.0
Col-0
salk011787
GK064H04
expb3
nrt2-12
hy5
tny
Mutants

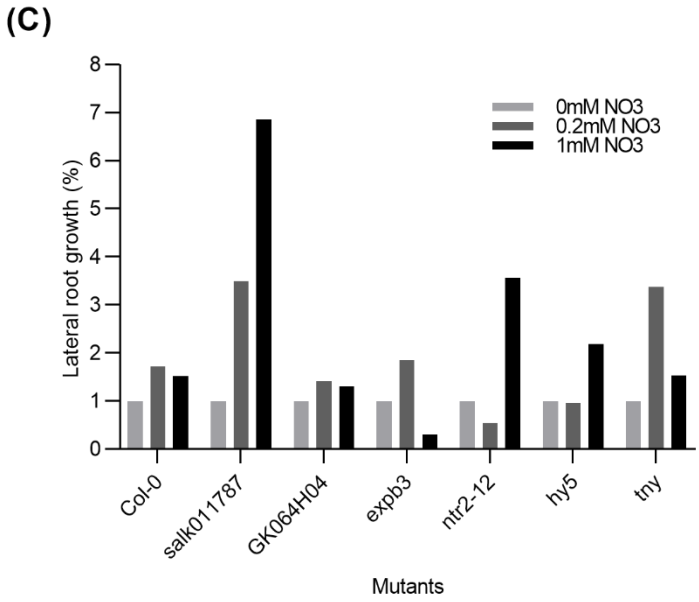


Figure 4 Lateral root density of single knockout mutants with 0 mM, 0.2mM and 1 mM of NO3, **a** 8 days in LD condition (n≥ 1), **b** 12 days in LD condition (n≥ 15) and **c** growth ratio (%) of 12 days in LD condiction. Statistical significance was determined by Kruskal-Wallis test with Dunn's post-test (* p≤ 0.05) and (** p≤ 0.01). Error bars indicate SD.

Discussion

Previously, phytohormones, sugars, mobile RNAs and proteins were once considered mobile signals produced by the shoot and mobilized to the roots, where they promote the development of the root system (Lee et al. 2017; Van Gelderen et al. 2018). Although these studies had a great importance in the elucidation of the genetic and molecular mechanisms involved in light responses, there are still many gaps to fulfill. In this work we searched for some possible candidates for light-responsive shoot-to-root mobile signals.

By comparing root expressed light-regulated genes from photomorphogenic seedlings with other available transcriptomic data, we found a list of candidate genes expressed in shoots that might act in root responses.

Some of the identified mutants displayed more pronounced root growth as well as lateral roots when compared to Col-0. Among them we can highlight AT1G46554 (*salk011787)* which is identified as a non-coding RNA and the loss of function mutant displays more LR formation and elongation, which suggests it might act as a repressor of lateral roots. The fact that these genes produces a light-inducible and phloem-mobile

non-coding RNA suggests that a putative long acting post-transcriptional and/or epigenetic mechanism might act to control light-responsive lateral root development.

Another gene, AT5G24880 (*GK06H04*), is described as a "chromo domain cec-like protein" expressed specifically in root hairs, stamens, and pollen in the eFP-Browser expression atlas. Although there is no further functional information regarding this protein, our results suggest that this gene acts as a negative regulator for the emergence of lateral roots, although this remains to be evaluated further.

Another interesting mutant is *tny* (AT5G25810), which showed more LR formation in control conditions and more LR growth in high NO_3 conditions. *TNY* encodes a member of the DREB A-4 subfamily of the ERF/AP2 family of TFs and is also known as *ERF40*. This gene is induced by ethylene and light and appears to stimulate cytokinin biosynthesis (Wilson et al. 1996; Sakuma et al. 2006). TINY was described to reduce cell expansion when overexpressed. Recently, it was described to inhibit plant growth and promote drought response via a repressive effect on BR signaling in drought conditions (Xie et al. 2019). Our results reinforce the repressive effect of TNY in root growth, especially regarding LRs. Nevertheless, its role in shoot-to-root signaling could be accessed via grafting or tissue specific gene-ablation.

The mutant *exp3* stood out in our analysis displaying reduced root growth in most of the tested conditions. EXP3 encodes EXPANSINβ3, first identified more than a decade ago as the main cell wall factors responsible for “acid growth” (Wieczorek et al. 2006). Expansins comprise two major gene families: α-expansins (EXPA) and β-expansins (EXPB). Most isoforms are expressed in both shoots and roots, which include EXPB3 (Wieczorek et al. 2006). Our results suggest that the mutation affects the cellular expansion and thus compromising the growth of the roots.

These four genes are promising candidates for studies on how light affects main root and lateral root growth. Here, we show that root growth responses are affected by light and this affects primary and lateral root development in *Arabidopsis*. Our results indicate that the majority mutants did not show differences related to shoot and root growth. However, the development of experiments with a greater number of plants evaluated and with different light intensities will allow a more accurate analysis of the effect on the behavior of mutants. In addition to enabling the evaluation of the participation of these genes in long-distance signaling when the aerial part is illuminated.

References

Carella P, Merl-Pham J, Wilson DC, Dey S, Hauck SM, Vlot AC and Cameron RK (2016) Comparative Proteomics Analysis of Phloem Exudates Collected during the Induction of Systemic Acquired Resistance. Plant Physiol 171:1495. doi: 10.1104/PP.16.00269

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C et al. (2007) FT protein movement contributes to long-distance signaling in floral induction of Arabidopsis. Science 316:1030–1033. doi: 10.1126/SCIENCE.1141752

Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett M and Sandberg G (2002) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. Plant J 29:325–332. doi: 10.1046/j.0960-7412.2001.01217.x

Dobin A, Davis CA, Schlesinger F, Drenkow J, Zaleski C, Jha S, Batut P, Chaisson M, Gingeras TR (2013) Sequence analysis STAR: ultrafast universal RNA-seq aligner. 29:15–21 . https://doi.org/10.1093/bioinformatics/bts635

Gautier L, Cope L, Bolstad BM, Irizarry RA (2004) affy-analysis of Affymetrix GeneChip data at the probe level. BIOINFORMATICS 20:307–315. https://doi.org/10.1093/bioinformatics/btg405

Ham B-K and Lucas WJ (2017) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Hannapel DJ, Sharma P and Lin T (2013) Phloem-mobile messengerRNAs and root development. Front Plant Sci 4:257. doi: 10.3389/FPLS.2013.00257/BIBTEX

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J, Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363 . https://doi.org/10.1111/j.1365-313X.2007.03052.x

Lau OS and Deng XW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci 17:584–593. doi: 10.1016/J.TPLANTS.2012.05.004

Lee HJ, Park YJ, Ha JH, Baldwin IT, Park CM (2017) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22: 803–812

Leivar P, Tepperman JM, Cohn MM, Monte E, Al-Sady B, Erickson E, Quail PH (2012) Dynamic antagonism between phytochromes and PIF family basic helix-loop-helix factors induces selective reciprocal responses to light and shade in a rapidly responsive transcriptional network in Arabidopsis. Plant Cell 24:1398–419. https://doi.org/10.1105/tpc.112.095711

Liao Y, Smyth GK, Shi W (2014) featureCounts: an efficient general purpose program for assigning sequence reads to genomic features. Bioinformatics 30:923–930. https://doi.org/10.1093/bioinformatics/btt656

Liu M-J, Wu S-H, Chen H-M, Wu S-H (2012) Widespread translational control contributes to the regulation of Arabidopsis photomorphogenesis. Mol Syst Biol 8:566. https://doi.org/10.1038/msb.2011.97

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Ritchie ME, Phipson B, Wu D, Hu Y, Law CW, Shi W, Smyth GK (2015) limma powers differential expression analyses for RNA-sequencing and microarray studies. Nucleic Acids Res 43:. https://doi.org/10.1093/nar/gkv007

Rolland F, Moore B and Sheen J (2002) Sugar sensing and signaling in plants. Plant Cell 14 Suppl:S185-205. doi: 10.1105/TPC.010455

Sun N, Wang J, Gao Z, Dong J, He H, Terzaghi W, Wei N, Deng XW, Chen H (2016) Arabidopsis SAURs are critical for differential light regulation of the development of various organs. Proc Natl Acad Sci U S A 113:6071–6. https://doi.org/10.1073/pnas.1604782113

Spiegelman Z, Ham BK, Zhang Z, Toal TW, Brady SM, Zheng Y, Fei Z, Lucas WJ and Wolf S (2015) A tomato phloem-mobile protein regulates the shoot-to-root ratio by mediating the auxin response in distant organs. Plant J 83:853–863. doi: 10.1111/TPJ.12932

Tabata R, Sumida K, Yoshii T, Ohyama K, Shinohara H and Matsubayashi Y (2014) Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. Science 346:343–346. doi: 10.1126/SCIENCE.1257800

Thieme CJ, Rojas-Triana M, Stecyk E, Schudoma C, Zhang W, Yang L, Minãmbres M, Walther D, Schulze WX, Paz-Ares J et al. (2015) Endogenous Arabidopsis messenger RNAs transported to distant tissues. Nat Plants 2015 14 1:1–9. doi: 10.1038/nplants.2015.25

Xie Z, Nolan T, Jiang H, Tang B, Zhang M, Li Z and Yin Y (2019) The AP2/ERF transcription factor TINY modulates brassinosteroid-regulated plant growth and drought responses in arabidopsis. Plant Cell 31:1788–1806. doi:

10.1105/tpc.18.00918

Zhang X-N, Wu Y, Tobias JW, Brunk BP, Deitzer GF, Liu D (2008) HFR1 Is Crucial for Transcriptome Regulation in the Cryptochrome 1-Mediated Early Response to Blue Light in Arabidopsis thaliana. PLoS One 3:e3563 . https://doi.org/10.1371/journal.pone.0003563

- Considerações finais -

Os últimos 10 anos foram bastante esclarecedores quanto ao estudo da luz no desenvolvimento das plantas. Embora descobertas notáveis tenham sido feitas sobre as respostas fotomorfogênicas da parte aérea a jusante dos fotorreceptores, os eventos de sinalização que controlam a fotomorfogênese da raiz foram deixados um pouco de lado. Descobertas recentes mostraram que a comunicação de longa distância desempenha um papel importante na fotomorfogênese, estresses abióticos e bióticos, sinalização de nutrientes, termomorfogênese e ciclo circadiano entre parte aérea e raízes. As plantas vêm desenvolvendo ao longo de toda a evolução inúmeros mecanismos para se proteger de condições adversas impostas pelo meio ambiente, ou seja, estão em um processo constante de adaptação. A relação luz x crescimento radicular, está bastante atrelada a comunicação que se dá entre parte aérea e raiz, esta comunicação é complexa e desencadeada por um ou vários sinais de longa distância.

Avaliamos nos Capítulos II a IV o efeito da iluminação da parte aérea na regulação de genes e processos que ativam o crescimento das raízes. As considerações do Capítulo II se baseiam na tentativa de esclarecer os mecanismos de sinalização no desenvolvimento inicial das plântulas de *Arabidopsis thaliana* revisando os hubs centrais de sinalização luminosa. A luz não é apenas uma fonte de energia, mas também um sinal de coordenação nas plantas e a maioria das pesquisas se concentra na resposta dos órgãos acima do solo apenas. No entanto, o desenvolvimento radicular subterrâneo é altamente responsivo aos sinais de luz da parte aérea e a compreensão desses mecanismos de sinalização fornecerá uma melhor visão do desenvolvimento inicial das plântulas.

No capítulo III, nos utilizamos da análise de *datasets* públicas de transcriptomas para avaliar de forma abrangente o efeito da iluminação da parte aérea na regulação da fotomorfogênese. Visando melhor aproveitar o número de genes diferencialmente expressos que encontramos, acabamos por optar pela utilização de duas ferramentas/metodologias distintas na análise destas *datasets*, o DEseq e o Transcriptograma. Apesar de serem abordagens com estratégias diferentes, ambas nos remeteram um pequeno conjunto de genes (fatores de transcrição) possivelmente envolvidos no processo de sinalização por luz. A combinação dos dados obtidos por essa análise (dados de bancos de dados públicos) possibilitou o levantamento da

participação de fatores de transcrição relacionados ao ABA na transmissão do sinal recebido da parte aérea.

O fitohormônio auxina e os açúcares fotossintetizados eram os principais candidatos a sinais de longa distância enviados pela parte aérea iluminada para as raízes, abaixo do solo. A participação de genes da rota do ABA apareceram em nossas análises, como estando envolvidos neste processo. Com base em nossas observações de que a maioria das respostas precoces transcricionais à luz pode depender de fatores de resposta ao ABA que já estão presentes na plântula cultivada no escuro, propomos um modelo em que a sinalização de luz reaproveita parte dessa maquinaria transcricional disponível para ativar os genes responsivos precoces na inativação de PIF e mais tarde, a estabilização de reguladores positivos de respostas à luz assume para sustentar o crescimento fotomorfogênico, esse efeito pode ocorrer por interação direta com bZIPs responsivos a ABA (interação entre HY5 e ABI5). São necessárias, porém, novas análises envolvendo fusão com outras proteínas e RNAs para investigação mais aprofundada do comportamento e mecanismos dos fatores de resposta ao ABA na via de sinalização luminosa.

A diversa gama e disponibilidade de mutantes perda-de-função permite avaliar geneticamente o papel de genes de interesse. No Capítulo IV, realizamos diversas filtragens baseadas em artigos publicados, *datasets* e bancos de dados e definimos um conjunto de genes candidatos como sendo responsivos à luz. A avaliação fenotípica dos mesmos nos conduziu a quatro genes promissores para esse estudo. Porém, os dados não foram totalmente explorados e torna-se necessário o desenvolvimento de mais experimentos para garantir este envolvimento.

