光对真菌影响的研究进展

段庆虎,张应香,龚凤萍,竹　玮,韩玉玲,尹川川

(信阳市农业科学院,河南 信阳 464000)

摘　要:光代表自然界信息的主要载体。把光能转化为细胞中的化学语言的分子机制传递了每一个生物体对其栖息地适应的重要信号。与植物相比,真菌使用光作为信息源而不是能源。真菌对光照的反应有很多种。该文主要从光强和光质对真菌的影响,光对真菌生物钟、新陈代谢和基因表达的影响及光信号传导等方面进行阐述,以期明确光对真菌生长发育的意义。

关键词:光;真菌;生物钟;新陈代谢;信号传导

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光对每一个活细胞来说是一个非常重要的信号,为了使生物体适应光的有害和有益影响从而显著增强其适应力,光被视为自然界中优胜劣汰的关键因素。与植物相比,真菌使用光作为信息源而不是能源。几十年真菌研究中,至少有100种真菌代表了所有的门,都发现了光反应[1]。它们有蓝光、近紫外、绿光和红光感知机制[2-3]。然而,在大多数情况下光对代谢过程的影响还有很多细节没有被研究,因此,在该次评述中描述的光响应主要涉及白光或日光影响。通常观察光对真菌诱导或抑制性发育和分生孢子生物钟产生复位及孢子释放抑制的作用[4]。

光的作用机制是复杂的,不同真菌对不同波长可见光的反应不一,不同生长发育阶段对光照强度、光质要求均有差异;光照既可刺激真菌发育,也可抑制真菌发育[5-6],并受其它环境因子或营养因子的影响[7-8]。真菌对光照的反应有很多种,该文主要从光强和光质对真菌的影响,光对真菌生理钟的影响,光对真菌代谢途径的影响,光对基因表达的影响,光信号如何传输等方面进行阐述,以期明确光对真菌生长发育的意义。

第一作者简介:段庆虎(1986-),男,河南固始人,硕士,现主要从事食药用菌选育与栽培及生理生化和分子生物学等研究工作。E-mail:duanqinghu0529@163.com.

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Research Progress on Flowering Integrator Gene,*FT* in Plants

LI Qiu-hong[1],FEI Yuan[1],PANG Ji-liang[1,2]

(1. College of Life and Environmental Sciences,Hangzhou Normal University,Hangzhou,Zhejiang 310036;2. Zhejiang Province Key Laboratory for Medicinal Plant Germplasm Improvement and Quality Control Technology,Hangzhou,Zhejiang 310036)

Abstract:Flowering is an important process for higher plants to transfer vegetative to reproductive development. The related genes expression and regulation is the molecular basis of realization of this transformation. *FT*(FLOWERING LOCUS T) is one of the crucial integrator in flowering regulatory pathways. The protein encoded by *FT* gene,which is able to transfer long distance,is a flowering hormone,and has key functions on the process of flower bud formation. This paper reviewed *FT* and its orthologue's functions,evolution and the effect of them on the switch of floral development.

Keywords:*FT* gene;florigen;floral development

1　光强和光质对真菌的影响

1.1　光强对真菌的影响

真菌光强需求研究涉及到菌丝体和子实体生长2个阶段。适宜的散射光照不仅能够促进食用菌原基分化，而且与子实体的形态有密切关系，但不同种类食用菌其子实体需要散射光的程度不同。适量地给予光照能够加速樟芝菌丝体的生长，但当光强大于600 lx时抑制了菌丝体的生长[9]。50～100 lx弱光对蛹虫草原基分化、子实体诱导有促进作用，光照强度1 000 lx其子实体生长好、产量高[10]。光照可以促进真菌 *A. lactariolens* 和 *H. vinosophyllum* 子实体的形成，光照强度增加使2个真菌的菌柄变短变粗[11]。总之，真菌所需光强较低，一般为几十到1 500 lx的弱光，最佳光强因真菌种类而异。

