



光信号与激素调控种子休眠和萌发研究进展

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摘要 休眠是种子植物在长期进化过程中产生的适应性性状, 通过抑制种子在不适宜的环境中萌发进而保证植物能够在逆境中生存。此外, 休眠有助于种子的长距离运输和扩散, 因此休眠对种子延续和物种保存具有重要意义。种子由休眠向萌发的发育转变不仅关系到物种的繁衍, 而且对保证农业生产中作物的产量和品质也具有重要作用。种子的休眠和萌发受到内源激素和外源光信号的共同调控。其中, 外源光信号主要通过调控内源ABA和GA的生物合成及信号转导进而调控种子休眠和萌发。该文系统综述了外源光信号和内源激素调控种子休眠和萌发的作用通路以及两类信号通路之间的交互作用, 旨在为农业生产中利用光和激素调控种子休眠与萌发提供参考。

关键词 种子休眠, 种子萌发, 光信号, 激素, 交互作用

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1 种子休眠和萌发相关研究背景

休眠是种子植物在长期进化过程中产生的适应性性状, 植物通过抑制种子萌发保证其在不适宜的环境中生存, 因此休眠对于种子能够“适时萌发”具有重要意义。在实际生产中, 为了保证种子的高萌发率, 大部分作物的种子往往呈现出较低的休眠水平(Lenser and Theißen, 2013)。然而过低的休眠水平导致成熟的种子在母体上直接萌发(“胎萌”)或出现穗发芽现象, 致使农业生产中种子的产量和质量下降(Simsek et al., 2014; Shu et al., 2015; Liu et al., 2019)。因此, 研究种子休眠和萌发的调控机制对农业生产具有重要指导意义。

种子休眠是指有活力的种子在适宜的条件下暂时不萌发的现象(Bewley, 1997; Finch-Savage and Leubner-Metzger, 2006)。种子的休眠包括休眠的诱导、维持和释放3个阶段(Shu et al., 2016)。成熟的种子释放休眠后, 在适宜的条件下即可萌发。*DOG1* (*DELAY OF GERMINATION 1*)在种子休眠诱导和维持中发挥重要作用。它既能通过抑制脱落酸(abscisic acid, ABA)通路的负调控因子——*AHG1* (*ABA HYPERSENSITIVE GERMINATION 1*)的磷

酸酶活性促进种子休眠(Nishimura et al., 2018); 也能通过调控响应赤霉素(gibberellin, GA)信号的细胞壁重塑相关基因的表达促进种子休眠(Graeber et al., 2014)。在种子吸胀初期, 胚乳中PHYB (PHYTOCHROME B)吸收远红光后以生理失活型存在, 此时PIF1 (PIF3-LIKE 5, PIL5)蛋白逐渐积累, 使胚乳中ABA水平逐渐升高。胚乳中的ABA信号能够释放到胚中并抑制GA的生物合成, 使种子保持休眠状态。随着种子吸胀时间的延长, 胚乳中ABA水平逐渐下调。此时胚中的PHYA介导远红光促进GA的生物合成, 进而促进种子萌发(Lee et al., 2012)。因此, 种子的休眠和萌发是两个相互独立的生物学过程。

研究表明, 种子的休眠及萌发受到内源激素和外源光信号的共同调控(Bassel, 2016; Shu et al., 2016)。本文主要从外源光信号和内源激素对种子休眠和萌发的调控以及两类信号通路的互作3方面对模式植物拟南芥(*Arabidopsis thaliana*)种子休眠和萌发的调控机制进行综述, 以期农业生产中利用光和激素调控种子休眠与萌发提供参考。

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2 激素调控种子休眠和萌发

2.1 ABA-GA动态平衡是调控种子休眠和萌发的关键

激素在种子休眠和萌发过程中发挥重要调控作用。其中, ABA和GA在调控种子休眠和萌发行使主要功能。ABA促进种子休眠, 而GA促进种子萌发(Shu et al., 2016; Née et al., 2017a)。在种子成熟过程中, ABA在种子内逐渐积累, 使种子的休眠水平逐渐升高。相比之下, 当种子受到吸胀或层积处理时, ABA含量逐渐降低, GA含量逐渐升高, 使种子萌发。与野生型种子相比, ABA合成缺陷突变体种子萌发更快(Frey et al., 2012); 而过表达ABA合成基因的种子以及ABA代谢突变体种子保持较高的休眠水平(Matakiadis et al., 2009; Martinez-Andújar et al., 2011; Nonogaki et al., 2014), 表明ABA能够通过其生物合成通路调控种子的休眠和萌发。ABA信号通过PYR/PYL/RCAR (PYRABACTIN RESISTANCE 1/PYR-LIKE PROTEINS/REGULATORY COMPONENTS OF ABA RECEPTORS)-PP2C (PROTEIN PHOSPHATASE 2C)-SnRKs (SNF1-RELATED PROTEIN KINASES)级联反应向下传递(Cutler et al., 2010; Hubbard et al., 2010)。目前鉴定到的PP2C类蛋白包括ABI1 (ABSCISIC ACID INSENSITIVE 1)、ABI2、HON (HONSU)和RDO5 (REDUCED DORMANCY 5)。其中, ABI1和ABI2通过与ABA信号受体蛋白PYR/PYL/RCAR互作进而抑制ABA信号转导(Ma et al., 2009; Park et al., 2009)。HON蛋白能够通过抑制ABA信号转导及促进GA信号转导抑制种子休眠(Kim et al., 2013), 说明HON能够整合ABA和GA信号以调控种子休眠。*rdo5*突变体的休眠水平降低, 但其ABA含量和ABA敏感性并未发生显著变化(Xiang et al., 2014), 说明RDO5通过不依赖ABA的途径调控种子休眠。ABI3、ABI4和ABI5是ABA信号通路下游的关键组分, 能够抑制种子萌发、促进种子休眠(Bentsink and Koornneef, 2008; Kanai et al., 2010; Shu et al., 2013)。响应ABA信号的R2R3型MYB转录因子MYB96通过调控ABI4以及ABA合成相关基因NCED2 (9-CIS-EPOXYCAROTENOID DIOXYGENASE 2)和NCED6的转录进而促进种子休眠、抑制种子萌发(Lee et al., 2015a, 2015b)。上述