Com base nos apontamentos relatados nesta tese fomos capazes de corroborar alguns aspectos da nossa hipótese inicial, assim como inserir novas possibilidades nesse modelo de desenvolvimento. Inúmeras questões no que diz respeito a como e de que forma determinados genes participam da fotomorfogênese permanecem não respondidas e necessitam de investigação aprofundada.

- Referências –

Abbas N, Maurya JP, Senapati D, Gangappa SN and Chattopadhyaya S (2014) Arabidopsis CAM7 and HY5 physically interact and directly bind to the HY5 promoter to regulate its expression and thereby promote photomorphogenesis. Plant Cell 26:1036–1052. doi: 10.1105/tpc.113.122515

Achard P, Liao L, Jiang C, Desnos T, Bartlett J, Fu X and Harberd NP (2007) DELLAs contribute to plant photomorphogenesis. Plant Physiol 143:1163–1172. doi: 10.1104/pp.106.092254

Achard P, Renou J-P, Berthomé R, Harberd NP and Genschik P (2008) Plant DELLAs Restrain Growth and Promote Survival of Adversity by Reducing the Levels of Reactive Oxygen Species. Curr Biol 18:656–660. doi: 10.1016/J.CUB.2008.04.034

Agurla S, Gahir S, Munemasa S, Murata Y, Raghavendra AS, Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I et al. (2020) Light and abscisic acid coordinately regulate greening of seedlings. Plant Physiol 183:1281–1294. doi: 10.1104/pp.20.00503

Al-Sady B, Ni W, Kircher S, Schäfer E and Quail PH (2006) Photoactivated Phytochrome Induces Rapid PIF3 Phosphorylation Prior to Proteasome-Mediated Degradation. Mol Cell 23:439–446. doi: 10.1016/j.molcel.2006.06.011

Albertos P, Romero-Puertas MC, Tatematsu K, Mateos I, Sánchez-Vicente I, Nambara E and Lorenzo O (2015) S-nitrosylation triggers ABI5 degradation to promote seed germination and seedling growth. Nat Commun 6:1–10. doi: 10.1038/ncomms9669

Ali F, Qanmber G, Li F and Wang Z (2022) Updated role of ABA in seed maturation, dormancy, and germination. J Adv Res 35:199–214. doi: 10.1016/J.JARE.2021.03.011

An F, Zhang X, Zhu Z, Ji Y, He W, Jiang Z, Li M and Guo H (2012) Coordinated regulation of apical hook development by gibberellins and ethylene in etiolated Arabidopsis seedlings. Cell Res 2012 225 22:915–927. doi: 10.1038/cr.2012.29

Ang Lay Hong and Deng Xing Wang (1994) Regulatory hierarchy of photomorphogenic loci: Allele-specific and light-dependent interaction between the HY5 and COP1 loci. Plant Cell 6:613–628. doi: 10.1105/tpc.6.5.613

Ang LH, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A and Deng XW (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. Mol Cell 1:213–222. doi: 10.1016/S1097-2765(00)80022-2

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012a) Photomorphogenesis. Arab B 10:e0147. doi: 10.1199/tab.0147

Arsovski AA, Galstyan A, Guseman JM and Nemhauser JL (2012b) Photomorphogenesis Photomorphogenesis. Society. doi: 10.1199/tab.0147

Bai MY, Shang JX, Oh E, Fan M, Bai Y, Zentella R, Sun TP and Wang ZY (2012) Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. Nat Cell Biol 14:810–817. doi: 10.1038/ncb2546

Bai S, Yao T, Li M, Guo X, Zhang Y, Zhu S and He Y (2014) PIF3 Is Involved in the Primary Root Growth Inhibition of Arabidopsis Induced by Nitric Oxide in the Light. Mol Plant 7:616–625. doi: 10.1093/MP/SST142

Balcerowicz M, Fittinghoff K, Wirthmueller L, Maier A, Fackendahl P, Fiene G, Koncz C and Hoecker U (2011) Light exposure of Arabidopsis seedlings causes rapid de-stabilization as well as selective post-translational inactivation of the repressor of photomorphogenesis SPA2. Plant J 65:712–723. doi: 10.1111/J.1365-313X.2010.04456.X

Balcerowicz M, Kerner K, Schenkel C and Hoecker U (2017) SPA proteins affect the subcellular localization of COP1 in the COP1/SPA ubiquitin ligase complex during photomorphogenesis. Plant Physiol 174:1314–1321. doi: 10.1104/pp.17.00488

Banerjee A and Roychoudhury A (2017) Abscisic-acid-dependent basic leucine zipper (bZIP) transcription factors in plant abiotic stress. Protoplasma 254:3–16. doi: 10.1007/S00709-015-0920-4/FIGURES/1

Bao F, Shen J, Brady SR, Muday GK, Asami T and Yang Z (2004) Brassinosteroids interact with auxin to promote lateral root development in arabidopsis. Plant Physiol 134:1624–1631. doi: 10.1104/pp.103.036897

Bhagat PK, Verma D, Sharma D and Sinha AK (2021a) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z/FIGURES/6

Bhagat PK, Verma D, Sharma D and Sinha AK (2021b) HY5 and ABI5 transcription factors physically interact to fine tune light and ABA signaling in Arabidopsis. Plant Mol Biol 107:117–127. doi: 10.1007/S11103-021-01187-Z

Bhalerao RP, Eklo J, Ljung K, Marchant A, Bennett M and Sandberg È (2002a) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. 29:

Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett M and Sandberg G (2002b) Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. Plant J 29:325–332. doi: 10.1046/j.0960-7412.2001.01217.x

Bhatia S, Gangappa SN, Kuswaha R, Kundu S and Chattopadhyay S (2008) Short Hypocotyl in White Light1, a serine-arginine-aspartate-rich protein in Arabidopsis, acts as a negative regulator of photomorphogenic growth. Plant Physiol 147:169–178. doi: 10.1104/pp.108.118174

Bhatnagar A, Singh S, Khurana JP and Burman N (2020) HY5-COP1: the central module of light signaling pathway. J Plant Biochem Biotechnol 29:590–610. doi: 10.1007/s13562-020-00623-3

Binder BM, Walker JM, Gagne JM, Emborg TJ, Hemmann G, Bleecker AB and Vierstra RD (2007) The Arabidopsis EIN3 Binding F-Box Proteins EBF1 and EBF2 Have Distinct but Overlapping Roles in Ethylene Signaling. Plant Cell 19:509–523. doi: 10.1105/TPC.106.048140

Binenbaum J, Weinstain R and Shani E (2018) Gibberellin Localization and Transport in Plants. Trends Plant Sci 23:410–421. doi: 10.1016/J.TPLANTS.2018.02.005

Bouché F, D'Aloia M, Tocquin P, Lobet G, Detry N and Périlleux C (2016) Integrating roots into a whole plant network of flowering time genes in Arabidopsis thaliana. Sci Reports 2016 61 6:1–12. doi: 10.1038/srep29042

Brumos J, Robles LM, Yun J, Vu TC, Jackson S, Alonso JM and Stepanova Correspondence AN (2018) Local Auxin Biosynthesis Is a Key Regulator of Plant Development. Dev Cell 47:306–318. doi: 10.1016/j.devcel.2018.09.022

Brunetti C, Sebastiani F and Tattini M (2019) Review: ABA, flavonols, and the evolvability of land plants. Plant Sci 280:448–454. doi: 10.1016/j.plantsci.2018.12.010

Buer CS, Muday GK and Djordjevic MA (2007) Flavonoids are differentially taken up and transported long distances in Arabidopsis. Plant Physiol 145:478–490. doi: 10.1104/pp.107.101824

Bulgakov VP and Koren OG (2022) Basic Protein Modules Combining Abscisic Acid and Light Signaling in Arabidopsis. Front Plant Sci 12:2986. doi: 10.3389/FPLS.2021.808960/BIBTEX

Burko Y, Gaillochet C, Seluzicki A, Chory J and Busch W (2020a) Local HY5 Activity Mediates Hypocotyl Growth and Shoot-to-Root Communication. Plant Commun 1:100078. doi: 10.1016/j.xplc.2020.100078

Burko Y, Seluzicki A, Zander M, Pedmale U V., Ecker JR and Chory J (2020b) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/TPC.19.00772

Burko Y, Seluzicki A, Zander M, Pedmale U V, Ecker JR and Chory J (2020c) Chimeric Activators and Repressors Define HY5 Activity and Reveal a Light-Regulated Feedback Mechanism. Plant Cell 32:967–983. doi: 10.1105/tpc.19.00772

Cabrera J, Conesa CM and Pozo JC (2022) May the dark be with roots: a perspective on how root illumination may bias in vitro research on plant–environment interactions. New Phytol 233:1988–1997. doi: 10.1111/nph.17936

Canamero RC, Bakrim N, Bouly J-P, Garay A, Dudkin EE, Habricot Y and Ahmad M (2006) Cryptochrome photoreceptors cry1 and cry2 antagonistically regulate primary root elongation in Arabidopsis thaliana. Planta 2006 2245 224:995–1003. doi: 10.1007/S00425-006-0280-6

Cañibano E, Bourbousse C, García-León M, Garnelo Gómez B, Wolff L, García-Baudino C, Lozano-Durán R, Barneche F, Rubio V and Fonseca S (2021) DET1-mediated COP1 regulation avoids HY5 activity over second-site gene targets to tune plant photomorphogenesis. Mol Plant 14:963–982. doi: 10.1016/j.molp.2021.03.009

Caño-Delgado A, Lee J-Y and Demura T (2010) Regulatory Mechanisms for Specification and Patterning of Plant Vascular Tissues. Annu Rev Cell Dev Biol 26:605–637. doi: 10.1146/annurev-cellbio-100109-104107

Carella P, Merl-Pham J, Wilson DC, Dey S, Hauck SM, Vlot AC and Cameron RK (2016) Comparative Proteomics Analysis of Phloem Exudates Collected during the Induction of Systemic Acquired Resistance. Plant Physiol 171:1495. doi: 10.1104/PP.16.00269

Chaiwanon J, Wang W, Zhu J-Y, Oh E and Wang Z-Y (2016) Information Integration and Communication in Plant Growth Regulation. Cell 164:1257–1268. doi: 10.1016/j.cell.2016.01.044

Chaiwanon J and Wang ZY (2015) Spatiotemporal brassinosteroid signaling and antagonism with auxin pattern stem cell dynamics in Arabidopsis roots. Curr Biol 25:1031–1042. doi: 10.1016/j.cub.2015.02.046

Chamovitz D a, Wei N, Osterlund MT, von Arnim a G, Staub JM, Matsui M and Deng XW (1996) The COP9 complex, a novel multisubunit nuclear regulator involved in light control of a plant developmental switch. Cell 86:115–21.

Chen G-H, Liu M-J, Xiong Y, Sheen J and Wu S-H (2018) TOR and RPS6 transmit light signals to enhance protein translation in deetiolating Arabidopsis seedlings. Proc Natl Acad Sci 115:12823–12828. doi: 10.1073/pnas.1809526115

Chen H, Huang X, Gusmaroli G, Terzaghi W, Lau OS, Yanagawa Y, Zhang Y, Li J, Lee JH, Zhu D et al. (2010) Arabidopsis CULLIN4-damaged DNA binding protein 1 interacts with CONSTITUTIVELY PHOTOMORPHOGENIC1-SUPPRESSOR OF PHYA complexes to regulate photomorphogenesis and flowering time. Plant Cell 22:108–123. doi: 10.1105/tpc.109.065490

Chen H, Zhang J, Neff MM, Hong S-WW, Zhang H, Deng X-WW, Xiong L and Korea S (2008a) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen H, Zhang J, Neff MM, Hong SW, Zhang H, Deng XW and Xiong L (2008b) Integration of light and abscisic acid signaling during seed germination and early seedling development. Proc Natl Acad Sci U S A 105:4495–4500. doi: 10.1073/pnas.0710778105

Chen Q, Dai X, De-Paoli H, Cheng Y, Takebayashi Y, Kasahara H, Kamiya Y and Zhao Y (2014) Auxin overproduction in shoots cannot rescue auxin deficiencies in arabidopsis roots. Plant Cell Physiol 55:1072–1079. doi: 10.1093/pcp/pcu039

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016a) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Chen X, Yao Q, Gao X, Jiang C, Harberd NP and Fu X (2016b) Shoot-to-Root Mobile Transcription Factor HY5 Coordinates Plant Carbon and Nitrogen Acquisition. Curr Biol 26:640–646. doi: 10.1016/j.cub.2015.12.066

Cheng ZJ, Zhao XY, Shao XX, Wang F, Zhou C, Liu YG, Zhang Y and Zhang XS (2014) Abscisic acid regulates early seed development in arabidopsis by ABI5-Mediated transcription of SHORT HYPOCOTYL UNDER BLUE1. Plant Cell 26:1053–1068. doi: 10.1105/tpc.113.121566

Chory J (1993) Out of darkness: mutants reveal pathways controlling light-regulated development in plants. Trends Genet 9:167–172. doi: 10.1016/0168-9525(93)90163-C

Christians MJ, Gingerich DJ, Hua Z, Lauer TD and Vierstra RD (2012) The Light-Response BTB1 and BTB2 Proteins Assemble Nuclear Ubiquitin Ligases That Modify Phytochrome B and D Signaling in Arabidopsis. Plant Physiol 160:118–134. doi: 10.1104/pp.112.199109

Christie JM, Blackwood L, Petersen J and Sullivan S (2015) Plant Flavoprotein Photoreceptors. Plant Cell Physiol 56:401–413. doi: 10.1093/pcp/pcu196

Collin A, Daszkowska-Golec A and Szarejko I (2021) Updates on the Role of ABSCISIC ACID INSENSITIVE 5 (ABI5) and ABSCISIC ACID-RESPONSIVE ELEMENT BINDING FACTORs (ABFs) in ABA Signaling in Different Developmental Stages in Plants. Cells 2021, Vol 10, Page 1996 10:1996. doi: 10.3390/CELLS10081996