1.2　光质对真菌的影响

近年来，不少学者开始关注光质对真菌形态及代谢方面的影响。蓝光抑制病原真菌灰葡萄孢菌孢子形成[12]。光抑制病原真菌 *Peronospora belbahrii* 孢子的形成和蔓延[13]。也有报道红光和蓝光都较黑暗下使 *Monascus pilosus* 产生更多的闭囊壳和分生孢子[14]。Sumathy等[15]发现光照条件下促进紫红曲霉生长而导致其色素产量降低，其中红光对生长和色素产量影响较小，绿光下生物量显著增加，但绿光和蓝光下色素产量与黑暗相比明显减少。另有报道红光激发 *Aspergillus nidulans* 无性发育和压制其有性发育[16]。Velmurugan等[17]发现黑暗、红光、蓝光和白光影响 *Monascus purpureus* 色素和生物量产量。Cai等[18]报道白色、红色、蓝色光对 *Aspergillus glaucus* 菌丝体生长有促进作用；红色和蓝色光促进 *Xylaria* sp. (No. 2508)菌丝体形成，但其受到黑暗和白光的抑制。应正河等[19]报道红光对绣球菌菌丝生长最为有利，黄光对原基形成有较强的诱导作用。LED光质对滑子菇和鸡腿菇的子实体发育有调控作用，光质间差异明显[20]。蓝色光质可以使灵芝子实体维持较高的抗氧化酶水平，促进可溶性蛋白合成，从而增强灵芝代谢，延缓灵芝衰老[21]。总之，光质对真菌的生长发育有调控作用，真菌对光质具有选择性，最佳光质因种类而异。

2　光对生物钟的影响

生理钟在真核细胞生物中无处不在[22]。在自然界中，生物对温度和光条件变化的适应对生存是至关重要的。生物钟和代谢过程之间的关系已经在粗糙脉胞菌中系统研究了[23]DNA代谢、RNA代谢、细胞周期、蛋白代谢、碳代谢、氮代谢及异戊二醇(包括胡萝卜素)产物生物合成涉及的基因已经在生物钟控制下被发现[24]。因此，生物钟不但影响新陈代谢，代谢也参与生理钟控制，从而构成了一个复杂的调控体系[25]。不过，除了粗糙脉胞菌，在大多数真菌中，生物钟的存在尚未被证明。然而，可以预料，每一个生物体对光敏感需要处理昼夜环境的变化。因此，生物钟触发过程很可能是一定程度上受光调控。

3　光对真菌代谢途径的影响

真菌适应地球自转带来变化的能力在很大程度上被低估了。许多研究表明光控制类胡萝卜素代谢，早期研究表明光也影响其它常常不被考虑的代谢过程，后来的研究都是关于代谢基因的转录和表达[26-28]。

3.1　类胡萝卜素代谢

类胡萝卜素是细菌、真菌和植物中普遍存在的可溶性天然色素。须霉是研究在对光响应和类胡萝卜素生产的模式菌株。这种真菌，除了性刺激，光对类胡萝卜素生产有促进作用[29]。蓝光增强carA和carB表达的积累，它们是编码类胡萝卜素生物合成酶，对光响应和类胡萝卜素生产是至关重要的[30-32]。须霉菌丝经光照后胡萝卜素含量明显增加[33]。此外，*G. fujikuroi* 在敲除wc-1后靠类胡萝卜素上调来响应光照[34-35]。光对 *P. blakesleeanus* 类胡萝卜素合成是正调控[36]。

3.2　多糖/碳水化合物代谢

不同碳源有效吸收和质量与光响应密切相关[37-38]。光控制曲霉的几个代谢过程，如多糖发生[39]，如葡萄糖[40]或糖原成分[41]。在 *B. emersonii* 中，光激活多糖合成和降低葡萄糖-6-磷酸脱氢酶活性[42]。经过光照后在分生孢子发生阶段磷酸甘油酸激酶和甘油醛-3-磷酸脱氢酶被下调[43-44]。ENVOY不仅对光强烈地响应而且显著影响纤维素酶基因的表达[45]。G-α亚基GNA3仅在光照下正调控这一基因表达过程[46]，另一个G-α亚基，GNA1被确定[47]，在光照条件下主导废除纤维素酶转录和黑暗条件下强烈增加其转录水平。菌体生长、多糖体、β-1,3-葡聚糖、大分子多糖、β-1,3-葡聚糖酶活性在光照强度为1 000 lx较高，此光照强度下生产的多糖体生物活性最高[48]。