研究表明, ABA不仅通过其生物合成通路调控种子的休眠和萌发, 还能以ABA信号的形式发挥作用。

GA能够通过抑制ABA诱导的种子休眠促进种子萌发(Gubler et al., 2005; Graeber et al., 2012)。在植物体内, 具有生物活性的GA主要包括GA₁和GA₄, 它们通过软化种皮、促进胚乳层细胞的水解和胚的生长打破种子休眠, 进而促进种子萌发(Holdsworth et al., 2008)。GA缺失突变体*ga1* (*gibberellic acid-requiring 1*)和*ga2*表现出强烈的休眠表型, 需要外源施加GA方可萌发(Lee et al., 2002; Shu et al., 2013)。GA20ox (GA 20-OXIDASE)和GA3ox基因编码参与GA生物合成的氧化酶; GA2ox编码的GA2-氧化酶主要参与GA的代谢过程。在PHYB-off条件下, *ga2ox*突变体萌发水平升高(Oh et al., 2006; Yamau-chi et al., 2007)。上述研究结果表明, GA能通过其生物合成通路调控种子的休眠和萌发。在GA信号转导过程中, DELLA蛋白扮演着重要角色, 它能响应GA信号快速降解, 对GA信号转导起限速作用(Silverstone et al., 1998; Itoh et al., 2002; Zentella et al., 2007; Nemoto et al., 2017)。GA受体蛋白GID1 (GA-INSENSITIVE DWARF 1)能够负调控DELLA蛋白的稳定性, 促进GA信号转导(Davière and Achard, 2013)。拟南芥SLY1 (SLEEPY1)和水稻GID2 (GA-INSENSITIVE DWARF2)是SCF聚合体中的F-box亚基, 依赖其C端的GGF和LSL基序与DELLA蛋白C端VHIID和LHR2基序结合, 促进DELLA多聚泛素化(Hirano et al., 2010; Ariizumi et al., 2011)。研究表明, DELLA蛋白GAI (GA-INSENSITIVE)能够通过抑制TCP14 (TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR 14)和TCP15的表达减缓细胞周期的进程, 最终使种子保持休眠状态(Resentini et al., 2015)。作为转录调节子, DELLA如何实现对下游基因的转录调控? 有研究指出, DELLA能够通过与染色质重塑因子互作调控下游基因的转录。DELLA蛋白RGL2 (RGA-LIKE 2)和RGL3与染色质重塑因子SWI3C (SWITCH3C)发生互作, 进而影响GID1a以及GA3ox基因的转录(Sarnowska et al., 2013)。此外, DELLA还能通过与种子萌发相关转录因子互作进而实现其对萌发的调控。RGL2通过与转录因子NF-YC互作, 诱导下游ABI5的转录, 进而抑制种子萌发(Liu et al., 2016)。此外,

RGL2还能通过与转录因子DOF6 (BINDING1 ZINC FINGER 6)互作诱导GATA12的表达, 进而促进种子休眠(Ravindran et al., 2017)。DELLA通过与ICE1 (INDUCER OF CBF EXPRESSION 1)互作解除其对ABA响应基因EM1 (LATE EMBRYOGENESIS ABUNDANT 1)和EM6的转录抑制作用, 最终抑制种子萌发(Hu et al., 2019)。

