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光质对植物生长发育、光合作用和碳氮代谢的影响研究进展

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摘要: 本文总结了光质对植物生长发育的调控作用, 分析了光质对植物光合作用的影响, 解析了光质调控植物碳氮代谢的过程, 并就此领域未来的研究方向提出了建议, 以期为光质在植物生长发育调控机制方面的进一步研究和作物栽培补光技术拓展提供参考。

关键词: 光质; 生长发育; 光合作用; 碳氮代谢

Research progress on the effects of light quality on plant growth and development, photosynthesis, and carbon and nitrogen metabolism

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Abstract: This review summarizes the regulation of light quality on plant growth and development, analyzes the effect of light quality on plant photosynthesis and the regulation of light quality on plant carbon and nitrogen metabolism. Furthermore, the key points in future studies are also proposed, in the hope of offering theoretical reference for dissecting the regulation mechanism of light quality in plant growth and development and the supplementary light technology in crop cultivation.
Key words: light quality; growth and development; photosynthesis; carbon and nitrogen metabolism

光环境是植物生长发育的重要生态环境因素之一, 主要通过光周期、光密度、光分布、光质等方面影响植物生长发育。光质是影响植物生长发育的重要调控因子。光质是一种触发信号因子, 可以引发种子发芽、组织分化、花芽分化, 也是一种调控能源, 不同波段的光携带不同级别的能量, 影响植物的生长发育(Devlin等2007)。植物对290~850 nm的光谱敏感(Paradiso等2022; 苗妍秀2015), 具体包括紫外光、蓝光、绿光、红光、远红光; 蓝光和红光是对植物光合作用最有效的光(Wang等

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2022; Nguyen等2021; Saengtharatip等2021)。

近年来, 随着相关生物及工程技术的不断进步以及研究的不断加深, 国内外学者在不同光质对植物生长发育的诸多方面(包括植物形态建成、光合作用、基因表达、调节植物生长、增强抗逆能力等)进行了深入研究。本文主要综述了光质对植物生长发育(种子萌发、根系、茎部、叶片、开花、果实发育与品质)、光合作用(气孔导度、光合色素、光系统、光合速率)以及碳氮代谢等方面影响的研究进展, 以期为光质调节植物生长发育的研究和作物栽培补光技术提供参考。

1 光质对植物生长发育的影响

1.1 光质对植物种子萌发的影响

植物种子的萌发需要适宜的水分、温度、氧气或光照等环境条件。根据种子萌发对光质的响应不同, 将种子分为需光性、嫌光性和光中性三类(杨期和等2003)。需光性种子, 是指种子萌发需要一定的光照; 没有光照的情况下, 种子不会萌发或萌发率很低。嫌光性种子, 是指种子的萌发需要无光的条件; 在有光照情况下, 种子不会萌发或萌发率很低, 或光照条件诱导种子产生休眠。光中性种子, 是指种子的萌发不会由于光照的有无或变化而发生变化。光周期(Fosket等1970; 赵笃乐1995a, b; McElroy等2004)、光密度(Mckinnon等2004; Gonzlez等2009: Liu等2018a, b)、光照时间与光通量(Grubišić等1990; Milberg等1996; Poppe等1997; Ohadi等2009; 刘青青等2019)、光质等光的属性都会影响植物种子萌发。

光质能决定某些植物种子的萌发与否或萌发率高低(Barrero等2012; Nawaz等2018)。光质对植物种子萌发的影响是一个复杂的生理过程, 也会受到激素调控的信号传递和相关基因的表达的影响。在特定波长的光谱环境中, 其对种子萌发具有促进或抑制作用(Barrero等2012)。对莴苣(*Lactuca sativa*) (Borthwick等1952; 杨期和等2003; 李雯琳2009; 程晓奕等2018)、尾穗苋(*Amaranthus caudatus*)和钟穗花属植物(Shinomura 1997)、远志(*Polygala tenuifolia*) (赵停等2018)的研究均发现红光对种子萌发有促进作用, 而远红光对种子萌发有抑制作用(Lindig等2001; 张敏等2012; Nawaz等2018; 栗昕羽等2022)。