3.3　几丁质和细胞壁其它成分

光照射真菌菌丝，细胞壁是光影响的第一个站。在 *P. blakesleeanus* 中发现了光照引起细胞壁结构瞬间变化[49]，*A. giganteus* 在光照下培养细胞壁中几丁质含量是黑暗培养的2倍[39]。*A. giganteus* 菌丝中葡聚糖的质量和数量受光照和葡萄糖浓度控制[50]。在 *Trichoderma harzianum* 中，光照10 min与黑暗对照相比，β-1,3-葡聚糖合成酶活性增加了130%，几丁质合成酶活性降低了50%，几丁质含量不变，β-1,3-葡聚糖含量提高了50%[51]。

3.4　脂肪酸代谢

N. crassa 光照培养下脂肪浓度高于黑暗条件[28]。在 *Alternaria alternate* 中也有相似的结果[52]。光下异柠檬酸脱氢酶活性降低导致柠檬酸积累，为合成脂肪和

类胡萝卜素提供原料[28]。另外,脂肪酸组成受光以及velvet(veA)影响[53-54]。在 *T. viride* 中也证实了光照后脂肪积累[55]。

3.5　核苷酸和核苷代谢

尽管核苷酸和核苷在能量代谢和调节氧化还原反应对真菌细胞来说是重要的,但是关于它们的光响应调控知识是有限的。NAD^+ 激酶是调控细胞同化和分裂途径相关的关键酶之一。NAD^+ 激酶活性仅在光照几分钟内就上升到 2 倍[56]。*B. emersonii* 生长在光下较黑暗核酸含量快速提高了 28%[42]。而 *N. crassa* 核酸含量和生物合成的生理周期大约是 24 h,其它许多生物也是这样[57]。尽管这一生理活动反映了光照的调节,生物钟的发现支持光对核苷酸代谢的影响。

3.6　cAMP

环腺苷磷酸(cAMP)是真核生物的第二信使。这一化合物在响应胞外刺激时产生,可调控多种生理过程。腺苷酸环化酶和磷酸二酯酶是调控真菌中 cAMP 水平的主要酶[58]。在 *T. viride* 中光照显著影响 cAMP 水平[59-60]。因此,光照导致胞内 ATP 和 cAMP 的快速增加,这可能在响应光照而偶联蛋白磷酸化。添加 3 mmol/L cAMP 可以替代光照的影响[61]。在 *A. nidulans* 中,也有报道磷酸二酯酶受光调控[62]。cAMP-蛋白激酶 A(PKA)和蓝光感知有关系,PKA 活性不仅在野生型而且在光感受器 BLR-1 和 BLR-2 突变体中随光照增加[63]。尽管这些菌株显示扰乱了光响应,这一现象可能由于光直接激活了腺苷酸环化酶。在 *N. crassa* 中发现 cAMP 水平和类胡萝卜素积累的联系[64]。cAMP 代谢和碳代谢之间有关系[65-66]。有学者发现光照与 cAMP 的代谢有关,而且 cAMP 是子实体形成的诱导物[67-68]。

3.7　氨基酸代谢

作为蛋白的构成单元,光照显著影响氨基酸的质量和含量。在 *P. blakesleeanus* 中,光照降低鸟氨酸脱羧酶活性[69]。在 *T. viride* 中,谷氨酸脱羧酶被光诱导,该酶催化 L-谷氨酸 α-脱羧变为 γ-氨基酪酸(GABA)[70-71]。这一反应属于叫做 GABA 回返的代谢途径[72],为分生孢子寄生和萌发提供能量。Miyake T 发现 *Monascus pilosus* 菌丝中 GABA 含量在光照后增加[14]。