综上所述, ABA和GA通过其生物合成通路和信号转导通路拮抗地调控种子休眠与萌发, 两者之间的动态平衡是决定种子保持休眠还是萌发的关键。

2.2 多种激素参与调控种子休眠和萌发

除ABA和GA之外, 种子的休眠和萌发还受到7类激素的调控, 包括生长素(auxin)、乙烯(ethylene, ET)、油菜素内酯(brassinosteroids, BRs)、水杨酸(salicylic acid, SA)、茉莉酸(jasmonic acid, JA)、细胞分裂素(cytokinins, CTKs)和独脚金内酯(strigolactones, SLs)。这些激素均通过影响ABA或GA通路间接调控种子的休眠和萌发(Shu et al., 2016; Née et al., 2017a)。生长素能够通过调控ABI3的转录水平影响种子的休眠和萌发。当内源生长素水平升高时, 生长素信号通路中的负调控因子AXR2/3 (AUXIN- RESISTANT 2/3)发生降解。此时AXR2/3对响应生长素信号的ARF10 (AUXIN RESPONSE FACTOR 10)和ARF16基因的转录抑制作用被解除, 而ARF10和ARF16能够激活ABI3的表达, 从而使种子保持休眠状态(Liu et al., 2013a)。然而, ARF10和ARF16不能直接结合在ABI3的启动子上(Liu et al., 2013a), 因此有待深入研究以揭示完整的生长素信号传递链。ET能够通过ABA生物合成和信号转导通路调控种子萌发(Cheng et al., 2009; Linkies et al., 2009; Corbineau et al., 2014), 但具体机制还不清楚。在盐胁迫条件下, ET受体蛋白ETR1 (ETHYLENE RESPONSE 1)和ETR2可能通过不依赖ET信号的通路调控ABA生物合成, 进而影响种子萌发(Wilson et al., 2014)。最近的研究发现, ETR1通过解除ERF12 (ETHYLENE RESPONSE FACTOR 12)/TPL (TOPLESS)模块对DOG1基因的转录抑制作用而促进DOG1的转录, 进而促进种子休眠(Li et al., 2019)。BR通过依赖MFT (MOTHER OFFT AND TFL 1)的途径拮抗ABA

信号转导通路, 促进种子萌发(Xi and Yu, 2010; Xi et al., 2010)。进一步的研究发现, BR信号通路中的负调控因子——BIN2 (BRASSINOSTEROID INS-ENSITIVE 2), 能够磷酸化并稳定ABI5蛋白, 进而促进ABA信号转导。BR信号通过抑制BIN2-ABI5互作解除ABA对种子萌发的抑制作用(Hu and Yu, 2014)。SA在调控种子萌发上发挥双重作用。在正常生长条件下, SA通过抑制GA诱导的 α 淀粉酶编码基因的表达抑制种子萌发(Xie et al., 2007); 而在高盐胁迫下, SA通过其它通路促进种子萌发(Lee et al., 2010)。CTKs通过抑制ABI5的转录或促进ABI5蛋白的降解拮抗ABA效应, 从而促进种子萌发(Wang et al., 2011; Guan et al., 2014)。外源施加JA能够延迟种子萌发(Nambara et al., 2010), 表明JA能够抑制种子萌发。有研究表明, JA通过抑制ABA合成相关基因的表达、促进ABA代谢相关基因的表达拮抗ABA, 从而促进种子萌发(Jacobsen et al., 2013)。JAZ3 (JASMONATE-ZIM DOMAIN PROTEIN 3)通过与ABI5互作抑制ABI5的转录激活活性, 进而促进种子萌发(Ju et al., 2019)。目前关于JA调控种子萌发功能上存在矛盾的原因还有待深入探究。SLs通过降低ABA/GA值促进种子萌发(Toh et al., 2012)。此外, SLs信号通路组分也能参与调控种子萌发, 如SMAX1 (SUPPRESSOR OF MORE AXILLARY GROWTH2 1) (Stanga et al., 2013)。但目前SLs调控种子萌发的具体机制还不清楚。综上, 生长素、ET、BR、CTKs、JA和SLs通过调控ABA生物合成或信号通路调控种子的休眠和萌发。然而生长素、ET、BR、CTKs、JA与GA之间的交互作用还有待深入研究。

3 光信号调控种子休眠和萌发

种子既是上一轮生命周期的终点, 也是下一轮生命周期的起点。因此, 种子能否适时完成休眠向萌发的发育转变对于植物整个生命周期能否顺利完成起着决定性作用。作为影响种子休眠和萌发的环境因子之一, 光信号能够促进种子萌发、抑制种子休眠。那么, 种子如何识别外源光信号, 并将其转变为发育信号进而调控休眠和萌发? 下文主要针对光信号调控种子休眠和萌发的研究进展进行系统综述。