Corbesier L, Vincent C, Jang S, Fornara F, Fan Q, Searle I, Giakountis A, Farrona S, Gissot L, Turnbull C et al. (2007) FT protein movement contributes to long-distance

signaling in floral induction of Arabidopsis. Science 316:1030–1033. doi: 10.1126/SCIENCE.1141752

Correll MJ and Kiss JZ (2005a) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Correll MJ and Kiss JZ (2005b) The Roles of Phytochromes in Elongation and Gravitropism of Roots. Plant Cell Physiol 46:317–323. doi: 10.1093/pcp/pci038

Cosme M, Fernández I, Declerck S, van der Heijden MGA and Pieterse CMJ (2021) A coumarin exudation pathway mitigates arbuscular mycorrhizal incompatibility in Arabidopsis thaliana. Plant Mol Biol 1:3. doi: 10.1007/s11103-021-01143-x

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011a) Root-localized phytochrome chromophore synthesis is required for photoregulation of root elongation and impacts root sensitivity to jasmonic acid in Arabidopsis. Plant Physiol 157:1138–50. doi: 10.1104/pp.111.184689

Costigan SE, Warnasooriya SN, Humphries BA and Montgomery BL (2011b) Root-Localized Phytochrome Chromophore Synthesis Is Required for Photoregulation of Root Elongation and Impacts Root Sensitivity to Jasmonic Acid in Arabidopsis. Plant Physiol 157:1138–1150. doi: 10.1104/pp.111.184689

da Silva SR, Perrone GC, Dinis JM and de Almeida RM (2014a) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics 15:1181. doi: 10.1186/1471-2164-15-1181

da Silva SRM, Perrone GC, Dinis JM and de Almeida RMC (2014b) Reproducibility enhancement and differential expression of non predefined functional gene sets in human genome. BMC Genomics. doi: 10.1186/1471-2164-15-1181

Datta S, Hettiarachchi GHCM, Deng X-W and Holm M (2006) Arabidopsis CONSTANS-LIKE3 Is a Positive Regulator of Red Light Signaling and Root Growth. Plant Cell 18:70–84. doi: 10.1105/TPC.105.038182

de Lucas M, Davière J-M, Rodríguez-Falcón M, Pontin M, Iglesias-Pedraz JM, Lorrain S, Fankhauser C, Blázquez MA, Titarenko E and Prat S (2008) A molecular framework for light and gibberellin control of cell elongation. Nature 451:480–484. doi: 10.1038/nature06520

de Wit M, Keuskamp DH, Bongers FJ et al. (2016) Integration of Phytochrome and Cryptochrome Signals Determines Plant Growth during Competition for Light. Curr Biol 26:3320–3326. doi: 10.1016/j.cub.2016.10.031

De Wit M, Galvão VC and Fankhauser C (2016) Light-Mediated Hormonal Regulation of Plant Growth and Development. Annu Rev Plant Biol 67:513–537. doi: 10.1146/annurev-arplant-043015-112252

Deng X-WX -W and Quail PH (1992) Genetic and phenotypic characterization of cop1 mutants of Arabidopsis thaliana. Plant J 2:83–95. doi: 10.1111/j.1365-313X.1992.00083.x

Deng XW, Caspar T and Quail PH (1991) cop1: a regulatory locus involved in light-controlled development and gene expression in Arabidopsis. Genes Dev 5:1172–1182. doi: 10.1101/GAD.5.7.1172

Dobin A, Davis CA, Schlesinger F, Drenkow J, Zaleski C, Jha S, Batut P, Chaisson M and Gingeras TR (2013) Sequence analysis STAR: ultrafast universal RNA-seq

aligner. 29:15–21. doi: 10.1093/bioinformatics/bts635

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017a) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Ni W, Yu R, Deng XW, Chen H and Wei N (2017b) Light-Dependent Degradation of PIF3 by SCFEBF1/2 Promotes a Photomorphogenic Response in Arabidopsis. Curr Biol 27:2420-2430.e6. doi: 10.1016/J.CUB.2017.06.062

Dong J, Tang D, Gao Z, Yu R, Li K, He H, Terzaghi W, Deng XW and Chen H (2014) Arabidopsis DE-ETIOLATED1 Represses Photomorphogenesis by Positively Regulating Phytochrome-Interacting Factors in the Dark. Plant Cell 26:3630–3645. doi: 10.1105/tpc.114.130666

Du M, Daher FB, Liu Y, Steward A, Tillmann M, Zhang X, Wong JH, Ren H, Cohen JD, Li C et al. (2022) Biphasic control of cell expansion by auxin coordinates etiolated seedling development. Sci Adv 8:1570. doi: 10.1126/SCIADV.ABJ1570/SUPPL_FILE/SCIADV.ABJ1570_MOVIES_S1_TO_S8.ZIP

Duan L, Pérez-Ruiz JM, Cejudo FJ and Dinneny JR (2021) Characterization of CYCLOPHILLIN38 shows that a photosynthesis-derived systemic signal controls lateral root emergence. Plant Physiol 185:503–518. doi: 10.1093/PLPHYS/KIAA032

Durinck S, Spellman PT, Birney E and Huber W (2009) Mapping identifiers for the integration of genomic datasets with the R/ Bioconductor package biomaRt. Nat Protoc 4:1184–1191. doi: 10.1038/nprot.2009.97

Dyachok J, Zhu L, Liao F, He J, Huq E and Blancaflor EB (2011) SCAR Mediates Light-Induced Root Elongation in Arabidopsis through Photoreceptors and Proteasomes. Plant Cell 23:3610–3626. doi: 10.1105/tpc.111.088823

Feng S, Martinez C, Gusmaroli G, Wang Y, Zhou J, Wang F, Chen L, Yu L, Iglesias-Pedraz JM, Kircher S et al. (2008) Coordinated regulation of Arabidopsis thaliana development by light and gibberellins. Nature 451:475–479. doi: 10.1038/nature06448

Fernández-Milmanda GL and Ballaré CL (2021) Shade Avoidance: Expanding the Color and Hormone Palette. Trends Plant Sci 26:509–523. doi: 10.1016/j.tplants.2020.12.006

Fernando VCD, Al Khateeb W, Belmonte MF and Schroeder DF (2018) Role of Arabidopsis ABF1/3/4 during det1 germination in salt and osmotic stress conditions. Plant Mol Biol 97:149–163. doi: 10.1007/S11103-018-0729-6/FIGURES/10

Forde BG (2002) Local and long-range signaling pathways regulating plant responses to nitrate. Annu Rev Plant Biol 53:203–224. doi: 10.1146/annurev.arplant.53.100301.135256

Franceschini A, Szklarczyk D, Frankild S, Kuhn M, Simonovic M, Roth A, Lin J, Minguez P, Bork P, von Mering C et al. (2012) STRING v9.1: protein-protein interaction networks, with increased coverage and integration. Nucleic Acids Res 41:D808–D815. doi: 10.1093/nar/gks1094

Fu L, Liu Y, Qin G, Wu P, Zi H, Xu Z, Zhao X, Wang Y, Li Y, Yang S et al. (2021) The TOR–EIN2 axis mediates nuclear signalling to modulate plant growth. Nature 591:288–292. doi: 10.1038/s41586-021-03310-y

Fu X and Harberd NP (2003) Auxin promotes Arabidopsis root growth by modulating gibberellin response. Nature 421:740–743. doi: 10.1038/nature01387

Fukaki H, Taniguchi N and Tasaka M (2006) PICKLE is required for SOLITARY-ROOT/IAA14-mediated repression of ARF7 and ARF19 activity during Arabidopsis lateral root initiation. Plant J 48:380–389. doi: 10.1111/J.1365-313X.2006.02882.X

Gaillochet C, Burko Y, Platre MP, Zhang L, Simura J, Willige BC, Kumar SV, Ljung K, Chory J and Busch W (2020) HY5 and phytochrome activity modulate shoot to root coordination during thermomorphogenesis. Development. doi: 10.1242/dev.192625

Galen C, Rabenold JJ and Liscum E (2007) Functional ecology of a blue light photoreceptor: effects of phototropin-1 on root growth enhance drought tolerance in Arabidopsis thaliana. New Phytol 173:91–99. doi: 10.1111/J.1469-8137.2006.01893.X

Galvã VC and Fankhauser C (2015) Sensing the light environment in plants: photoreceptors and early signaling steps. Curr Opin Neurobiol 34:46–53. doi: 10.1016/j.conb.2015.01.013

Gangappa SN, Crocco CD, Johansson H, Datta S, Hettiarachchi C, Holm M and Botto JF (2013a) The Arabidopsis B-BOX Protein BBX25 Interacts with HY5, Negatively Regulating BBX22 Expression to Suppress Seedling Photomorphogenesis. Plant Cell 25:1243–1257. doi: 10.1105/TPC.113.109751

Gangappa SN, Holm M and Botto JF (2013b) Molecular interactions of BBX24 and BBX25 with HYH, HY5 HOMOLOG, to modulate Arabidopsis seedling development. Plant Signal Behav. doi: 10.4161/psb.25208

Gao YQ, Bu LH, Han ML, Wang YL, Li ZY, Liu HT and Chao DY (2021) Long-distance blue light signalling regulates phosphate deficiency-induced primary root growth inhibition. Mol Plant 14:1539–1553. doi: 10.1016/j.molp.2021.06.002

García-González J, Lacek J, Weckwerth W and Retzer K (2021) Exogenous carbon source supplementation counteracts root and hypocotyl growth limitations under increased cotyledon shading, with glucose and sucrose differentially modulating growth curves. Plant Signal Behav. doi: 10.1080/15592324.2021.1969818

Gautier L, Cope L, Bolstad BM and Irizarry RA (2004) affy-analysis of Affymetrix GeneChip data at the probe level. BIOINFORMATICS 20:307–315. doi: 10.1093/bioinformatics/btg405

Ge S, He L, Jin L, Xia X, Li L, Ahammed GJ, Qi Z, Yu J and Zhou Y (2022) Light-dependent activation of HY5 promotes mycorrhizal symbiosis in tomato by systemically regulating strigolactone biosynthesis. New Phytol 233:1900–1914. doi: 10.1111/nph.17883

Gil K-E, Ha J-H and Park C-M (2018) Abscisic acid-mediated phytochrome B signaling promotes primary root growth in Arabidopsis. Plant Signal Behav 13:e1473684. doi: 10.1080/15592324.2018.1473684

Gommers CMM and Monte E (2018) Seedling Establishment: A Dimmer Switch-Regulated Process between Dark and Light Signaling. Plant Physiol 176:1061–1074. doi: 10.1104/pp.17.01460

Grunewald W, De Smet I, Lewis DR, Löfke C, Jansen L, Goeminne G, Vanden Bossche R, Karimi M, De Rybel B, Vanholme B et al. (2012) Transcription factor

WRKY23 assists auxin distribution patterns during Arabidopsis root development through local control on flavonol biosynthesis. Proc Natl Acad Sci U S A 109:1554–9. doi: 10.1073/pnas.1121134109

Guo Z, Xu J, Wang Y, Hu C, Shi K, Zhou J, Xia X, Zhou Y, Foyer CH and Yu J (2021) The phyB-dependent induction of HY5 promotes iron uptake by systemically activating FER expression. EMBO Rep 22:e51944. doi: 10.15252/embr.202051944

Ha J-HH, Kim J-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-HJ-IIJH and Park C-MM (2018a) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant J 94:790–798. doi: 10.1111/tpj.13902

Ha J-HH, Kim J-IJ-HJ-IIJH, Kim S-GG, Sim H-JJ, Lee G, Halitschke R, Baldwin IT, Kim J-IJ-HJ-IIJH and Park C-MM (2018b) Shoot phytochrome B modulates reactive oxygen species homeostasis in roots via abscisic acid signaling in Arabidopsis. Plant J 94:790–798. doi: 10.1111/tpj.13902

Hacham Y, Holland N, Butterfield C, Ubeda-Tomas S, Bennett MJ, Chory J and Savaldi-Goldstein S (2011) Brassinosteroid perception in the epidermis controls root meristem size. Development 138:839–848. doi: 10.1242/DEV.061804

Ham B-K and Lucas WJ (2017a) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Ham B-K and Lucas WJ (2017b) Phloem-Mobile RNAs as Systemic Signaling Agents. Annu Rev Plant Biol 68:173–195. doi: 10.1146/annurev-arplant-042916-041139

Hamon-josse M, Villaecija-aguilar JA, Ljung K and Leyser O (2021) KAI2 regulates seedling development by mediating light- induced remodelling of auxin transport. bioRxiv 2021.05.06.443001. doi: 10.1101/2021.05.06.443001

Hamon-Josse M, Villaécija-Aguilar JA, Ljung K, Leyser O, Gutjahr C and Bennett T (2022) KAI2 regulates seedling development by mediating light-induced remodelling of auxin transport. New Phytol 235:126–140. doi: 10.1111/NPH.18110

Han X, Huang X and Deng XW (2020) The Photomorphogenic Central Repressor COP1: Conservation and Functional Diversification during Evolution. Plant Commun 1:100044. doi: 10.1016/j.xplc.2020.100044

Hannapel DJ, Sharma P and Lin T (2013) Phloem-mobile messengerRNAs and root development. Front Plant Sci 4:257. doi: 10.3389/FPLS.2013.00257/BIBTEX

Harkey AF, Watkins JM, Olex AL, DiNapoli KT, Lewis DR, Fetrow JS, Binder BM and Muday GK (2018) Identification of Transcriptional and Receptor Networks That Control Root Responses to Ethylene. Plant Physiol 176:2095–2118. doi: 10.1104/PP.17.00907