3.8　氮和硫代谢

氮饥饿导致菌丝分化和子囊孢子形成[73-74],它一旦被氮饥饿诱导,子囊孢子的形成被蓝光强烈增强[74-75],表明光响应和氮代谢之间存在联系。并且,有报道几个蓝光调控基因也被氮饥饿调控[76],这几个基因也被生物钟控制,这些基因参与了氮代谢[77]。进一步研究发现硝酸还原酶在光下比黑暗中活性强说明光起作用了[78]。在 *N. crassa* 中,硝酸还原酶活性降低,它的小亚基活性在蓝光感应中增强[79]。

对于光响应,硫代谢也需要阐述。虽然这一代谢途径在真菌中被很好地研究[80],仅有一个研究报道说光影响硫代谢。在 *T. reesei* 中,硫代谢和纤维素酶基因表达联系被确定,其依赖光照[81]。真菌吸收硫酸盐似乎在响应光时被调整[81]。所以,光响应中碳代谢和硫代谢之间的关系开辟了一个新的复杂的调控网络,这需要进一步地研究。

3.9　次生代谢

真菌在星球上进化成功不仅由于它们多样的代谢来适应不同的环境,而且由于它们在化学战争中的有效性。真菌分泌化合物去帮助它们和其它微生物竞争,这不仅仅对真菌有益,而且作为抗生素或真菌毒素,对社会也至关重要[82-83]。*Aspergillus flavus* 中黄曲霉毒素早在 40 年前表面受光负调控[84]。对 *A. alternata* 而言,光抑制真菌毒素格链孢酚和甲基格链孢酚的产生[85-86]。相反,另一研究报道黄曲霉毒素 B1 和赭曲霉素 1 分别由 *A. flavus* 和 *Aspergillus ochraceus* 产生,在光照条件下增强[87],除了加快生长的影响,光周期没有影响赭曲霉素[88]。研究发现 25 个参与黄曲霉毒素的生物合成与调控的基因是成簇的[89]。阐述这些基因在光调控黄曲霉毒素产生中的潜在作用将可能帮助澄清光调控黄曲霉毒素是怎样产生的。光是尾孢菌素生物合成的基本诱导物和对尾孢菌素毒性是绝对必需的[90]。

对比这些真菌毒素,许多次生代谢物具有高的工业价值,它们被应用于食品或抗生素生产。曲霉被用于生产传统东方食品,这一真菌产生许多有益的次生代谢物[91]。青霉素是最重要的次生代谢产物,与上面提及的几个次生代谢产物一样青霉素的合成受光抑制[92]。

4　光对基因表达的影响

早在 1989 年就有关于蓝光诱导基因的研究[93]。Bluhm 等[94]报道了与光裂合酶同源的 PHL1 的特性,并提供了 PHL1 调节紫外线照射响应的证据;方喆等[95]得到海洋真菌灰绿曲霉蓝光调节受体基因 *Agwc1*,并且 *Agwc1* 很有可能在灰绿曲霉蓝光感应系统中发挥重要功能;李海峰[96]报道 *Le. phrA* 基因在香菇子实体形成的整个阶段中都有转录,在光照环境下生长原基之前的菌丝体细胞中的转录量比黑暗环境中生长的多,这表明 *Le. phrA* 是一个强光照表达基因。高雅报道真菌 *Mucor amphibiorum* RCS1 中一个类 S-腺苷-L-高半胱氨酸水解酶基因(S-adenosyl-L-homocysteine hydrolase-like,sahhl)受蓝光诱导表达[97]。杨涛等[98]克隆蓝光受体基因 *Cmwc-1* 并测定在不同光照条件下其表达量的变化,*Cmwc-1* 在黑暗条件下表达,光照刺激后表达量增加,待光照时间持续 30 min,其表达量将不再上升,即光适应现象。蓝光对须霉热激蛋白 HSP100 基因的具有激活作用[99]。另外有报道木霉的疏水基因 *tvsrh1* 是光依赖性拼接[100]。

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5 光信号工作如何传导

光信号的感知和传导是由一个复杂的调控网络组成的，在粗糙脉胞菌中，与生物钟共用相同的关键元件而相互联系[101-103]。关于光响应，在真菌中的主要调节蛋白是 PAS 结合域，其包含光受体 WC-1 和 WC-2，它们相互作用作为一个转录因子复合体(WCC)，在粗糙脉胞菌中所有的蓝光响应由 WCC 居间促成，这些光受体也是生物钟的关键元件[104-107]。此外，WCC 激活一定数量的生物钟调控基因，这是光与生物钟相互联系的结果。