3.1 光信号转导通路

植物依赖光受体蛋白识别外源环境中的光信号。根据吸收光谱成分的不同可以将植物光受体分为3类: 吸收红光/远红光(600–750 nm)的光敏色素(PHY) (Quail et al., 1995)、吸收蓝光/UV-A (320–500 nm)的向光素(PHOTOTROPIN, PHOT)、隐花色素(CRYPTOCHROME, CRY)和ZTL (ZEITLUPE)/FK-F1 (FLAVIN BINDING KELCH REPEAT F-BOX 1)/LKP2 (LOV KELCH PROTEIN 2)基因家族(Briggs and Huala, 1999; Cashmore, 2003; Lin and Shalitin, 2003)以及吸收UV-B (280–320 nm)的UVR8 (UV RESISTANCE LOCUS 8) (Rizzini et al., 2011)。近年来, 人们在PHY、CRY以及UVR8介导的光信号转导通路研究中取得了重要进展。其中, PHY和CRY均能通过与转录因子互作进而直接调控下游基因的转录。此类信号通路主要包括: PHYB-PIFs通路、CRY-PIF4/5通路、CRY2-CIBs (CRYPTOCHROME-INTERACTING BASIC-HELIX-LOOP-HELIX)信号通路、PHYA-AUX/IAA (AUXIN/INDOLE-3-ACETIC ACID)信号通路以及PHYB/CRY1-AUX/IAA信号通路。PHYB通过与PIFs互作促使PIFs发生泛素化降解, 进而调控PIFs下游基因的转录(Oh et al., 2006); PHYA/B和CRY1/2通过与PIFs互作进而影响PIFs对靶基因的转录调控(Chen et al., 2014; Pedmale et al., 2016; Ma et al., 2016); CRY2通过与CIBs蛋白互作提高CIBs对*FT*基因的激活水平(Liu et al., 2008a, 2013b; 马朝峰和戴思兰, 2019); PHYA通过与生长素信号转导通路的负调控因子AUX/IAA互作稳定其蛋白活性, 进而调控植物的避荫反应(Yang et al., 2018a); PHYB和CRY1分别介导红光和蓝光, 通过抑制AUX/IAA的泛素化降解抑制生长素信号转导(Xu et al., 2018)。此外, PHY和CRY亦可通过与COP1 (CONSTITUTIVE PHOTOMORPHO-GENESIS 1)互作抑制其E3泛素连接酶活性, 促进COP1靶蛋白的积累, 从而间接调控基因转录(Hardtke et al., 2000; Seo et al., 2003; Jang et al., 2005, 2015; Liu et al., 2008b; Luo et al., 2014)。在UVR8介导的信号通路中, COP1作为正调控因子发挥作用。UVR8通过与COP1互作促进下游HY5 (LONG HYPOCOTYL 5)蛋白的积累, 进而诱导光响应基因的转录(Huang et al., 2013; 景艳军和林荣呈, 2017)。最近的研究发现,

RUP1 (REPRESSOR OF UV-B PHOTOMORPHO-GENESIS 1)和RUP2作为UVR8介导的信号转导通路中的负调控因子, 能够促进HY5蛋白降解; 而COP1能够与RUP1/RUP2互作介导其泛素化降解。RUP1/RUP2-HY5以及COP1-RUP1/RUP2构成植物响应UVB信号的分子开关(Ren et al., 2019)。此外, UVR8通过与BES1 (BRI1-EMS-SUPPRESSOR 1)/BIM1 (BES1-INTERACTING MYC-LIKE 1)蛋白互作抑制BES1/BIM1对下游BR响应基因的转录激活活性(Liang et al., 2018)。UVR8通过与WRKY36 (WRKY DNA-BINDING PROTEIN 36)互作进而解除WRKY36对HY5的转录抑制作用, 最终促进HY5转录和植物光形态建成(Yang et al., 2018b)。

3.2 PHY与种子休眠和萌发

PHY在黑暗条件下以生理失活的红光吸收型(Pr)存在, 吸收红光之后转变成其生理激活型(Pfr)。两种光吸收型的PHY在Pr和Pfr两种状态间相互转变。早在20世纪50年代, 研究人员以莴苣(*Lactuca sativa*)种子为材料, 研究红光和远红光对其萌发的影响。结果表明红光促进种子萌发, 而远红光能够逆转红光的作用(Borthwick et al., 1952)。红光和远红光对种子萌发的可逆调控暗示着PHY参与调控种子的萌发过程(Shinomura et al., 1994; Hennig et al., 2002)。拟南芥PHY基因家族包含5个成员——PHYA-PHYE (Sharrock and Quail, 1989; Clack et al., 1994)。种子萌发受到PHYA和PHYB的调控。其中, PHYB发挥主要功能。研究表明, PHYA蛋白在干种子中表达量很低, 随着种子在黑暗条件下吸胀时间的延长其蛋白表达量逐渐增加, 说明PHYA参与调控种子的萌发过程(Shinomura et al., 1996)。PHYA主要在种子吸胀后期通过介导红光和远红光条件下的极低辐照度反应(VLFR)和远红光下的高辐照度反应(FR-HIR)调控种子萌发。相比之下, PHYB在干种子和吸胀种子中表达量均很高, 能够在种子吸胀初期(几个小时以内)介导红光和远红光下的低辐照度反应(LFR)调控种子萌发(Seo et al., 2009; Li et al., 2011)。除了PHYA和PHYB外, PHYE也参与光调控的种子萌发过程, 而且三者 in 调控种子萌发方面功能冗余(Hennig et al., 2002)。最近有研究表明, PHYB除了调控种子萌发, 还参与调控种子休眠(Jiang et al., 2016)。

3.3 调控种子休眠和萌发的主要光信号因子

PHY作为光信号的受体蛋白, 如何调控下游基因的转录并影响种子休眠和萌发? 研究表明, 在外源光信号的刺激下, PHY由细胞质转移至细胞核。PHY依赖一系列光信号因子调控种子休眠和萌发(de Wit et al., 2016)。