Hartmann L, Drewe-Boß P, Wießner T, Wagner G, Geue S, Lee H-C, Obermüller DM, Kahles A, Behr J, Sinz FH et al. (2016) Alternative Splicing Substantially Diversifies the Transcriptome during Early Photomorphogenesis and Correlates with the Energy Availability in Arabidopsis. Plant Cell 28:2715–2734. doi: 10.1105/tpc.16.00508

He S-B, Wang W-X, Zhang J-Y, Xu F, Lian H-L, Li L and Yang H-Q (2015a) The CNT1 Domain of Arabidopsis CRY1 Alone Is Sufficient to Mediate Blue Light Inhibition of Hypocotyl Elongation. Mol Plant 8:822–825. doi:

10.1016/J.MOLP.2015.02.008

He SB, Wang WX, Zhang JY, Xu F, Lian HL, Li L and Yang HQ (2015b) The CNT1 domain of arabidopsis CRY1 alone is sufficient to mediate blue light inhibition of hypocotyl elongation. Mol Plant 8:822–825. doi: 10.1016/j.molp.2015.02.008

He Z, Zhao X, Kong F, Zuo Z and Liu X (2016) TCP2 positively regulates HY5/HYH and photomorphogenesis in Arabidopsis. J Exp Bot 67:775–785. doi: 10.1093/JXB/ERV495

Hellmann H and Estelle M (2002a) Plant development: regulation by protein degradation. Science 297:793–7. doi: 10.1126/science.1072831

Hellmann H and Estelle M (2002b) Plant development: Regulation by protein degradation. Science (80-) 297:793–797. doi: 10.1126/science.1072831

Heo J-O, Chang KS, Kim IA, Lee M-H, Lee SA, Song S-K, Lee MM and Lim J (2011) Funneling of gibberellin signaling by the GRAS transcription regulator SCARECROW-LIKE 3 in the Arabidopsis root. Proc Natl Acad Sci 108:2166–2171. doi: 10.1073/pnas.1012215108

Hoecker U and Quail PH (2001) The Phytochrome A-specific Signaling Intermediate SPA1 Interacts Directly with COP1, a Constitutive Repressor of Light Signaling inArabidopsis. J Biol Chem 276:38173–38178. doi: 10.1074/jbc.M103140200

Hoecker U, Tepperman JM and Quail PH (1999) SPA1, a WD-Repeat Protein Specific to Phytochrome A Signal Transduction. Science (80-) 284:496–499. doi: 10.1126/science.284.5413.496

Holm M, Ma LG, Qu LJ and Deng XW (2002) Two interacting bZIP proteins are direct targets of COP1-mediated control of light-dependent gene expression in Arabidopsis. Genes Dev 16:1247–1259. doi: 10.1101/gad.969702

Holtan HE, Bandong S, Marion CM, Adam L, Tiwari S, Shen Y, Maloof JN, Maszle DR, Ohto M, Preuss S et al. (2011) BBX32, an Arabidopsis B-Box Protein, Functions in Light Signaling by Suppressing HY5-Regulated Gene Expression and Interacting with STH2/BBX21. Plant Physiol 156:2109–2123. doi: 10.1104/PP.111.177139

Hornitschek P, Kohnen M V., Lorrain S, Rougemont J, Ljung K, López-Vidriero I, Franco-Zorrilla JM, Solano R, Trevisan M, Pradervand S et al. (2012) Phytochrome interacting factors 4 and 5 control seedling growth in changing light conditions by directly controlling auxin signaling. Plant J 71:699–711. doi: 10.1111/j.1365-313X.2012.05033.x

Hu W, Su Y-S and Lagarias JC (2009a) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant • 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009b) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Hu W, Su Y-S and Lagarias JC (2009c) A Light-Independent Allele of Phytochrome B Faithfully Recapitulates Photomorphogenic Transcriptional Networks. Mol Plant 2:166–182. doi: 10.1093/mp/ssn086

Humplík JF, Bergougnoux V and Van Volkenburgh E (2017) To Stimulate or Inhibit? That Is the Question for the Function of Abscisic Acid. Trends Plant Sci 22:830–841.

doi: 10.1016/j.tplants.2017.07.009

Jaillais Y and Vert G (2016) Brassinosteroid signaling and BRI1 dynamics went underground. Curr Opin Plant Biol 33:92–100. doi: 10.1016/J.PBI.2016.06.014

Jeong J and Choi G (2013) Phytochrome-interacting factors have both shared and distinct biological roles. Mol Cells 35:371–380. doi: 10.1007/s10059-013-0135-5

Jeong J, Kim K, Kim ME, Kim HG, Heo GS, Park OK, Park Y Il, Choi G and Oh E (2016) Phytochrome and ethylene signaling integration in Arabidopsis occurs via the transcriptional regulation of genes co-targeted by PIFs and EIN3. Front Plant Sci 7:1055. doi: 10.3389/fpls.2016.01055

Jiang K, Yung V, Chiba T and Feldman LJ (2017) Longitudinal patterning in roots: a GATA2–auxin interaction underlies and maintains the root transition domain. Planta 2017 2474 247:831–843. doi: 10.1007/S00425-017-2831-4

Jiao Y, Lau OS and Deng XW (2007a) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jiao Y, Lau OS and Deng XW (2007b) Light-regulated transcriptional networks in higher plants. Nat Rev Genet 8:217–230. doi: 10.1038/nrg2049

Jing Y and Lin R (2013) Plant Signaling & Behavior PICKLE is a repressor in seedling de-etiolation pathway. doi: 10.4161/psb.25026

Jing Y and Lin R (2020) Transcriptional regulatory network of the light signaling pathways. New Phytol 227:683–697. doi: 10.1111/nph.16602

Jing Y, Zhang D, Wang X, Tang W, Wang W, Huai J, Xu G, Chen D, Li Y and Lin R (2013) Arabidopsis chromatin remodeling factor PICKLE interacts with transcription factor HY5 to regulate hypocotyl cell elongation. Plant Cell 25:242–256. doi: 10.1105/tpc.112.105742

Job N and Datta S (2021) PIF3/HY5 module regulates BBX11 to suppress protochlorophyllide levels in dark and promote photomorphogenesis in light. New Phytol 230:190–204. doi: 10.1111/nph.17149

Job N, Yadukrishnan P, Bursch K, Datta S and Johansson H (2018) Two B-Box Proteins Regulate Photomorphogenesis by Oppositely Modulating HY5 through their Diverse C-Terminal Domains. Plant Physiol 176:2963–2976. doi: 10.1104/PP.17.00856

Khanna R, Huq E, Kikis EA, Al-Sady B, Lanzatella C and Quail PH (2004) A novel molecular recognition motif necessary for targeting photoactivated phytochrome signaling to specific basic helix-loop-helix transcription factors. Plant Cell 16:3033–3044. doi: 10.1105/tpc.104.025643

Kilian J, Whitehead D, Horak J, Wanke D, Weinl S, Batistic O, D'Angelo C, Bornberg-Bauer E, Kudla J and Harter K (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363. doi: 10.1111/j.1365-313X.2007.03052.x

Kim B, Jeong YJ, Corvalán C, Fujioka S, Cho S, Park T and Choe S (2014) Darkness and gulliver2/phyB mutation decrease the abundance of phosphorylated BZR1 to activate brassinosteroid signaling in Arabidopsis. Plant J 77:737–747. doi: 10.1111/tpj.12423

Kim J, Kang H, Park J, Kim W, Yoo J, Lee N, Kim J, Yoon T-Y and Choi G (2016) PIF1-Interacting Transcription Factors and Their Binding Sequence Elements Determine the in Vivo Targeting Sites of PIF1. doi: 10.1105/tpc.16.00125

Kircher S and Schopfer P (2012) Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. Proc Natl Acad Sci U S A 109:11217–11221. doi: 10.1073/pnas.1203746109

Kircher S and Schopfer P Photosynthetic sucrose acts as cotyledon-derived long-distance signal to control root growth during early seedling development in Arabidopsis. doi: 10.1073/pnas.1203746109

Ko D and Helariutta Y (2017) Shoot–Root Communication in Flowering Plants. Curr Biol 27:R973–R978. doi: 10.1016/j.cub.2017.06.054

Kondhare KR, Patil NS and Banerjee AK (2021) A historical overview of long-distance signalling in plants. J Exp Bot 72:4218–4236. doi: 10.1093/JXB/ERAB048

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010a) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/j.devcel.2010.05.008

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K et al. (2010b) Nitrate-regulated auxin transport by NRT1.1 defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937. doi: 10.1016/J.DEVCEL.2010.05.008

Kulkarni SR, Vaneechoutte D, de Velde J Van and Vandepoele K (2018) TF2Network: predicting transcription factor regulators and gene regulatory networks in Arabidopsis using publicly available binding site information. Nucleic Acids Res.

Kumar P, Montgomery CE and Kiss JZ (2008) The role of phytochrome C in gravitropism and phototropism in Arabidopsis thaliana. Funct Plant Biol 35:298–305. doi: 10.1071/FP08013

Kumari S, Yadav S, Patra D, Singh S, Sarkar AK and Panigrahi KCS (2019) Uncovering the molecular signature underlying the light intensity-dependent root development in Arabidopsis thaliana. BMC Genomics 20:1–23. doi: 10.1186/s12864-019-5933-5

Kurata T and Yamamoto KT (1997) Light-stimulated root elongation in Arabidopsis thaliana. J Plant Physiol 151:346–351. doi: 10.1016/S0176-1617(97)80263-5

Kurihara Y, Makita Y, Shimohira H and Matsui M (2020) Time-Course Transcriptome Study Reveals Mode of bZIP Transcription Factors on Light Exposure in Arabidopsis. Int J Mol Sci 21:1993. doi: 10.3390/ijms21061993

Kushwaha R, Singh A and Chattopadhyay S (2008) Calmodulin7 Plays an Important Role as Transcriptional Regulator in Arabidopsis Seedling Development. Plant Cell 20:1747–1759. doi: 10.1105/TPC.107.057612

Kwok SF, Piekos B, Miśera S and Deng XW (1996) A complement of ten essential and pleiotropic arabidopsis COP/DET/FUS genes is necessary for repression of photomorphogenesis in darkness. Plant Physiol 110:731–742. doi: 10.1104/pp.110.3.731

Lacek J, García-González J, Weckwerth W and Retzer K (2021a) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 22:12784. doi: 10.3390/ijms222312784

Lacek J, García-González J, Weckwerth W and Retzer K (2021b) Lessons Learned from the Studies of Roots Shaded from Direct Root Illumination. Int J Mol Sci 2021, Vol 22, Page 12784 22:12784. doi: 10.3390/IJMS222312784

Lau K, Podolec R, Chappuis R, Ulm R and Hothorn M (2019) Plant photoreceptors and their signaling components compete for COP 1 binding via VP peptide motifs. EMBO J 38:e102140. doi: 10.15252/embj.2019102140

Lau OS and Deng XW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trends Plant Sci 17:584–593. doi: 10.1016/J.TPLANTS.2012.05.004

Lau OS, Huang X, Charron J-B, Lee J-H, Li G and Deng XW (2011) Interaction of Arabidopsis DET1 with CCA1 and LHY in mediating transcriptional repression in the plant circadian clock. Mol Cell 43:703. doi: 10.1016/J.MOLCEL.2011.07.013

Laxmi A, Pan J, Morsy M and Chen R (2008a) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Laxmi A, Pan J, Morsy M and Chen R (2008b) Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. PLoS One 3:e1510. doi: 10.1371/journal.pone.0001510

Leasure CD, Tong H, Yuen G, Hou X, Sun X and He ZH (2009) Root UV-B sensitive2 acts with root UV-B sensitive1 in a root ultraviolet B-sensing pathway. Plant Physiol 150:1902–1915. doi: 10.1104/pp.109.139253

Lee H-J, Ha J-H, Kim S-G, Choi H-K, Kim ZH, Han Y-J, Kim J-I, Oh Y, Fragoso V, Shin K et al. (2016a) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal 9:1–9. doi: 10.1126/scisignal.aaf6530

Lee HJ, Ha JH, Kim SG, Choi HK, Kim ZH, Han YJ, Kim J Il, Oh Y, Fragoso V, Shin K et al. (2016b) Stem-piped light activates phytochrome B to trigger light responses in Arabidopsis thaliana roots. Sci Signal. doi: 10.1126/SCISIGNAL.AAF6530

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017a) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/j.tplants.2017.06.009

Lee HJ, Park YJ, Ha JH, Baldwin IT and Park CM (2017b) Multiple Routes of Light Signaling during Root Photomorphogenesis. Trends Plant Sci 22:803–812. doi: 10.1016/J.TPLANTS.2017.06.009

Lee S, Wang W and Huq E (2021) Spatial regulation of thermomorphogenesis by HY5 and PIF4 in Arabidopsis. Nat Commun 2021 121 12:1–12. doi: 10.1038/s41467-021-24018-7

Leivar P and Monte E (2014) PIFs: Systems Integrators in Plant Development. Plant Cell 26:56–78. doi: 10.1105/TPC.113.120857

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008a) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi:

10.1016/j.cub.2008.10.058

Leivar P, Monte E, Oka Y, Liu T, Carle C, Castillon A, Huq E and Quail PH (2008b) Multiple Phytochrome-Interacting bHLH Transcription Factors Repress Premature Seedling Photomorphogenesis in Darkness. Curr Biol 18:1815–1823. doi: 10.1016/J.CUB.2008.10.058

Leivar P and Quail PH (2011) PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci 16:19–28. doi: 10.1016/j.tplants.2010.08.003

Leivar P, Tepperman JM, Monte E, Calderon RH, Liu TL and Quail PH (2009) Definition of early transcriptional circuitry involved in light-induced reversal of PIF-imposed repression of photomorphogenesis in young Arabidopsis seedlings. Plant Cell 21:3535–3553. doi: 10.1105/tpc.109.070672

Lejay L, Wirth J, Pervent M, Cross JMF, Tillard P and Gojon A (2008) Oxidative pentose phosphate pathway-dependent sugar sensing as a mechanism for regulation of root ion transporters by photosynthesis. Plant Physiol 146:2036–2053. doi: 10.1104/pp.107.114710