光信号感知是通过变构和相互作用得到的：WC-1 的 LOV 型和 PAS 结构域是光受体蛋白的功能位，包含黄素结合域，以及在 LOV 结构域和黄素间有一个保守的半胱氨酸残基，还有一个蓝光依赖化合物形成[108-109]。光诱导构象改变最终导致与下游光传感元件相互作用，启动光信号传输[108-110]。

一旦感知，光信号引起生物钟启动，调整内部生物钟适应生长环境。研究粗糙脉胞菌的 PAS/LOV 结构域蛋白 VIVID(VVD)对生物钟启动是重要的[111-112]。VVD 代表了一种蓝光依赖光受体，抑制光响应，可以感受光强度变化[113-114]。它可以减弱 WCC 的活性，是光响应调节的关键元件[112,115]。

在粗糙脉胞菌中除了直接传输信号，调控机制还包括由蛋白激酶 C(PKC)调控的光依赖基因[116]。它以一种光依赖形式与 WC-1 相互作用，使其磷酸化导致 WC-1 蛋白的减少[117]。由 PKC 调控的过程一旦被光激活也会受光的影响，PKC 不仅作用于各自的调控过程，也干扰光响应，这表明经由 PKC 的信号传输有光依赖性[118]。此外，在粗糙脉胞菌中，另一个激酶 cAMP 依赖蛋白激酶 A(PKA)对生物钟功能也是必不可少的，其在几个代谢过程中已被清晰地研究了，这个激酶通过启动随后的酪蛋白激酶抑制 WC 活性[119]。PKC 和 PKA 激酶可能是光响应和调控代谢过程的关键酶[120-121]。此外，调控生物钟的元件 FREQUENCY(FRQ)也是通过磷酸化激活或抑制 WCC[115]。因此，磷酸化是调控生物钟和光响应的一个关键事件。

6 结论与展望

总之，因为地球的自转导致日常环境变化清晰地影响着真菌的代谢活动。实际上，每一个重要生命活动都是避免光伤害和(或)准备发育的需要，这一调控与光信号精密联系。在许多情况下，光的输出效果在不同物种中是类似的。然而，调控机制导致各自的影响不太一致。因此，光的影响在一个物种发现，也可能被另一个物种的试验排除。明显的昼夜适应意味着一方面更详细了解底层调控机制不仅会增加人们的真菌生理学知识，也可以帮助提高对生物技术过程认识。可以通过在没有光刺激的时候敲除负调节机制或增强某些基因的表达等来确认关键基因的调控。另一方面，光对所有重要代谢途径的宽泛调控影响说明随机光照，其与真菌传统培养和分析是不可避免的，严重危害生殖和所得数据的准确性。因此，需要谨慎地看待没有光调控的结果。尤其是在信号传导中调控基因和基因经常显示在光响应几分钟内的显著转录。

相信随着真菌中新型光源、细胞生物学、基因功能和光信号传导等方面研究的深入，将有助于人们了解光对真菌的影响机制。

(该文作者还有段仁周，单位同第一作者。)

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Researches Advances on the Effect of Light on Fungi Growth and Development

DUAN Qing-hu,ZHANG Ying-xiang,GONG Feng-ping,ZHU Wei,HAN Yu-ling,YIN Chuan-chuan,DUAN Ren-zhou
(Xinyang City Academy of Agricultural Sciences,Xinyang,Henan 464000)

Abstract:Light represents a major carrier of information in nature. The molecular machineries translating its electromagnetic energy (photons) into the chemical language of cells transmit vital signals for adjustment of virtually every living organism to its habitat. In contrast to plants,fungi use light as a source of information but not as a source of energy. Fungi react to illumination in various ways. This review mainly elaborated the effect of light intensity and quality on fungi,the effects of light on fungi biological clock,metabolism and gene expression and light signal transduction,etc. , and illustrated the growth and development significance of light for fungi.

Keywords:light;fungi;circadian clock;metabolism;signal transduction