拟南芥基因组编码8个PIFs (PHYTOCHROME-INTERACTING FACTORS, PIF1–PIF8)蛋白。其中, PIF1和PIF6分别调控种子萌发和休眠(Oh et al., 2006; Penfield et al., 2010)。PIF1作为种子萌发的负调控因子, 能够将内源激素和外源光信号连接起来, 在光介导的种子萌发过程中发挥关键作用。研究表明, 外源光信号通过调控PIF1蛋白稳定性或转录活性影响其对下游基因的转录调控。光照条件下, PIF1蛋白能够通过与Pfr形式的PHY互作, 进而发生泛素化降解(Oh et al., 2004; 2006); HFR1 (LONG HYPOCOTYL IN FAR-RED 1)通过PIF1的C端与之发生互作, 进而干扰PIF1的转录活性, 最终促进种子萌发(Shi et al., 2013)。在黑暗条件下, DET1 (DE-ETIOLOGATED 1)和COP10以一种未知的机制稳定PIF1蛋白的活性(Shi et al., 2015)。bHLH转录因子SPT (SPATULA)作为种子萌发的正调控因子, 在种子萌发中也发挥重要作用(Vaistij et al., 2018)。此外, SPT还能调控种子休眠。然而, 在不同的生态型背景下SPT调控种子休眠的功能不同。在Ler背景下, SPT抑制种子休眠; 而在Col背景下, SPT促进种子休眠(Vaistij et al., 2013)。外源光信号能否影响SPT对下游基因的转录调控? 目前还需阐释PHY调控SPT转录活性的作用机制, 以解答上述问题。最近的研究表明, 昼夜节律钟的关键组分CCA1 (CIRCADIAN CLOCK ASSOCIATED 1)、LHY (LATE ELONGATED HYPOCOTYL)以及RVE1 (REVEILLE1)均能介导外源光信号调控的种子休眠(Penfield and Hall, 2009; Jiang et al., 2016)。此外, RVE1还能调控种子萌发(Jiang et al., 2016)。IMB1 (IMBIBITION-INDUCIBLE1)是染色质域蛋白家族成员, 在PHYA介导的种子萌发中发挥作用。IMB1在干种子中的表达量很低, 随着种子吸胀呈现上调表达, 暗示IMB1能够促进种子萌发(Duque and Chua, 2003)。目前, 关于IMB1调控PHYA介导的种子萌发的分子机制还有待深入探究。CSN (COP9 SIGNALO-

SOME)蛋白复合体是一类保守的蛋白复合体, 能够调控RING型E3泛素化连接酶的活性。CSN包含8个亚基(CSN1–CSN8) (Wei and Deng, 2003)。其中, CSN1和CSN5参与调控种子萌发。*csn1-10*和*csn5a-1*突变体呈现出种子延迟萌发的表型(Jin et al., 2018)。

3.4 光信号通过调控激素的生物合成影响种子休眠和萌发

PIF1能够介导外源光信号, 通过调控ABA和GA的生物合成调控种子萌发(图1A)。统计Col和*pif1*突变体的种子在PHYB-on和PHYB-off条件下的萌发率, 发现Col只能在PHYB-on条件下萌发, *pif1*在PHYB-on和PHYB-off条件下均能萌发; 使用GA合成抑制剂PAC (paclobutrazol)能够抑制Col和*pif1*萌发。上述研究结果表明, PIF1在PHYB介导的种子萌发过程中发挥重要作用, 它可能通过调控GA的生物合成抑制种子萌发。进一步研究证实, PIF1能够抑制GA合成相关基因GA3ox1和GA3ox2的表达, 促进GA代谢相关基因GA2ox2的表达, 进而下调内源GA₄的水平, 抑制种子萌发(Oh et al., 2006)。与*ga1*单突变体相比, *pif1/ga1*双突变体中ABA合成相关基因的表达下调; 而ABA代谢相关基因的表达水平上调, 致使*pif1/ga1*双突变体中ABA的水平降低, 表现出持续萌发的表型(Oh et al., 2007)。那么, PIF1如何调控ABA和GA生物合成相关基因的转录? 后续的研究发现, PIF1能够通过诱导SOM (SOMNUS)和DAG1 (DOF AFFECTING GERMINATION 1)的转录间接抑制GA合成、促进ABA合成, 最终抑制种子萌发(Kim et al., 2008; Gabriele et al., 2010) (图1A)。其中, CCCH型锌指蛋白SOM通过调控组蛋白精氨酸去甲基化酶编码基因JM20 (JUMONJI 20)和JM22的表达, 进而影响GA合成基因GA3ox1和GA3ox2的甲基化水平, 最终抑制种子的萌发过程。此外, SOM还能激活GA代谢基因GA2ox2以及ABA合成基因ABA1 (ABA-DEFICIENT 1)、NCED6和NCED9的表达, 抑制ABA代谢基因CYP707A2表达, 从而抑制GA生物合成、促进ABA合成, 最终抑制种子萌发(Kim et al., 2008; de Wit et al., 2016)。包含Dof结构域的DAG1蛋白直接结合在GA3ox1启动子上抑制其表达, 进而抑制种子萌发(Gabriele et al., 2010)。