Li L, Ljung K, Breton G, Schmitz RJ, Pruneda-Paz J, Cowing-Zitron C, Cole BJ, Ivans LJ, Pedmale U V, Jung HS et al. (2012) Linking photoreceptor excitation to changes in plant architecture. Genes Dev 26:785–790. doi: 10.1101/gad.187849.112

Li L and Sheen J (2016) Dynamic and diverse sugar signaling. Curr Opin Plant Biol 33:116–125. doi: 10.1016/j.pbi.2016.06.018

Li L, Xu J, Xu ZH and Xue HW (2005) Brassinosteroids stimulate plant tropisms through modulation of polar auxin transport in Brassica and Arabidopsis. Plant Cell 17:2738–2753. doi: 10.1105/tpc.105.034397

Li S, Yamada M, Han X, Ohler U and Benfey PN (2016) High-Resolution Expression Map of the Arabidopsis Root Reveals Alternative Splicing and lincRNA Regulation. Dev Cell 39:508–522. doi: 10.1016/j.devcel.2016.10.012

Li T, Lei W, He R, Tang X, Han J, Zou L, Yin Y, Lin H and Zhang D (2020) Brassinosteroids regulate root meristem development by mediating BIN2-UPB1 module in Arabidopsis. PLOS Genet 16:e1008883. doi: 10.1371/JOURNAL.PGEN.1008883

Li X, Cai W, Liu Y, Li H, Fu L, Liu Z, Xu L, Liu H, Xu T and Xiong Y (2017) Differential TOR activation and cell proliferation in Arabidopsis root and shoot apexes. Proc Natl Acad Sci 114:2765–2770. doi: 10.1073/pnas.1618782114

Li Y, Ende W Van den and Rolland F (2014) Sucrose Induction of Anthocyanin Biosynthesis Is Mediated by DELLA. Mol Plant 7:570–572. doi: 10.1093/MP/SST161

Liang S, Gao X, Wang Y, Zhang H, Yin K, Chen S, Zhang M and Zhao R (2020) Phytochrome-interacting factors regulate seedling growth through ABA signaling. Biochem Biophys Res Commun 526:1100–1105. doi: 10.1016/j.bbrc.2020.04.011

Liao Y, Smyth GK and Shi W (2014) featureCounts: an efficient general purpose program for assigning sequence reads to genomic features. Bioinformatics 30:923–930. doi: 10.1093/bioinformatics/btt656

Lilley JLS, Gee CW, Sairanen I, Ljung K and Nemhauser JL (2012) An endogenous carbon-sensing pathway Triggers increased auxin flux and hypocotyl elongation. Plant

Physiol 160:2261–2270. doi: 10.1104/pp.112.205575

Liu G, Gao S, Tian H, Wu W, Robert HS and Ding Z (2016) Local Transcriptional Control of YUCCA Regulates Auxin Promoted Root-Growth Inhibition in Response to Aluminium Stress in Arabidopsis. PLOS Genet 12:e1006360. doi: 10.1371/journal.pgen.1006360

Liu M-J, Wu S-H, Chen H-M and Wu S-H (2012) Widespread translational control contributes to the regulation of Arabidopsis photomorphogenesis. Mol Syst Biol 8:566. doi: 10.1038/msb.2011.97

Liu TY, Chang CY and Chiou TJ (2009) The long-distance signaling of mineral macronutrients. Curr Opin Plant Biol 12:312–319. doi: 10.1016/j.pbi.2009.04.004

Liu X, Liu R, Li Y, Shen X, Zhong S and Shi H (2017) EIN3 and PIF3 form an interdependent module that represses chloroplast development in buried seedlings. Plant Cell 29:3051–3067. doi: 10.1105/tpc.17.00508

Ljung K, Bhalerao RP and Sandberg G (2001) Sites and homeostatic control of auxin biosynthesis in Arabidopsis during vegetative growth. Plant J 28:465–474. doi: 10.1046/j.1365-313X.2001.01173.x

Ljung K, Hull AK, Celenza J, Yamada M, Estelle M, Normanly J and Sandberg G (2005) Sites and regulation of auxin biosynthesis in arabidopsis roots. Plant Cell 17:1090–1104. doi: 10.1105/tpc.104.029272

Ljung K, Nemhauser JL and Perata P (2015) New mechanistic links between sugar and hormone signalling networks. Curr Opin Plant Biol 25:130–137. doi: 10.1016/j.pbi.2015.05.022

Luo X-M, Lin W-H, Zhu S, Zhu J-Y, Sun Y, Fan X-Y, Cheng M, Hao Y, Oh E, Tian M et al. (2010) Integration of Light- and Brassinosteroid-Signaling Pathways by a GATA Transcription Factor in Arabidopsis. Dev Cell 19:872–883. doi: 10.1016/J.DEVCEL.2010.10.023

Lyu G, Li D, Li S and Hu H (2019) STO and GA negatively regulate UV-B-induced Arabidopsis root growth inhibition. Plant Signal Behav. doi: 10.1080/15592324.2019.1675471

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008a) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Singh A, Ram H and Chattopadhyay S (2008b) GBF1, a Transcription Factor of Blue Light Signaling in Arabidopsis, Is Degraded in the Dark by a Proteasome-mediated Pathway Independent of COP1 and SPA1 *. doi: 10.1074/jbc.M803437200

Mallappa C, Yadav V, Negi P and Chattopadhyay S (2006) A basic leucine zipper transcription factor, G-box-binding factor 1, regulates blue light-mediated photomorphogenic growth in Arabidopsis. J Biol Chem 281:22190–22199. doi: 10.1074/jbc.M601172200

Mancini E, Sanchez SE, Romanowski A, Schlaen RG, Sanchez-Lamas M, Cerdán PD and Yanovsky MJ (2016) Acute Effects of Light on Alternative Splicing in Light-Grown Plants. Photochem Photobiol 92:126–133. doi: 10.1111/php.12550

Marchant A, Bhalerao R, Casimiro I, Eklöf J, Casero PJ, Bennett M and Sandberg G (2002) AUX1 promotes lateral root formation by facilitating indole-3-acetic acid distribution between sink and source tissues in the Arabidopsis seedling. Plant Cell 14:589–597. doi: 10.1105/tpc.010354

Matsubayashi Y (2014) Posttranslationally Modified Small-Peptide Signals in Plants. http://dx.doi.org/101146/annurev-arplant-050312-120122 65:385–413. doi: 10.1146/ANNUREV-ARPLANT-050312-120122

McAdam SAM, Brodribb TJ and Ross JJ (2016a) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McAdam SAM, Brodribb TJ and Ross JJ (2016b) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. doi: 10.1111/pce.12669

McNellis TW, von Arnim AG, Araki T, Komeda Y, Misera S and Deng X-W (1994) Genetic and Molecular Analysis of an Allelic Series of cop1 Mutants Suggests Functional Roles for the Multiple Protein Domains. Plant Cell 6:487. doi: 10.2307/3869929

Meng LS, Wei ZQ, Cao XY, Tong C, Lv MJ, Yu F and Loake GJ (2020) Cytosolic invertase-mediated root growth is feedback regulated by a glucose-dependent signaling loop. Plant Physiol 184:895–908. doi: 10.1104/pp.20.00778

Metsalu T and Vilo J (2015) ClustVis: A web tool for visualizing clustering of multivariate data using Principal Component Analysis and heatmap. Nucleic Acids Res 43:W566–W570. doi: 10.1093/nar/gkv468

Miotto YE, da Costa CT, Offringa R, Kleine-Vehn J and Maraschin F dos S (2021) Effects of Light Intensity on Root Development in a D-Root Growth System. Front Plant Sci 12:1–9. doi: 10.3389/fpls.2021.778382

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019a) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Miotto YE, Tesser da Costa C, de Oliveira BH, Guzman F, Margis R, de Almeida RMC, Offringa R and dos Santos Maraschin F (2019b) Identification of root transcriptional responses to shoot illumination in Arabidopsis thaliana. Plant Mol Biol 101:487–498. doi: 10.1007/s11103-019-00918-7

Mo M, Yokawa K, Wan Y and Baluska F (2015a) How and why do root apices sense light under the soil surface? Front Plant Sci 6:1–8. doi: 10.3389/fpls.2015.00775

Mo M, Yokawa K, Wan Y and Baluška F (2015b) How and why do root apices sense light under the soil surface? Front Plant Sci 6:775. doi: 10.3389/fpls.2015.00775

Möglich A, Yang X, Ayers RA and Moffat K (2010) Structure and function of plant photoreceptors. Annu Rev Plant Biol 61:21–47. doi: 10.1146/annurev-arplant-042809-112259

Molas ML, Kiss JZ and Correll MJ (2006) Gene profiling of the red light signalling pathways in roots. J Exp Bot 57:3217–3229. doi: 10.1093/jxb/erl086

Moni A, Lee A-Y, Briggs WR and Han I-S (2015) The blue light receptor Phototropin 1 suppresses lateral root growth by controlling cell elongation. Plant Biol 17:34–40. doi: 10.1111/PLB.12187

Morais DA DR (2017) Bioconductor - transcriptogramer. In: Morais DA, Dalmolin RJ (2017). Transcr. Transcr. Anal. based Transcr. doi 10.18129/B9.bioc.transcriptogramer, R Packag. https://bioconductor.org/packages/release/bioc/html/transcriptogramer.html. Accessed 12 Dec 2018

Mostafavi S, Ray D, Warde-Farley D, Grouios C and Morris Q (2008) GeneMANIA: A real-time multiple association network integration algorithm for predicting gene function. Genome Biol 9:S4. doi: 10.1186/gb-2008-9-s1-s4

Murashige T and Skoog F (1962) A Revised Medium for Rapid Growth and Bio Assays with Tobacco Tissue Cultures. Physiol Plant 15:473–497. doi: 10.1111/J.1399-3054.1962.TB08052.X

Ni M, Tepperman JM and Quail PH (1998a) PIF3, a phytochrome-interacting factor necessary for normal photoinduced signal transduction, is a novel basic helix-loop-helix protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Ni M, Tepperman JM and Quail PH (1998b) PIF3, a Phytochrome-Interacting Factor Necessary for Normal Photoinduced Signal Transduction, Is a Novel Basic Helix-Loop-Helix Protein. Cell 95:657–667. doi: 10.1016/S0092-8674(00)81636-0

Notaguchi M, Wolf S and Lucas WJ (2012) Phloem-Mobile Aux/IAA Transcripts Target to the Root Tip and Modify Root ArchitectureF. J Integr Plant Biol 54:760–772. doi: 10.1111/J.1744-7909.2012.01155.X

Novák J, Černý M, Pavlů J, Zemánková J, Skalák J, Plačková L and Brzobohatý B (2014) Roles of proteome dynamics and cytokinin signaling in root to hypocotyl ratio changes induced by shading roots of arabidopsis seedlings. Plant Cell Physiol 56:1006–1018. doi: 10.1093/pcp/pcv026

Oh E, Kang H, Yamaguchi S, Park J, Lee D, Kamiya Y and Choi G (2009) Genome-wide analysis of genes targeted by PHYTOCHROME INTERACTING FACTOR 3-LIKE5 during seed germination in arabidopsis. Plant Cell 21:403–419. doi: 10.1105/tpc.108.064691

Oh E, Seo PJ and Kim J (2018) Signaling Peptides and Receptors Coordinating Plant Root Development. Trends Plant Sci 23:337–351. doi: 10.1016/J.TPLANTS.2017.12.007/ATTACHMENT/BD6CC66E-2342-46C7-8AA9-996959725A60/MMC2.PDF

Oh J, Park E, Song K, Bae G and Choi G (2019) PHYTOCHROME INTERACTING FACTOR 8 Inhibits Phytochrome A-mediated Far-red Light Responses in Arabidopsis. Plant Cell Adv Publ. doi: 10.1105/tpc.19.00515

Osterlund MT and Deng XW (1998) Multiple photoreceptors mediate the light-induced reduction of GUS-COP1 from Arabidopsis hypocotyl nuclei. Plant J 16:201–208. doi: 10.1046/j.1365-313X.1998.00290.x

Osterlund MT, Hardtke CS, Ning W and Deng XW (2000) Targeted destabilization of HY5 during light-regulated development of Arabidopsis. Nature 405:462–466. doi: 10.1038/35013076

Oyama T, Shimura Y and Okada K (1997) The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus- induced development of root and hypocotyl. Genes Dev 11:2983–2995. doi: 10.1101/gad.11.22.2983

Pacín M, Legris M and Casal JJ (2014) Rapid decline in nuclear COSTITUTIVE

PHOTOMORPHOGENESIS1 abundance anticipates the stabilization of its target ELONGATED HYPOCOTYL5 in the light. Plant Physiol 164:1134–1138. doi: 10.1104/pp.113.234245

Paik I, Chen F, Ngoc Pham V, Zhu L, Kim J Il and Huq E (2019) A phyB-PIF1-SPA1 kinase regulatory complex promotes photomorphogenesis in Arabidopsis. Nat Commun 10:1–17. doi: 10.1038/s41467-019-12110-y

Pan Y and Shi H (2017) Stabilizing the Transcription Factors by E3 Ligase COP1. Trends Plant Sci 22:999–1001. doi: 10.1016/j.tplants.2017.09.012

Park BS, Eo HJ, Jang I-C, Kang H-G, Song JT and Seo HS (2010) Ubiquitination of LHY by SINAT5 regulates flowering time and is inhibited by DET1. Biochem Biophys Res Commun 398:242–246. doi: 10.1016/j.bbrc.2010.06.067

Peng P, Yan Z, Zhu Y and Li J (2008) Regulation of the Arabidopsis GSK3-like Kinase BRASSINOSTEROID-INSENSITIVE 2 through Proteasome-Mediated Protein Degradation. Mol Plant 1:338–346. doi: 10.1093/MP/SSN001