Borthwick等(1952)在不同波长对莴苣种子萌发的影响的研究中发现, 640~670 nm的红光可有效诱导在黑暗中浸泡过的莴苣种子萌发, 而这种促进效应会被远红光逆转, 720~750 nm的远红光会抑制莴苣种子萌发。在其后的相关研究中也发现了类似的现象(Sage 1992; Lindig-Cisneros等2001)。由此可知, 植物种子可能通过红光和远红光的比值(R/FR)来感受实际光谱环境, 尤其对于需光性种子, 主要通过R/FR判断光环境的适宜性(Franklin等2010)。不同植物种子的萌发对R/FR要求不同(Smith 1991)。在对杉树(*Cunninghamia lanceolata*)种子的研究中, 发现R-FR-R间断处理能够促进杉木种子萌发, 而R-FR-R间接处理与林下光环境的变化相似(刘青青等2019), 可能是因为远红光逆转红光促进萌发作用的功能具有时间性(童哲等2000)。

1.2 光质对植物根系生长的影响

根系是植物重要的生理器官, 具有固定、吸收养分和水分的作用。光与植物的根系看似没有直接的关系, 但光可以通过影响植物叶片的光合作用及光合产物的合成与转运, 通过植物的茎等器官传导, 来影响根系的生长发育和功能(Sun等2005)。

不同植物根系对光质的响应不同, 研究表明蓝光是改善根系形成的有效光源(You等2013; Feldman 1984), 可以促进水稻(*Oryza sativa*) (李韶山等1994)、烟草(*Nicotiana tabacum*) (林叶春等2014)、番茄(*Lycopersicon esculentum*) (刘振威等2015; 蒲高斌等2005)、罗勒(*Ocimum basilicum*) (You等2013)、莴苣(Dougher等2001; Lin等2013)、兜兰(Lee等2011)等植物根系生长, 增加根系活力, 但Nhut等(2003)和Rizzini等(2011)的研究发现蓝光显著影响草莓(*Fragaria* × *ananassa*)根系的生长。红光可以显著促进作物主侧根生长, 增加根系长度和侧根数量, 增强根系活力以及根系对磷的吸收(Moon等2006; Son等2013; 闫萌萌等2014; 董桑婕等2022), 但相关研究也发现红光会抑制番茄根系的生长(孙娜2015), 降低菊花(*Dendranthema morifolium*)组培苗的根系活力(魏星等2008)。

在生产研究中, 发现复合光质对根系具有很

好的调控作用。Xiong等(2011)和闫晓花等(2016)发现, 红蓝复合光对黄瓜(*Cucumis sativus*)根系的促进作用优于单色光, 复合光显著提高根系的活力, 增加根系生长速率和干物质的积累。在菊花(Kim等2004)、棉花(*Gossypium hirsutum*) (Li等2010)、草莓(Choi等2015)、番茄(Eguchi等2016)、莴苣(Son等2013)、牡丹(*Paeonia suffruticosa*) (郭丽丽等2015)和油菜(*Brassica campestris*) (Li等2013)上有关复合光的研究都有类似的结论。

1.3 光质对植物茎部生长的影响

植物的生长需要不断对环境进行适应, 植物茎的生长是植物生长最具特征的指标, 尤其是在植物幼苗期, 是对生长环境的直接响应。植物茎的生长主要通过株高、胚轴长、茎节长、茎粗等指标来衡量。相关研究表明, 红光有利于细胞伸长, 进而增加植物的株高; 蓝光能抑制细胞伸长, 进而增加茎粗(Paradiso 2022; Trouwborst等2010)。

红光的波长与植物色素吸收的峰值相符合(Schoefs 2002), 能够促进细胞的分裂, 扩大细胞体积, 因此红光促进植物生长, 尤其是纵向生长(Dou 2017; Paradiso等2022)。单色红光的照射, 促进植物干物质的积累, 影响根冠比(Yu 2017), 促进莴苣(Naznin等2019; Darko等2014)、白菜(*Brassica pekinensis*) (Fan等2013)、香椿(*Toona sinensis*) (张立伟等,2010)、南瓜(*Cucurbita moschata*) (黄枝等2016)等植物株高或胚轴的伸长。单色蓝光的照射, 有利于控制生菜(Paradiso 2022)、白菜(Fan等2013)、葫芦(*Lagenaria siceraria*) (Hernández等2014)等植物株高。