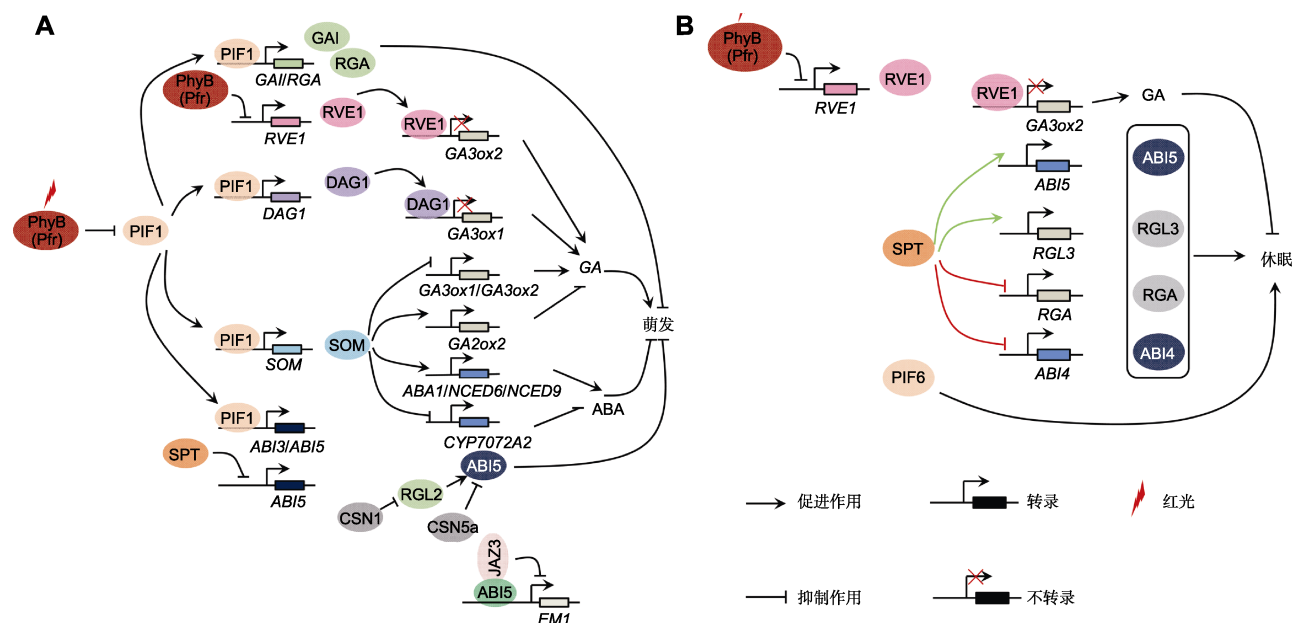


图1 光信号通过调控内源脱落酸(ABA)和赤霉素(GA)的生物合成及信号转导调控种子休眠与萌发

(A) 光信号通过调控ABA和GA通路调控种子萌发。PHYB能够介导红光促进PIF1发生泛素化降解,从而促进种子萌发。PIF1能够通过直接激活DAG1和SOM的转录进而间接调控GA生物合成相关基因的表达,或者直接诱导DELLA蛋白编码基因RGA和GAI的转录,最终抑制种子萌发。同样地,PIF1也能通过调控ABA的生物合成和信号转导调控种子萌发。PIF1通过依赖于SOM的途径促进ABA生物合成,进而抑制种子萌发;抑或直接诱导ABI3和ABI5的转录进而促进ABA信号转导,抑制种子萌发。除PIF1之外,PHYB还能调控RVE1的转录间接促进GA的生物合成,最终促进种子萌发。SPT和CSN蛋白复合体通过依赖于ABI5途径调控种子萌发。SPT通过抑制ABI5的转录抑制ABA信号转导,促进种子萌发。CSN1通过促进RGL2的泛素化降解进而抑制ABI5的蛋白稳定性,最终促进种子萌发;而CSN5a能够直接抑制ABI5蛋白的积累进而促进种子萌发。JAZ3通过抑制ABI5对ABA响应基因EM1的转录激活功能进而促进种子萌发。**(B)** 光信号通过调控ABA和GA通路调控种子休眠。PHYB能够介导红光抑制RVE1转录,进而促进下游GA3ox2的转录,最终抑制种子休眠。在不同生态型拟南芥背景下,SPT调控种子休眠的功能不同。其中,在Col背景下,SPT通过促进RGL3和ABI5的转录进而促进种子休眠(绿色标识线);在Ler背景下,SPT通过抑制RGA和ABI4的转录进而抑制种子休眠(红色标识线)。此外,PIF6也参与调控种子休眠。

Figure 1 Light signal regulates seed germination and dormancy via endogenous abscisic acid (ABA) and gibberellin (GA) biosynthesis pathway