Petersson S V., Johansson AI, Kowalczyk M, Makoveychuk A, Wang JY, Moritz T, Grebe M, Benfey PN, Sandberg G and Ljung K (2009) An Auxin Gradient and Maximum in the Arabidopsis Root Apex Shown by High-Resolution Cell-Specific Analysis of IAA Distribution and Synthesis. Plant Cell 21:1659–1668. doi: 10.1105/tpc.109.066480

Pham VN, Kathare PK and Huq E (2018a) Phytochromes and phytochrome interacting factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Kathare PK and Huq E (2018b) Phytochromes and phytochrome interacting factors. Plant Physiol 176:1025–1038. doi: 10.1104/pp.17.01384

Pham VN, Paik I, Hoecker U and Huq E (2020) Genomic evidence reveals SPA-regulated developmental and metabolic pathways in dark-grown Arabidopsis seedlings. Physiol Plant 169:380–396. doi: 10.1111/PPL.13095

Pham VN, Xu X and Huq E (2018c) Molecular bases for the constitutive photomorphogenic phenotypes in Arabidopsis. Development. doi: 10.1242/dev.169870

Podolec R and Ulm R (2018a) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Podolec R and Ulm R (2018b) Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. Curr Opin Plant Biol 45:18–25. doi: 10.1016/j.pbi.2018.04.018

Ponnu J and Hoecker U (2021a) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/FPLS.2021.662793/BIBTEX

Ponnu J and Hoecker U (2021b) Illuminating the COP1/SPA Ubiquitin Ligase: Fresh Insights Into Its Structure and Functions During Plant Photomorphogenesis. Front Plant Sci 12:486. doi: 10.3389/fpls.2021.662793

Ponnu J, Riedel T, Penner E, Schrader A and Hoecker U (2019) Cryptochrome 2 competes with COP1 substrates to repress COP1 ubiquitin ligase activity during Arabidopsis photomorphogenesis. Proc Natl Acad Sci U S A 116:27133–27141. doi: 10.1073/PNAS.1909181116/-/DCSUPPLEMENTAL

Prát T, Hajný J, Grunewald W, Vasileva M, Molnár G, Tejos R, Schmid M, Sauer M

and Friml J (2018) WRKY23 is a component of the transcriptional network mediating auxin feedback on PIN polarity. PLOS Genet 14:e1007177. doi: 10.1371/journal.pgen.1007177

Qi L, Liu S, Li C, Fu J, Jing Y, Cheng J, Li H, Zhang D, Wang X, Dong X et al. (2020) PHYTOCHROME-INTERACTING FACTORS Interact with the ABA Receptors PYL8 and PYL9 to Orchestrate ABA Signaling in Darkness. Mol Plant 13:414–430. doi: 10.1016/j.molp.2020.02.001

Qu Y, Liu S, Bao W, Xue X, Ma Z, Yokawa K, Baluška F and Wan Y (2017) Expression of root genes in Arabidopsis seedlings grown by standard and improved growing methods. Int J Mol Sci 18:951. doi: 10.3390/ijms18050951

Quail PH (2007) Phytochrome-regulated Gene Expression. J Integr Plant Biol. doi: 10.1111/j.1672-9072.2007.00422.x

Ram H, Priya P, Jain M and Chattopadhyay S (2014) Genome-wide DNA binding of GBF1 is modulated by its heterodimerizing protein partners, HY5 and HYH. Mol Plant 7:448–451. doi: 10.1093/mp/sst143

Ranjan A, Fiene G, Fackendahl P and Hoecker U (2011) The Arabidopsis repressor of light signaling SPA1 acts in the phloem to regulate seedling de-etiolation, leaf expansion and flowering time. Development 138:1851–1862. doi: 10.1242/dev.061036

Regnault T, Davière J-M, Wild M, Sakvarelidze-Achard L, Heintz D, Carrera Bergua E, Lopez Diaz I, Gong F, Hedden P and Achard P (2015) The gibberellin precursor GA_{12}acts as a long-distance growth signal in <italic>Arabidopsis</italic>. doi: 10.1038/NPLANTS.2015.73

Ritchie ME, Phipson B, Wu D, Hu Y, Law CW, Shi W and Smyth GK (2015) limma powers differential expression analyses for RNA-sequencing and microarray studies. Nucleic Acids Res. doi: 10.1093/nar/gkv007

Rolland F, Moore B and Sheen J (2002) Sugar sensing and signaling in plants. Plant Cell 14 Suppl:S185-205. doi: 10.1105/TPC.010455

Rosado D, Ackermann A, Spassibojko O, Rossi M and Pedmale U V (2021) WRKY transcription factors and ethylene signaling modify root growth during the shade-avoidance response. Plant Physiol. doi: 10.1093/PLPHYS/KIAB493

Rybarczyk-Filho JL, Castro MAA, Dalmolin RJS, Moreira JCF, Brunnet LG and de Almeida RMC (2011) Towards a genome-wide transcriptogram: the Saccharomyces cerevisiae case. Nucleic Acids Res 39:3005–16. doi: 10.1093/nar/gkq1269

Saijo Y, Sullivan J a, Wang H, Yang J, Shen Y, Rubio V, Ma L, Hoecker U and Deng XW (2003) The COP1-SPA1 interaction defines a critical step in phytochrome A-mediated regulation of HY5 activity. Genes Dev 17:2642–7. doi: 10.1101/gad.1122903

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013a) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sairanen I, Novák O, Pěnčík A, Ikeda Y, Jones B, Sandberg G and Ljung K (2013b) Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in arabidopsis. Plant Cell 24:4907–4916. doi: 10.1105/tpc.112.104794

Sakaguchi J, Matsushita T and Watanabe Y (2019) DWARF4 accumulation in root tips is enhanced via blue light perception by cryptochromes. Plant Cell Environ 42:1615–1629. doi: 10.1111/pce.13510

Sakaguchi J and Watanabe Y (2017a) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakaguchi J and Watanabe Y (2017b) Light perception in aerial tissues enhances DWF4 accumulation in root tips and induces root growth. Sci Rep 7:1–11. doi: 10.1038/s41598-017-01872-4

Sakamoto K and Briggs WR (2002) Cellular and Subcellular Localization of Phototropin 1. Plant Cell 14:1723–1735. doi: 10.1105/TPC.003293

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K and Yamaguchi-Shinozaki K (2006) Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. Plant Cell 18:1292–1309. doi: 10.1105/tpc.105.035881

Sakuraba Y, Kanno S, Mabuchi A, Monda K, Iba K and Yanagisawa S (2018) A phytochrome-B-mediated regulatory mechanism of phosphorus acquisition. Nat Plants 4:1089–1101. doi: 10.1038/s41477-018-0294-7

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007a) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Salisbury FJ, Hall A, Grierson CS and Halliday KJ (2007b) Phytochrome coordinates Arabidopsis shoot and root development. Plant J 50:429–438. doi: 10.1111/j.1365-313X.2007.03059.x

Sanchez SE, Rugnone ML and Kay SA (2020) Light Perception: A Matter of Time. Mol Plant 13(3):363–385. doi: 10.1016/j.molp.2020.02.006

Sassi M, Lu Y, Zhang Y, Wang J, Dhonukshe P, Blilou I, Dai M, Li J, Gong X, Jaillais Y et al. (2012) COP1 mediates the coordination of root and shoot growth by light through modulation of PIN1- and PIN2-dependent auxin transport in Arabidopsis. Development 139:3402–3412. doi: 10.1242/dev.078212

Schepetilnikov M, Makarian J, Srour O, Geldreich A, Yang Z, Chicher J, Hammann P and Ryabova LA (2017) GTPase ROP2 binds and promotes activation of target of rapamycin TOR in response to auxin. EMBO J 36:886–903. doi: 10.15252/embj.201694816

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992a) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Schindler U, Menkens AE, Beckmann H, Ecker JR and Cashmore AR (1992b) Heterodimerization between light-regulated and ubiquitously expressed Arabidopsis GBF bZIP proteins. EMBO J 11:1261–1273. doi: 10.1002/j.1460-2075.1992.tb05170.x

Senapati D, Kushwaha R, Dutta S, Maurya JP, Biswas S, Gangappa SN and Chattopadhyay S (2019) COP1 regulates the stability of CAM7 to promote photomorphogenic growth. Plant Direct 3:1–14. doi: 10.1002/pld3.144

Seo HS, Yang J, Ishikawa M and Bolle C (2003) LAF1 ubiquitination by COP1 controls photomorphogenesis and is stimulated by SPA1. Nature 8:995–999. doi: 10.1038/nature01751.1.

Shaikhali J, Norén L, De Dios Barajas-López J, Srivastava V, König J, Sauer UH, Wingsle G, Dietz KJ and Strand Å (2012) Redox-mediated mechanisms regulate DNA binding activity of the G-group of basic region leucine zipper (bZIP) transcription factors in Arabidopsis. J Biol Chem 287:27510–27525. doi: 10.1074/jbc.M112.361394

Shani E, Weinstain R, Zhang Y, Castillejo C, Kaiserli E, Chory J, Tsien RY and Estelle M (2013) Gibberellins accumulate in the elongating endodermal cells of Arabidopsis root. Proc Natl Acad Sci U S A 110:4834–4839. doi: 10.1073/pnas.1300436110

Shannon P, Markiel A, Ozier O, Baliga NS, Wang JT, Ramage D, Amin N, Schwikowski B and Ideker T (2003) Cytoscape: A software Environment for integrated models of biomolecular interaction networks. Genome Res 13:2498–2504. doi: 10.1101/gr.1239303

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015a) Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant Cell 27:189–201. doi: 10.1105/tpc.114.134775

Sheerin DJ, Menon C, Oven-Krockhaus S Zur, Enderle B, Zhu L, Johnen P, Schleifenbaum F, Stierhof YD, Huq E and Hiltbrunner A (2015b) Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in arabidopsis by reorganizing the COP1/SPA complex. Plant Cell 27:189–201. doi: 10.1105/tpc.114.134775

Shi H, Liu R, Xue C, Shen X, Wei N, Deng XW and Zhong S (2016) Seedlings Transduce the Depth and Mechanical Pressure of Covering Soil Using COP1 and Ethylene to Regulate EBF1/EBF2 for Soil Emergence. Curr Biol 26:139–149. doi: 10.1016/J.CUB.2015.11.053

Shi QM, Yang X, Song L and Xue HW (2011) Arabidopsis MSBP1 is activated by HY5 and HYH and is involved in photomorphogenesis and brassinosteroid sensitivity regulation. Mol Plant 4:1092–1104. doi: 10.1093/mp/ssr049

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009a) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Shin J, Kim K, Kang H, Zulfugarov IS, Bae G, Lee CH, Lee D and Choi G (2009b) Phytochromes promote seedling light responses by inhibiting four negatively-acting phytochrome-interacting factors. Proc Natl Acad Sci U S A 106:7660–7665. doi: 10.1073/pnas.0812219106

Silva-Navas J, Moreno-Risueno MA, Manzano C, Pallero-Baena M, Navarro-Neila S, Téllez-Robledo B, Garcia-Mina JM, Baigorri R, Gallego FJ and Del Pozo JC (2015) D-Root: A system for cultivating plants with the roots in darkness or under different light conditions. Plant J 84:244–255. doi: 10.1111/tpj.12998

Silva-Navas J, Moreno-Risueno MA, Manzano C, Téllez-Robledo B, Navarro-Neila

S, Carrasco V, Pollmann S, Gallego FJ and Del Pozo JC (2016) Flavonols mediate root phototropism and growth through regulation of proliferation-to-differentiation transition. Plant Cell 28:1372–1387. doi: 10.1105/tpc.15.00857

Singh A, Ram H, Abbas N and Chattopadhyay S (2012a) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Singh A, Ram H, Abbas N and Chattopadhyay S (2012b) Molecular interactions of GBF1 with HY5 and HYH proteins during light-mediated seedling development in Arabidopsis thaliana. J Biol Chem 287:25995–26009. doi: 10.1074/jbc.M111.333906

Skubacz A, Daszkowska-Golec A and Szarejko I (2016) The role and regulation of ABI5 (ABA-insensitive 5) in plant development, abiotic stress responses and phytohormone crosstalk. Front Plant Sci 7:1–18. doi: 10.3389/fpls.2016.01884

Spaninks K, van Lieshout J, van Ieperen W and Offringa R (2020) Regulation of Early Plant Development by Red and Blue Light: A Comparative Analysis Between Arabidopsis thaliana and Solanum lycopersicum. Front Plant Sci. doi: 10.3389/fpls.2020.599982

Spiegelman Z, Ham BK, Zhang Z, Toal TW, Brady SM, Zheng Y, Fei Z, Lucas WJ and Wolf S (2015) A tomato phloem-mobile protein regulates the shoot-to-root ratio by mediating the auxin response in distant organs. Plant J 83:853–863. doi: 10.1111/TPJ.12932

Srivastava AK, Senapati D, Srivastava A, Chakraborty M, Gangappa SN and Chattopadhyay S (2015) Short Hypocotyl in White Light1 Interacts with Elongated Hypocotyl5 (HY5) and Constitutive Photomorphogenic1 (COP1) and Promotes COP1-Mediated Degradation of HY5 during Arabidopsis Seedling Development. Plant Physiol 169:2922–2934. doi: 10.1104/PP.15.01184

Stewart JL, Maloof JN and Nemhauser JL (2011) PIF Genes Mediate the Effect of Sucrose on Seedling Growth Dynamics. PLoS One 6:e19894. doi: 10.1371/JOURNAL.PONE.0019894

Stracke R, Favory JJ, Gruber H, Bartelniewoehner L, Bartels S, Binkert M, Funk M, Weisshaar B and Ulm R (2010) The Arabidopsis bZIP transcription factor HY5 regulates expression of the PFG1/MYB12 gene in response to light and ultraviolet-B radiation. Plant, Cell Environ 33:88–103. doi: 10.1111/j.1365-3040.2009.02061.x