红光和蓝光配合使用, 可以有效调节植株茎的生长。在红光的基础上加入适量的蓝光可以有效抑制植株的株高, 有关黄瓜(Trouwborst等2010)、金鱼草(*Antirrhinum majus*) (Randall等2014)、菊花(Ouzounis等2014)、玫瑰(*Rosa rugosa*) (Randall等2014; Terfa等2012a, b)、大戟(*Euphorbia pekinensis*) (Islam等2012)、凤仙(*Impatiens balsamina*) (Randall等2014)、矮牵牛(*Pharbitis nil*) (Randall等2014)等植物的研究中已有较多证明。

红光和远红光的配合使用, 也可以调节植株的株高。自然光中, 红光:远红光的比值在1.15~0.70之间变化(Craig等2016; Wang等2020); 随着远红光比例的增加, 会增加植株茎部养分的分配比例, 从而引起地上部分发育相比地下根系更快(Craig等2012; Demotes-Mainard等2016; Zheng等2019)。

1.4 光质对植物叶片生长的影响

植物叶片是植株进行光合作用的主要器官, 叶片生长的优劣程度直接关系到植物进行光合作用的能力, 进而影响植物的生长发育。植物生命活动依赖于叶片的光合作用, 在进化过程中植物的叶片形成了一种对光的感应机制, 以保证在植物的生命周期中维持和最大限度地提高叶片的光合能力和对光感应的灵敏度。植物通过调整叶片的光合生物化学(如Rubisco活性、PSII和PSI比率变化)、叶片的解剖结构(如叶绿体大小及其分布)和叶片的形态(如叶片面积及其厚度)来适应光照环境的变化, 以最大限度地收集光能和捕获二氧化碳, 进而进行光合作用来制造更多光合产物, 以供植物生长发育(Terashima等2006; Athanasiou等2010; Kono等2014; Vialet-Chabrand等2017; Zheng等2019)。

光质会影响植物叶片生长、结构形成、叶绿体发育和气孔开放, 直接或间接影响植物的光合作用。蓝光可以通过增加气孔开度和量子产量来提高每个叶面积单位的光合能力(Paradiso等2022)。单色蓝光增加莴苣叶片宽度(Stutte等2009)、形态指数(Lin等2013; Son等2013)、干物质积累(Dougher等2001)。单色红光促进莴苣叶片的伸长(Stutte等2009)。复合红蓝光可以促进莴苣(Wang等2016)、菠菜(*Spinacia oleracea*) (Naznin等2019)等叶菜作物叶片数、叶面积指数, 皂荚(*Gleditsia sinensis*)幼苗叶片的厚度以及黄瓜(Trouwborst等2010)等果菜作物叶片生长。

绿光在很多研究中被认为是无效光, 但最近研究发现绿光可以促进植物的生长发育从而适应不同光照环境, 直接作用于叶绿体, 从而影响植物的生长发育。在红蓝复合光源中增加绿光可以增加莴苣叶片长宽比(Ohashi-Kaneko等2007)、叶片数量、叶面积、叶面积指数(Li等2009)。绿光可以深入穿透叶幕层, 达到整个群体下部叶片, 促进下部叶片光合作用, 为叶片提供信号响应环境辐照度, 进而提高作物生产力和产量(Smith等2017)。

1.5 光质对植物开花的影响

开花是植物由营养生长转入生殖生长的显著标志, 与光周期的长短关系密切, 需要经历一定的光周期(Hemming等2008)。相关研究表明, 光质对植物开花也有着一定的影响(Heo等2002), 植物通过不同光受体接受光及转导光信号来完成响应光环境的变化。根据不同光质的响应, 可以将光受体分成光敏色素和隐花色素, 光敏色素是主要感受红光和远红光的色素, 隐花色素是主要感受蓝光和近紫外光的色素。光敏色素有5种, 分别是光敏色素A (phytochrome A, PHYA)、光敏色素B (phytochrome B, PHYB)、光敏色素C (phytochrome C, PHYC)、光敏色素D (phytochrome D, PHYD)和光敏色素E (phytochrome E, PHYE) (Gyula等2003; Franklin等2010); 隐花色素有两种, 分别是隐花色素1 (cryptochrome 1, CRY1)和隐花色素2 (cryptochrome 2, CRY2) (Gyula等2003)。