(A) Light signal regulates seed germination via ABA and GA pathway. PHYB regulates seed germination through promoting the degradation of PIF1 protein. The accumulation of PIF1 in nucleus activates the transcription of DAG1 and SOM, which indirectly regulates the expression of GA biosynthesis gene or directly induces RGA and GAI (DELLA protein encoding genes) transcription and leads to repressing seed germination. Similarly, PIF1 stimulates ABA biosynthesis and ABA signaling pathway to suppress seed germination. PIF1 induces ABA biosynthesis via SOM-dependent pathway to repress seed germination; or it induces the transcription of ABI3 and ABI5 in order to stimulate ABA signaling. Except for PIF1, PHYB also promotes seed germination via inhibiting RVE1 transcription which indirectly promote GA biosynthesis. SPT and CSN complex could regulate seed germination in an ABI5-dependent manner. SPT suppresses ABI5 transcript to destroy ABA pathway. CSN1 stimulates RGL2 degradation to inhibit ABI5 activity, while CSN5a directly decreases the accumulation of ABI5 in order to provoke seed germination. JAZ3 promotes seed germination by repressing the transcriptional activity of ABI5 which activates ABA-responding gene EM1 expression. **(B)** Light signal controls seed dormancy via ABA and GA pathway. PHYB mediates red light to repress the transcription level of GA3ox2, inhibiting seed dormancy. SPT plays different roles in regulating seed dormancy under Col and Ler background of *Arabidopsis*. SPT promotes seed dormancy through activating the expression of RGL3 and ABI5 under Col background (green line), however, SPT suppresses seed dormancy via inhibiting RGA and ABI4 transcript under Ler background (red line). In addition, PIF6 is also involved in controlling seed dormancy.

与PIF1不同,bHLH类转录因子RVE1不仅在PHYB介导的种子萌发过程中发挥重要作用,还能促

进种子休眠(图1B)。统计新收获及后熟的Col和rve1-2突变体种子萌发率,发现rve1-2突变体表现出休眠水

平降低和萌发水平升高的表型,表明RVE1能够促进种子休眠,抑制种子萌发。进一步研究发现,RVE1能够直接抑制GA3ox2的转录,进而抑制GA的生物合成。RVE1的转录受到PHYB的负调控。上述结果表明,PHYB能够介导外源光信号,通过抑制RVE1的转录解除RVE1对GA3ox2的转录抑制作用,最终实现对种子休眠和萌发的调控(Jiang et al., 2016)。然而,目前关于PHYB抑制RVE1转录的作用机制还有待进一步阐释。综上,光信号通过调控ABA与GA的生物合成影响种子的休眠和萌发。

3.5 光信号通过调控激素信号转导影响种子的休眠和萌发

为了进一步探究外源光信号能否通过调控GA的信号转导影响种子萌发,研究者检测了ga1突变体和pif1/ga1双突变体种子萌发对GA₃的敏感性。结果发现,与ga1突变体相比,pif1/ga1双突变体对GA₃的敏感性升高。说明PIF1可能参与调控GA信号转导。进一步检测GA信号转导通路中关键组分的转录水平,发现PIF1能够促进DELLA蛋白编码基因GAI和RGA (REPRESSOR OF GA1-3)的表达。该研究进一步证实PIF1能够直接结合在GAI和RGA的启动子上。上述结果表明,黑暗条件下,PIF1蛋白能够直接诱导GAI和RGA的表达,从而抑制GA信号转导,最终抑制种子萌发(Oh et al., 2007)。此外,PIF1还能通过诱导ABI3和ABI5的转录促进ABA信号转导,从而抑制种子萌发(Park et al., 2011)。SPT在不同生态型拟南芥背景下调控种子休眠的功能和作用机制不同。在Col背景下,SPT诱导ABI5和RGL3的表达,从而促进ABA、抑制GA的信号转导,最终促进种子休眠。在Ler背景下,SPT抑制ABI4和RGA的表达,从而抑制ABA、促进GA的信号转导,最终抑制种子休眠(Vaistij et al., 2013)。此外,SPT还能通过抑制ABI5表达促进种子萌发(Vaistij et al., 2018)。imb1功能缺失突变体的萌发率降低,对ABA超敏感。进一步研究发现,ABI5转录本的积累可能是造成imb1突变体对ABA超敏感的原因之一(Duque and Chua, 2003)。上述结果暗示,IMB1可能通过抑制ABA信号转导通路促进种子萌发(Duque and Chua, 2003)。CSN蛋白复合体亚基CSN1和CSN5a的功能缺失突变体表现出延迟萌发的表型。去除种皮后csn1-10和csn5a-1能够正常萌

发,说明csn1-10和csn5a-1延迟萌发的表型依赖于种皮。种皮抑制的种子萌发与胚乳中RGL2相关,RGL2通过促进ABA的合成以及稳定ABI5蛋白进而抑制种子萌发。说明CSN1和CSN5a可能通过调控GA和ABA的信号转导促进种子萌发。进一步研究发现,CSN1通过促进RGL2的泛素化降解促进GA信号转导,从而促进种子萌发;CSN5a通过抑制ABI5蛋白的稳定性进而抑制ABA信号转导,最终促进种子萌发(Jin et al., 2018)。上述研究结果表明,外源光信号还能通过调控GA和ABA信号转导影响种子的休眠与萌发(图1A, B)。