Sun N, Wang J, Gao Z, Dong J, He H, Terzaghi W, Wei N, Deng XW and Chen H (2016) Arabidopsis SAURs are critical for differential light regulation of the development of various organs. Proc Natl Acad Sci U S A 113:6071–6. doi: 10.1073/pnas.1604782113

Supek F, Bošnjak M, Škunca N and Šmuc T (2011) REVIGO Summarizes and Visualizes Long Lists of Gene Ontology Terms. PLoS One 6:e21800. doi: 10.1371/journal.pone.0021800

Swarup K, Benková E, Swarup R, Casimiro I, Péret B, Yang Y, Parry G, Nielsen E, De Smet I, Vanneste S et al. (2008) The auxin influx carrier LAX3 promotes lateral root emergence. Nat Cell Biol 10:946–954. doi: 10.1038/ncb1754

Szklarczyk D, Morris JH, Cook H, Kuhn M, Wyder S, Simonovic M, Santos A, Doncheva NT, Roth A, Bork P et al. (2017) The STRING database in 2017: quality-controlled protein-protein association networks, made broadly accessible. Nucleic

Acids Res 45:D362–D368. doi: 10.1093/nar/gkw937

Tabata R, Sumida K, Yoshii T, Ohyama K, Shinohara H and Matsubayashi Y (2014) Perception of root-derived peptides by shoot LRR-RKs mediates systemic N-demand signaling. Science 346:343–346. doi: 10.1126/SCIENCE.1257800

Tan H, Man C, Xie Y, Yan J, Chu J and Huang J (2019) A Crucial Role of GA-Regulated Flavonol Biosynthesis in Root Growth of Arabidopsis. Mol Plant 12:521–537. doi: 10.1016/j.molp.2018.12.021

Tang W, Ji Q, Huang Y, Jiang Z, Bao M, Wang H and Lin R (2013) FAR-RED ELONGATED HYPOCOTYL3 and FAR-RED IMPAIRED RESPONSE1 Transcription Factors Integrate Light and Abscisic Acid Signaling in Arabidopsis 1[C][W][OPEN]. doi: 10.1104/pp.113.224386

Tepperman JM, Hudson ME, Khanna R, Zhu T, Chang SH, Wang X and Quail PH (2004) Expression profiling of phyB mutant demonstrates substantial contribution of other phytochromes to red-light-regulated gene expression during seedling de-etiolation. Plant J 38:725–739. doi: 10.1111/j.1365-313X.2004.02084.x

Tepperman JM, Zhu T, Chang H-S, Wang X and Quail PH (2001) Multiple transcription-factor genes are early targets of phytochrome A signaling. Proc Natl Acad Sci 98:9437–9442. doi: 10.1073/pnas.161300998

Thieme CJ, Rojas-Triana M, Stecyk E, Schudoma C, Zhang W, Yang L, Miñambres M, Walther D, Schulze WX, Paz-Ares J et al. (2015) Endogenous Arabidopsis messenger RNAs transported to distant tissues. Nat Plants 2015 14 1:1–9. doi: 10.1038/nplants.2015.25

Tian T, Liu Y, Yan H, You Q, Yi X, Du Z, Xu W and Su Z (2017) agriGO v2.0: a GO analysis toolkit for the agricultural community, 2017 update. Nucleic Acids Res 45:W122–W129. doi: 10.1093/nar/gkx382

Tilbrook K, Arongaus AB, Binkert M, Heijde M, Yin R and Ulm R (2013) The UVR8 UV-B Photoreceptor: Perception, Signaling and Response. Arab B 11:e0164. doi: 10.1199/tab.0164

Tong H, Leasure CD, Hou X, Yuen G, Briggs W and He ZH (2008) Role of root UV-B sensing in Arabidopsis early seedling development. Proc Natl Acad Sci U S A 105:21039–21044. doi: 10.1073/pnas.0809942106

Ubeda-Tomás S, Federici F, Casimiro I, Beemster GTS, Bhalerao R, Swarup R, Doerner P, Haseloff J and Bennett MJ (2009) Gibberellin Signaling in the Endodermis Controls Arabidopsis Root Meristem Size. Curr Biol 19:1194–1199. doi: 10.1016/j.cub.2009.06.023

Ubeda-Tomás S, Swarup R, Coates J, Swarup K, Laplaze L, Beemster GTS, Hedden P, Bhalerao R and Bennett MJ (2008) Root growth in Arabidopsis requires gibberellin/DELLA signalling in the endodermis. Nat Cell Biol 10:625–628. doi: 10.1038/ncb1726

Unterholzner SJ, Rozhon W, Papacek M, Ciomas J, Lange T, Kugler KG, Mayer KF, Sieberer T and Poppenberger B (2015) Brassinosteroids are master regulators of gibberellin biosynthesis in Arabidopsis. Plant Cell 27:2261–2272. doi: 10.1105/tpc.15.00433

van Gelderen K, Kang C, Paalman R, Keuskamp D, Hayes S and Pierik R (2018a) Far-red light detection in the shoot regulates lateral root development through the HY5

transcription factor. Plant Cell 30:101–116. doi: 10.1105/tpc.17.00771

van Gelderen K, Kang C and Pierik R (2018b) Light Signaling, Root Development, and Plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Van Gelderen K, Kang C and Pierik R (2018) Light signaling, root development, and plasticity. Plant Physiol 176:1049–1060. doi: 10.1104/pp.17.01079

Vaseva II, Qudeimat E, Potuschak T, Du Y, Genschik P, Vandenbussche F and Van Der Straeten D (2018) The plant hormone ethylene restricts Arabidopsis growth via the epidermis. Proc Natl Acad Sci 115:E4130–E4139. doi: 10.1073/pnas.1717649115

von Arnim AG and Deng X-W (1994) Light inactivation of arabidopsis photomorphogenic repressor COP1 involves a cell-specific regulation of its nucleocytoplasmic partitioning. Cell 79:1035–1045. doi: 10.1016/0092-8674(94)90034-5

Vukašinović N, Wang Y, Vanhoutte I, Fendrych M, Guo B, Kvasnica M, Jiroutová P, Oklestkova J, Strnad M and Russinova E (2021) Local brassinosteroid biosynthesis enables optimal root growth. Nat Plants 7:619–632. doi: 10.1038/s41477-021-00917-x

Wan Y, Jasik J, Wang L, Hao H, Volkmann D, Menzel D, Mancuso S, Baluška F and Lin J (2012) The signal transducer NPH3 integrates the phototropin1 photosensor with PIN2-based polar auxin transport in Arabidopsis root phototropism. Plant Cell 24:551–565. doi: 10.1105/tpc.111.094284

Wan Y, Yokawa K and Baluška F (2019) Arabidopsis Roots and Light: Complex Interactions. Mol Plant 12:1428–1430. doi: 10.1016/j.molp.2019.10.001

Wan YL, Eisinger W, Ehrhardt D, Kubitscheck U, Baluska F and Briggs W (2008) The subcellular localization and blue-light-induced movement of phototropin 1-GFP in etiolated seedlings of Arabidopsis thaliana. Mol Plant 1:103–117. doi: 10.1093/mp/ssm011

Wang W, Chen Q, Botella JR and Guo S (2019) Beyond light: Insights into the role of constitutively photomorphogenic1 in plant hormonal signaling. Front Plant Sci 10:557. doi: 10.3389/FPLS.2019.00557/BIBTEX

Wang W, Paik I, Kim J, Hou X, Sung S and Huq E (2021) Direct phosphorylation of HY5 by SPA kinases to regulate photomorphogenesis in Arabidopsis. New Phytol 230:2311–2326. doi: 10.1111/nph.17332

Wei N, Kwok SF, von Arnim AG, Lee A, McNellis TW, Piekos B, Deng XW, Deng XW and Chen H (1994) Arabidopsis COP8, COP10, and COP11 Genes Are Involved in Repression of Photomorphogenic Development in Darkness. PLANT CELL ONLINE 6:629–643. doi: 10.1105/tpc.6.5.629

Wieczorek K, Golecki B, Gerdes L, Heinen P, Szakasits D, Durachko DM, Cosgrove DJ, Kreil DP, Puzio PS, Bohlmann H et al. (2006) Expansins are involved in the formation of nematode-induced syncytia in roots of Arabidopsis thaliana. Plant J 48:98–112. doi: 10.1111/J.1365-313X.2006.02856.X

Willige BC, Zander M, Yoo CY, Phan A, Garza RM, Trigg SA, He Y, Nery JR, Chen H, Chen M et al. (2021) PHYTOCHROME-INTERACTING FACTORs trigger environmentally responsive chromatin dynamics in plants. Nat Genet 53:955–961. doi: 10.1038/s41588-021-00882-3

Wilson K, Long D, Swinburne J and Coupland G (1996) A Dissociation insertion causes a semidominant mutation that increases expression of TINY, an arabidopsis gene related to APETALA2. Plant Cell 8:659–671. doi: 10.1105/tpc.8.4.659

Woerlen N, Allam G, Popescu A, Corrigan L, Pautot V and Hepworth SR (2017) Repression of BLADE-ON-PETIOLE genes by KNOX homeodomain protein BREVIPEDICELLUS is essential for differentiation of secondary xylem in Arabidopsis root. Planta 2017 2456 245:1079–1090. doi: 10.1007/S00425-017-2663-2

Wu Y, Shi L, Li L, Fu L, Liu Y, Xiong Y and Sheen J (2019) Integration of nutrient, energy, light, and hormone signalling via TOR in plants. J Exp Bot 70:2227–2238. doi: 10.1093/jxb/erz028

Xie Z, Nolan T, Jiang H, Tang B, Zhang M, Li Z and Yin Y (2019) The AP2/ERF transcription factor TINY modulates brassinosteroid-regulated plant growth and drought responses in arabidopsis. Plant Cell 31:1788–1806. doi: 10.1105/tpc.18.00918

Xiong Y, McCormack M, Li L, Hall Q, Xiang C and Sheen J (2013) Glucose–TOR signalling reprograms the transcriptome and activates meristems. Nature 496:181–186. doi: 10.1038/nature12030

Xiong Y and Sheen J (2012) Rapamycin and glucose-target of rapamycin (TOR) protein signaling in plants. J Biol Chem 287:2836–2842. doi: 10.1074/jbc.M111.300749

Xu D, Jiang Y, Li J, Holm M and Deng XW (2018) The B-Box Domain Protein BBX21 Promotes Photomorphogenesis. Plant Physiol 176:2365–2375. doi: 10.1104/PP.17.01305

Xu D, Jiang Y, Li J, Lin F, Holm M and Deng XW (2016) BBX21, an Arabidopsis B-box protein, directly activates HY5 and is targeted by COP1 for 26S proteasome-mediated degradation. Proc Natl Acad Sci 113:7655–7660. doi: 10.1073/PNAS.1607687113

Xu D, Li J, Gangappa SN, Hettiarachchi C, Lin F, Andersson MX, Jiang Y, Deng XW and Holm M (2014a) Convergence of Light and ABA Signaling on the ABI5 Promoter. PLoS Genet 10:e1004197. doi: 10.1371/journal.pgen.1004197

Xu P, Chen H, Li T, Xu F, Mao Z, Cao X, Miao L, Du S, Hua J, Zhao J et al. Blue light-dependent interactions of CRY1 with GID1 and DELLA proteins regulate gibberellin signaling and photomorphogenesis in Arabidopsis. doi: 10.1093/plcell/koab124

Xu W, Ding G, Yokawa K, Baluška F, Li QF, Liu Y, Shi W, Liang J and Zhang J (2013) An improved agar-plate method for studying root growth and response of Arabidopsis thaliana. Sci Rep 3:1–7. doi: 10.1038/srep01273

Xu X, Kathare PK, Pham VN, Bu Q, Nguyen A and Huq E (2017) Reciprocal proteasome-mediated degradation of PIFs and HFR1 underlies photomorphogenic development in Arabidopsis. Dev 144:1831–1840. doi: 10.1242/dev.146936

Xu X, Paik I, Zhu L, Bu Q, Huang X, Deng XW and Huq E (2014b) PHYTOCHROME INTERACTING FACTOR1 enhances the E3 ligase activity of CONSTITUTIVE PHOTOMORPHOGENIC1 to synergistically repress photomorphogenesis in Arabidopsis. Plant Cell 26:1992–2006. doi:

10.1105/tpc.114.125591

Xu X, Paik I, Zhu L and Huq E (2015a) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. Trends Plant Sci 20:641–650. doi: 10.1016/j.tplants.2015.06.010

Xu X, Paik I, Zhu L and Huq E (2015b) Illuminating Progress in Phytochrome-Mediated Light Signaling Pathways. doi: 10.1016/j.tplants.2015.06.010

Yadukrishnan P and Datta S (2021) Light and abscisic acid interplay in early seedling development. New Phytol 229:763–769. doi: 10.1111/NPH.16963

Yadukrishnan P, Rahul PV and Datta S (2020a) HY5 Suppresses, Rather Than Promotes, Abscisic Acid-Mediated Inhibition of Postgermination Seedling Development. Plant Physiol 184:574–578. doi: 10.1104/pp.20.00783

Yadukrishnan P, Rahul PV, Ravindran N, Bursch K, Johansson H and Datta S (2020b) CONSTITUTIVELY PHOTOMORPHOGENIC1 promotes ABA-mediated inhibition of post-germination seedling establishment. Plant J 103:481–496. doi: 10.1111/tpj.14844

Yang M, Li C, Cai Z, Hu Y, Nolan T, Yu F, Yin Y, Xie Q, Tang G and Wang X (2017a) SINAT E3 Ligases Control the Light-Mediated Stability of the Brassinosteroid-Activated Transcription Factor BES1 in Arabidopsis. Dev Cell 41:47. doi: 10.1016/J.DEVCEL.2017.03.014