蓝光和远红光主要通过CRY1、CRY2和PHYA等光受体来促进植物的开花(Putterill等2004; Lin等2000); 红光主要通过PHYB、PHYD和PHYE等光受体来抑制植物的开花; 光受体CRY2促进植物的开花依赖蓝光, 也受红光的影响(Lin等2000)。Fukuda等(2016)研究发现, 蓝光照射的牵牛花能促进花芽分化, 促进植株提前开花, 而红光在较强的光照强度下才能诱导牵牛花的花芽发育。Guo等(1998)研究表明, 在有蓝光受体或缺少红光受体情况下, 蓝光照射下的植株可以提早开花; 缺少蓝光受体CRY2时红光照射下的植株开花会推迟。但CRY2突变体植株在蓝光照射下能够正常开花, 这说明单独的CRY2受体在蓝光照射下是不能促进植物开花的。

光质不仅能够调控植物开花的时间, 对植物花性分化和性器官发育也有影响。Tong等(1990)间断使用红光打破暗期, 可以诱导光敏型不育水型的花粉高不育率, 而用红光/远红光间断打破暗期又会恢复花粉的育性, 说明红光/远红光可以通过光敏色素调节光敏型水稻的雄性器官的发育及育性转变。宋佳丽(2016)研究适宜红、蓝光配合使用能通过PHYA、PHYB、PHYC、PHYE、CRY1等光受体调控植株*CO*、*FT*的表达, 进而调控黄瓜开花, 较高蓝光比例的红、蓝光处理在黄瓜苗期通过茎尖激素信号的转导调控黄瓜花性分化, 增加黄瓜雌花数, 并促使较早出现雌花花芽、提早开花。

1.6 光质对植物果实发育的影响

果实的发育受植物营养、水分、温度、光照等因素影响。在光照的诸多因素中, 光质是能够影响果实的生长发育的重要因子。Lu等(2012)研究了温室栽培环境中单桁架番茄生产系统下, 在番茄果实快速发育阶段, 分别使用白光、红光和蓝光LED进行补光, 在相同能耗的基础上, 白光和红光处理不仅会提高番茄的生长速率, 而且分别使番茄鲜产量增加12%和14%, 干产量增加16%和14%。Naznin等(2019)和段青青等(2019)对在气候室生长的辣椒(*Capsicum annuum*)进行光照试验, 发现红蓝光照射能促进辣椒结果速率, 还能有效增加果实数量。Gómez等(2013)在温室对番茄的光照试验结果, 也证实了补光能促进果实尽早成熟, 增加节点数、果实数和果实总鲜重。Kaiser等(2019)为温室种植的番茄提供了不同比例的红蓝光(0%、6%、12%和24%)进行补光, 发现适当增加蓝光不仅抑制株高和茎间长度, 促进植株健壮, 还可以促进番茄总生物量, 增加果实数量和产量, 但24%的蓝光不利于番茄生长。

Guo等(2016)对温室中生长的迷你型黄瓜进行光照试验, 发现蓝光对黄瓜植株生长和果实产量有一定影响, 而在温室顶部照射远红光的处理可以增加果实体积, 增加产量。Särkkä等(2017)的试验也证实了添加远红光的复合光照下, 黄瓜果实的生长起始速率和产量都有增加。Yoshida等(2012)在封闭的植物生产系统中对草莓进行光照试验, 研究果实生产效率, 发现蓝光可以促进植物进入结果期, 而且产量比白色光源处理的更高, 能提高果实的生产效率。此外, Piovene等(2015)和刘庆等(2015)在草莓上进行光照试验, 也证明了红蓝光质复合光照可以促进草莓成熟, 增加果实产量。唐道彬等(2017)在马铃薯(*Solanum tuberosum*)光照试验中发现, 在马铃薯生长前期增加红光的比例, 可以诱导植株匍匐茎的形成; 在马铃薯生长后期增加蓝光的比例, 可以促进形成块茎和加快块茎的膨大, 以此提高块茎的数量和产量。宋寒冰等(2020)利

用不同光质光源对真姬菇(*Hypsizygus marmoreus*)进行培养发现, 在菌盖中光受体基因*WC1*和*WC2*均在蓝光下表达量最高, 在蓝光下形成的原基数量最多, 在红光下原基数量最少, 而蓝光下产量也较高。