4 展望

随着种子休眠和萌发调控机制相关研究的不断深入,外源环境信号协同内源激素影响种子休眠和萌发的分子调控网络已日渐清晰。然而,不同信号通路之间的互作机制仍不清楚,主要表现在以下3个方面。(1) ABA和GA是调控种子休眠和萌发的主要激素。其它激素如生长素、ET、BR、CTKs和JA,主要通过参与调控ABA的生物合成或信号转导影响种子的休眠与萌发。目前关于生长素、ET、BR、CTKs、JA与GA之间的交互作用还不清楚。(2) 外源光信号通过调控激素的生物合成以及信号转导通路影响种子的休眠和萌发。然而,目前的研究主要集中在光受体PHYA/B及其相关信号蛋白介导外源光信号,通过调控ABA和GA通路进而影响种子休眠与萌发的作用机制解析上。是否存在更多通过调控内源激素通路进而影响种子休眠和萌发的光响应蛋白? 外源光信号能否调控生长素或其它激素通路进而参与种子休眠和萌发过程? 这些问题都值得探讨。(3) 有研究表明,与黑暗条件下相比,红光、远红光以及蓝光处理的种子均能正常萌发。说明除红光和远红光外,蓝光亦能调控种子萌发。与Col相比,蓝光对phyA突变体种子萌发的促进作用减弱(Hennig et al., 2002)。这一现象暗示蓝光促进种子萌发部分由PHYA介导。那么,是否存在其它蓝光受体参与调控蓝光促进的种子萌发有待进一步验证。

休眠被称为“种子生物学中最神秘的现象之一”(Finch-Savage and Leubner-Metzger, 2006)。按照不同的休眠诱导时间,可以将种子休眠划分为主要休眠和次要休眠。主要休眠在种子成熟过程中逐渐

升高,在成熟的种子中休眠水平最高。主要休眠的种子经过一段时间的干燥储藏(后熟作用)后能够解除休眠。次要休眠是指已经完全后熟的种子在不适宜的环境条件下不能萌发的现象,层积处理可以解除种子次要休眠。按照不同的休眠部位可以将种子休眠划分为外壳引起的休眠和胚引起的休眠。去除或机械损伤种皮可以解除外壳引起的休眠,但不能解除胚引起的休眠。外源施加激素结合层积处理有助于解除胚引起的休眠。因此在实际生产中,生产者可以通过促进次要休眠从而延长种子的寿命和储存时间;通过打破主要休眠、解除胚(或种皮)引起的休眠从而促进种子萌发,缩短生产周期。

与野生种相比,经过驯化的栽培种种子休眠水平下调,如水稻(*Oryza sativa*)、小麦(*Triticum aestivum*)、大麦(*Hordeum vulgare*)和玉米(*Zea mays*)等禾本科作物(Bewley and Black, 1994)。近年来,育种学家们利用遗传学或组学的方法鉴定到一些与种子休眠相关的位点、转录本或蛋白(Alonso-Blanco et al., 2003; Argyris et al., 2005; Gu et al., 2006; Née et al., 2017b)。例如,研究者利用QTL方法鉴定到调控种子休眠的关键基因——*DOG1* (Alonso-Blanco et al., 2003; Bentsink et al., 2006)。后续研究发现,*DOG1*能够参与调控ABA信号通路以及GA的生物合成,进而调控种子休眠(Graeber et al., 2014; Nishimura et al., 2018)。那么,*DOG1*能否参与调控GA信号通路进而促进种子休眠?*DOG1*是否受到外源光信号和内源激素的调控?针对上述问题的研究不仅有助于人们更加清晰地理解种子如何监测环境因子的变化,从而决定是否完成从休眠到萌发的发育转变;还为利用光信号或激素人工调控种子的休眠和萌发,解决农业生产中“胎萌”以及穗发芽等问题提供了理论支撑。

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Advances in Light and Hormones in Regulating Seed Dormancy and Germination

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Abstract Plants have evolved to maintain the dormancy of freshly harvested seeds, which ensures that seeds do not germinate until environmental conditions are optimal. Therefore, dormancy helps seeds spread over long distances to ensure the survival of species. The transition from dormancy to germination is crucial to plant survival and for promoting yield and quality in agricultural production. Seed dormancy and germination are precisely regulated by diverse endogenous hormones and light signals. Light cues regulate seed dormancy and germination by affecting abscisic acid/gibberellic acid biosynthesis and signals. In this review, we summarize the key roles of the hormone pathway and light signal transduction pathways in regulating seed dormancy and germination. We also discuss the interactions (crosstalk) between phytohormone signals and light signals in seed dormancy and germination, in order to apply reference for regulating seed dormancy and germination by using light and hormones in agricultural production.

Key words seed dormancy, seed germination, light signal, hormones, crosstalk

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