Yang X, Song L and Xue H-W (2008) Membrane Steroid Binding Protein 1 (MSBP1) Stimulates Tropism by Regulating Vesicle Trafficking and Auxin Redistribution. Mol Plant 1:1077–1087. doi: 10.1093/MP/SSN071

Yang Y and Liu H (2020) Coordinated Shoot and Root Responses to Light Signaling in Arabidopsis. Plant Commun 1:100026. doi: 10.1016/j.xplc.2020.100026

Yang Y, Zhang L, Chen P, Liang T, Li X and Liu H (2020) UV-B photoreceptor UVR8 interacts with MYB73/MYB77 to regulate auxin responses and lateral root development. EMBO J. doi: 10.15252/embj.2019101928

Yang Z, Liu B, Su J, Liao J, Lin C and Oka Y (2017b) Cryptochromes Orchestrate Transcription Regulation of Diverse Blue Light Responses in Plants. Photochem Photobiol 93:112–127. doi: 10.1111/php.12663

Yeh C-M, Kobayashi K, Fujii S, Fukaki H, Mitsuda N and Ohme-Takagi M (2020) Blue Light Regulates Phosphate Deficiency-Dependent Primary Root Growth Inhibition in Arabidopsis. Front Plant Sci 0:1803. doi: 10.3389/FPLS.2019.01803

Yokawa K, Fasano R, Kagenishi T and BaluÅ¡ka F (2014) Light as stress factor to plant roots â€“ case of root halotropism. Front Plant Sci 5:1–9. doi: 10.3389/fpls.2014.00718

Yokawa K, Kagenishi T and Baluška F (2013) Root photomorphogenesis in laboratory-maintained Arabidopsis seedlings. Trends Plant Sci 18:117–119. doi: 10.1016/j.tplants.2013.01.002

Yokawa K, Kagenishi T, Kawano T, Mancuso S and Baluška F (2011) Illumination of arabidopsis roots induces immediate burst of ROS production. Plant Signal Behav 6:1460–1464. doi: 10.4161/psb.6.10.18165

Yu X, Liu H, Klejnot J and Lin C (2010) The Cryptochrome Blue Light Receptors. Arab B 8:e0135. doi: 10.1199/tab.0135

Yuan X, Xu P, Yu Y and Xiong Y (2020) Glucose-TOR signaling regulates PIN2 stability to orchestrate auxin gradient and cell expansion in Arabidopsis root. Proc Natl Acad Sci U S A 117:32223–32225. doi: 10.1073/pnas.2015400117

Zdanio M, Boron AK, Balcerowicz D, Schoenaers S, Markakis MN, Mouille G, Pintelon I, Suslov D, Gonneau M, Höfte H et al. (2020) The Proline-Rich Family Protein EXTENSIN33 Is Required for Etiolated Arabidopsis thaliana Hypocotyl Growth. Plant Cell Physiol 61:1191–1203. doi: 10.1093/PCP/PCAA049

Zeng J, Wang Q, Lin J, Deng K, Zhao X, Tang D and Liu X Arabidopsis cryptochrome-1 restrains lateral roots growth by inhibiting auxin transport. JI Plant Physiol 167:670–673. doi: 10.1016/j.jplph.2009.12.003

Zhang B, Holmlund M, Lorrain S, Norberg M, Bakó LS, Fankhauser C and Nilsson O (2017a) BLADE-ON-PETIOLE proteins act in an E3 ubiquitin ligase complex to regulate PHYTOCHROME INTERACTING FACTOR 4 abundance. Elife. doi: 10.7554/eLife.26759

Zhang H, He H, Wang X, Wang X, Yang X, Li L and Deng XW (2011a) Genome-wide mapping of the HY5-mediated genenetworks in Arabidopsis that involve both transcriptional and post-transcriptional regulation. Plant J 65:346–358. doi: 10.1111/J.1365-313X.2010.04426.X

Zhang Y, Li C, Zhang J, Wang J, Yang J, Lv Y, Yang N, Liu J, Wang X, Palfalvi G et al. (2017b) Dissection of HY5/HYH expression in Arabidopsis reveals a root-autonomous HY5-mediated photomorphogenic pathway. PLoS One 12:e0180449. doi: 10.1371/journal.pone.0180449

Zhang Y, Wang C, Xu H, Shi X, Zhen W, Hu Z, Huang J, Zheng Y, Huang P, Zhang KX et al. (2019) HY5 Contributes to Light-Regulated Root System Architecture Under a Root-Covered Culture System. Front Plant Sci 10:1490. doi: 10.3389/FPLS.2019.01490/BIBTEX

Zhang Z, Zhu J-Y, Roh J, Marchive C, Kim S-K, Meyer C, Sun Y, Wang W and Wang Z-Y (2016) TOR Signaling Promotes Accumulation of BZR1 to Balance Growth with Carbon Availability in Arabidopsis. Curr Biol 26:1854–1860. doi: 10.1016/j.cub.2016.05.005

Zhang ZL, Ogawa M, Fleet CM, Zentella R, Hu J, Heo JO, Lim J, Kamiya Y, Yamaguchi S and Sun TP (2011b) SCARECROW-LIKE 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in Arabidopsis. Proc Natl Acad Sci U S A 108:2160–2165. doi: 10.1073/pnas.1012232108

Zhong M, Zeng B, Tang D, Yang J, Qu L, Yan J, Wang X, Li X, Liu X and Zhao X (2021) The blue light receptor CRY1 interacts with GID1 and DELLA proteins to repress GA signaling during photomorphogenesis in Arabidopsis. Mol Plant 14:1328–1342. doi: 10.1016/J.MOLP.2021.05.011

Zhu L, Bu Q, Xu X, Paik I, Huang X, Hoecker U, Deng XW and Huq E (2015) CUL4 forms an E3 ligase with COP1 and SPA to promote light-induced degradation of PIF1. Nat Commun 6:1–10. doi: 10.1038/ncomms8245

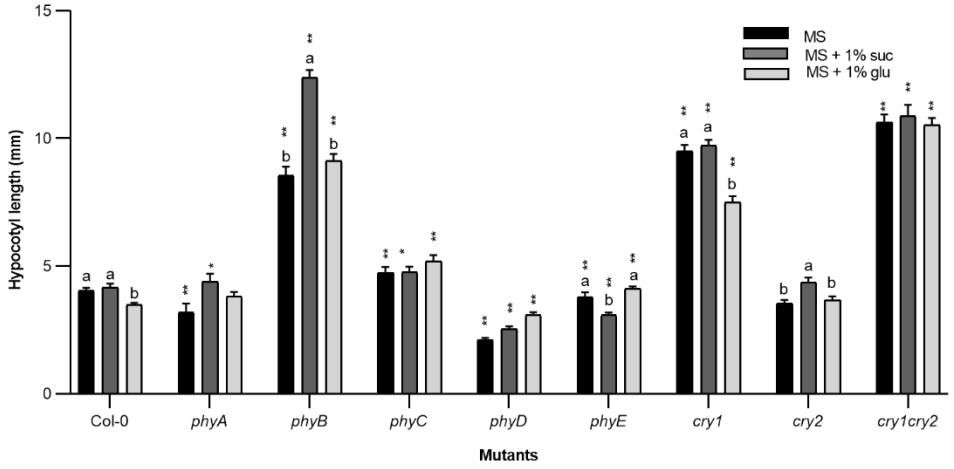
Zhang H, Han W, De Smet I, Talboys P, Loya R, Hassan A, Rong H, Jürgens G, Paul Knox J and Wang MH (2010) ABA promotes quiescence of the quiescent centre and suppresses stem cell differentiation in the Arabidopsis primary root meristem. Plant J 64:764–774. doi: 10.1111/j.1365-313X.2010.04367.x

Zhang Y, Wang C, Xu H, Shi X, Zhen W, Hu Z, Huang J, Zheng Y, Huang P, Zhang KX et al. (2019) HY5 Contributes to Light-Regulated Root System Architecture Under a Root-Covered Culture System. Front Plant Sci 10:1490. doi: 10.3389/FPLS.2019.01490/BIBTE

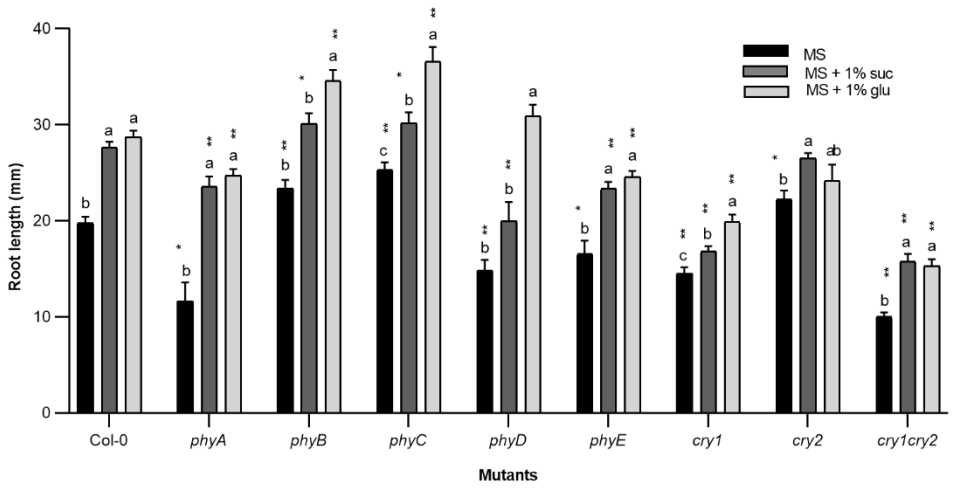
Anexos

1.

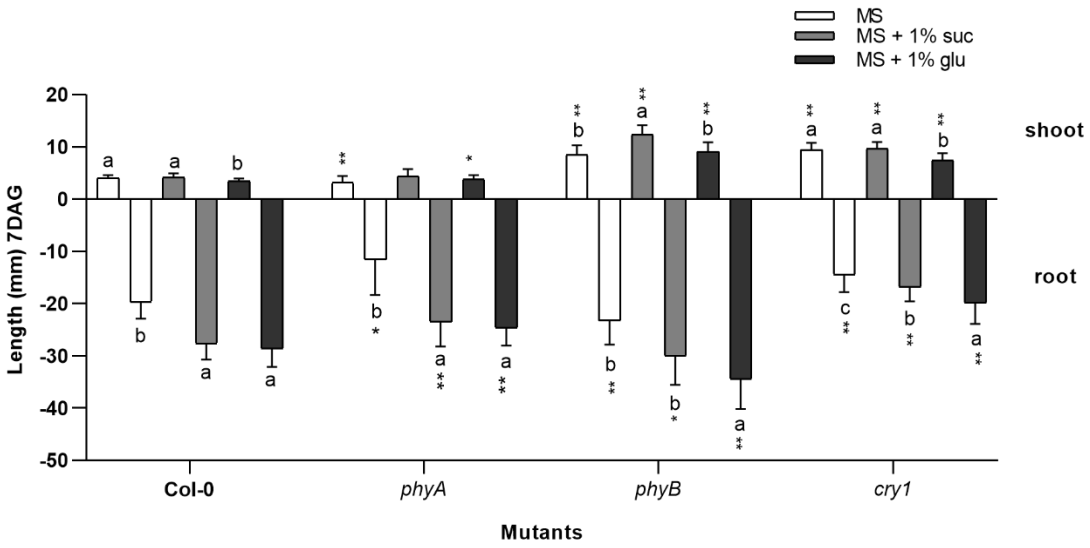
(A)



(B)

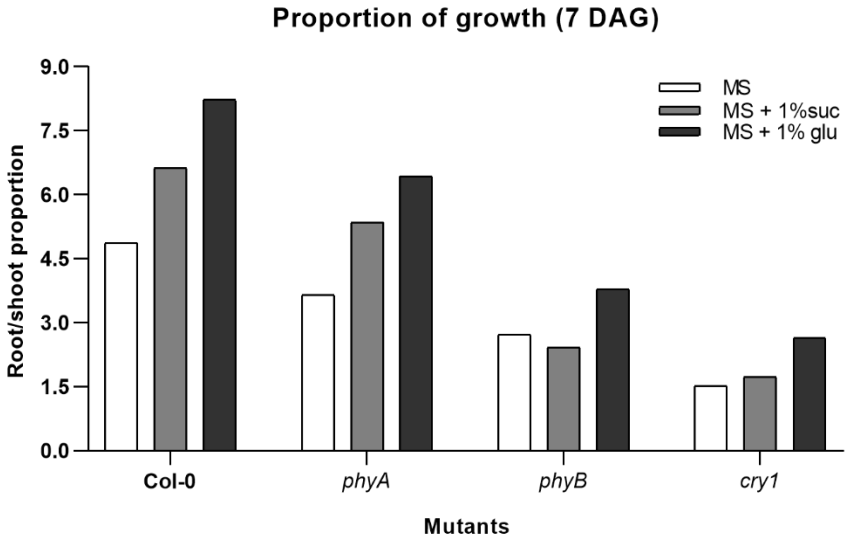


(C)



.

(D)



1. Fenótipos de mutantes estudados na condição LD = 7 e 10 dias com MS, ou MS + 1% SUC, ou MS + 1% GLUCOSE. WL (109,84 umol). Mensurações: **a** Comprimento de hipocótilo; **b** Comprimento da raiz; **c** Comprimento de hipocótilo e raiz de Col-0, *phyA*, *phyB* e *cry1*. **d** Proporção de crescimento (%) (relação raiz/hipocótilo). A significância estatística foi determinada pelo teste de Kruskal-Wallis com pós-teste de Dunn (* $p \leq 0,05$) e (** $p \leq 0,01$). As barras de erro indicam SD. As letras indicam comparações (ANOVA) dentro do genótipo, n = 20 ou mais.