1.7 光质对植物果实(食用器官)品质的影响

光质对粮油作物籽粒的品质有影响。Chen等(2021)通过4种不同光质在两种香型水稻上研究发现, 红光、蓝光以及红蓝组合光相比对照(自然光)产量有14.24%~35.36%增加, 并且蓝光和红蓝组合光通过降低吡咯林-5-羧酸含量, 降低了稻米中2-乙酰基-1吡咯啉(香稻中关键芳香族化合物)的含量, 调节了稻米中脯氨酸和γ-氨基丁酸含量, 进而影响了香稻的品质。常建伟等(2021)在不同光质对食品用小麦(*Triticum aestivum*)芽苗酚类物质累积调节的研究中发现, 相比对照处理, 蓝光、绿光和黄光的处理提高了酚类合成途径中苯丙氨酸解氨酶(PAL)、4-香豆酸-CoA连接酶(C4H)、肉桂酸4-羟化酶(4CL)等相关酶的活性, 同时上调了PAL、C4H和4CL mRNA的表达水平, 以此提高了阿魏酸、对香豆酸和咖啡酸等酚酸类物质的含量, 总酚含量增加。方临志(2019)在大豆(*Glycine max*)中的研究也证明增加蓝光的比例有利于大豆籽粒中可溶性蛋白和游离氨基酸的积累。

光质影响茎叶蔬菜的营养品质。高波(2015)研究了不同光质照射下的水培芹菜(*Apium graveliens*), 红蓝光质配比(10:1)能够显著提高芹菜的地上鲜重、可溶性糖含量等各项生长指标, 同时有效降低了芹菜的根冠比、纤维素及硝态氮含量, 芹菜在此光质配比下具有良好的生长、品质特性。孟力力等(2022)在人工光照的植物工厂中对冰草(*Agropyron cristatum*)进行不同光质的光照试验, 发现一定比例的远红光可以有效提高冰草叶片中维生素C、可溶性渗透物、挥发性酮类及酯类物质等的含量, 提高冰草的品质。张玉彬等(2021)用不同比例红蓝光质的光源连续培养生菜发现, 提高蓝光比例可以显著增加生菜可溶性糖、抗坏血酸(ascorbic acid, AsA)含量和提高单脱氢抗坏血酸还原酶(MDHAR)活性。龚春燕等(2018)在研究不同光质对西兰花(*Brassica oleracea*)的营养品质和抗氧化特性研究中, 发现蓝光可以有效提高西兰花叶片中可溶性蛋白、可溶性糖、酚类物质及花青苷含量, 增强西兰花的营养品质。

光质对植物果实的品质也有一定的影响。蓝光显著诱导辣椒花青素合成相关基因表达并促进花青素积累(王晓通等2022)。杨俊伟等(2019)用不同比例的红蓝光源照射在植物工厂栽培的番茄, 研究表明红蓝光质配比(2:1)处理能显著提高番茄果实的可溶性蛋白、抗坏血酸及番茄红素的含量, 并且红光照射下番茄果实的可溶性固形物含量、可滴定酸质量分数及糖酸比均显著高于白光的处理。李岩等(2017)、Hao等(2016)和孙娜(2015)也报道了复合光质的光源可以提高番茄的品质, 改善番茄的外观品质。张克坤等(2017)在设施栽培的早熟葡萄(*Vitis vinifera*)上研究不同光质补光对果实品质的影响发现, 蓝光、紫外光的补光处理可显著加快葡萄果实发育, 并且有利于果实糖含量的提高和有机酸含量的下降, 蓝光补光处理还可以有效加快果实中α-萜品醇、橙花醇、里那醇等萜烯类物质的生成, 而紫外光补光处理的葡萄果实己醛、香叶醇、E-2-己烯醛等香气物质含量最高。Samuolienė等(2010)在草莓上的光照研究表明, 红蓝光质配比(7:1)培养的草莓, 果实中含糖量等指标更高, 品质更佳。戚行江等(2021)利用5种颜色(红、黄、绿、紫、白)避雨膜在杨梅(*Myrica rubra*)上试验表明, 黄膜处理的果实可溶性糖和花色苷含量比对照分别增加了12.05%和12.21%; 红膜处理与对照较接近; 紫膜处理的果实可溶性糖含量比对照减少11.14%。

2 光质对植物光合作用的影响

植物光合作用直接决定其生长发育和产量。植物的干物质主要来源于其光合作用的产物, 光照对光合作用的影响至关重要。光照(光强、光质、光周期等)的变化会直接或间接影响植物的生长发育, 同时植物的光合作用相关生理活动也会对光照的变化及时地作出相应的响应。光质对植物的光合作用具有重要的调节作用(Modarelli等2020; Eugeniusz等2021; Esmaeilizadeh等2021; Moazzen等2021)。

2.1 光质对植物叶片气孔导度的影响

植物叶片气孔是光合作用的通道, 氧气、二氧化碳、水等光合作用的原料和产物能否与外界进行及时的交换取决于叶片气孔的开放程度, 直接决定光合作用的强弱(Lee等2007)。气孔开放是通过叶片保卫细胞中的钾离子和可溶性渗透物等物质的积累来调控的。保卫细胞中钾离子和可溶性渗透物含量的增加可以提高细胞的渗透势, 降低细胞的水势, 保卫细胞吸水, 体积变大, 进而引起细胞气孔开放; 如果保卫细胞中钾离子和可溶性渗透物含量下降, 则细胞渗透势降低, 水势提高, 保卫细胞失水, 体积变小, 进而使细胞气孔关闭。相关研究表明, 光质能通过植物叶片的气孔导度调节植物的光合作用(D'Onofrio等1998; Ramalho等2002)。

不同光质对植物叶片气体交换、叶绿素形成等生理过程具有调控作用(Ramalho等2002), 叶片细胞的光受体(光敏色素、隐花色素)、叶绿体等可以通过不同光质感应调节气孔体积大小和气孔数量(Khattak等2006; Qin等2005; Lin等2004; Sing等1996)。Roni等(2017)在环境可控的设施中用不同光质处理杜仲, 发现相比白光和单色红光处理, 单色蓝光处理的杜仲叶片下表皮层厚度和栅栏细胞的长度、宽度更大, 其叶片的保卫细胞面积、气孔密度及气孔导度更大, 进而增加叶片的光量子通量, 调节光合作用。Lim等(2021)利用不同光质对罗勒照射, 发现含有蓝光的组合光照下光合速率和气孔导度均高于单色红光照射, 绿光和蓝光共同促进植物的气孔发育, 调节植物的水分利用率, 进而影响植物的光合作用。Sakhonwasee等(2017)在牵牛花上的试验、Pichler等(2007)在苹果(*Malus pumila*)上的试验, 以及Clavijo-Herrera等(2018)和Hyeon-Hye等(2004)在生菜上的试验, 也都发现光质对植株叶片的气孔密度、气孔宽度有显著影响。

2.2 光质对植物光合色素含量的影响

植物叶片的光合色素对光能具有吸收、传递和转化的作用, 是植株进行光合作用的基础, 光合色素的构成及其含量对叶片的光合作用有重要的影响作用。光合色素依据其功能作用的不同, 可以具体分为反应中心色素和天线色素等两类, 多数藻类和高等植物的光合色素主要有叶绿素a、叶绿素b、类葫芦卜素等。在光合作用反应中, 叶绿素a、叶绿素b等叶绿素是参加光合作用的主要色素, 类葫芦卜素等色素在光合作用中作为辅助色素吸收叶绿素无法吸收的光波, 然后再将吸收转化的光能传递给叶绿素用于光合作用。类葫芦卜素由胡萝卜素和叶黄素组成, 其在吸收转化光能给叶绿素的同时, 还会通过叶黄素循环来调节天线传递能力, 进而转化过剩激发能来保护叶绿素不受破坏。

相关研究表明, 光质会影响植物光合色素的形成和积累(Bercel等2022; Naif等2021; Zhang等2020)。Qing等(2021)以茄子(*Solanum melongena*)为试验材料, 研究了单色光和不同比例红蓝光对茄子生长的影响, 研究表明叶绿素a、叶绿素b和类胡萝卜素含量在单色红光处理下均有显著升高, 而在蓝光处理下显著降低, 适宜的红蓝(3:1)复合光下, 植物生长、叶片发育、光合色素及特性、碳氮代谢等参数值均达到最大值, 促进茄子生长效果显著。Nguyen等(2021)用不同比例复合光质照射菠菜, 表明红蓝(4:1)复合光可有效调节菠菜的生长, 对叶片和光合色素有显著的影响, 而且得到的菠菜品质更优。de Hsie等(2019)研究不同光质对圆叶李(*Lippia rotundifolia*)的影响, 发现红蓝(2.5:1)复合光促进圆叶李的生长效果最好, 此光质组合下植株的生物特征数据最优, 总叶绿素含量最高。Pawłowska等(2020)在非洲菊(*Gerbera jamesonii*)和Zhao等(2020)在紫花苜蓿(*Medicago sativa*)的研究中, 也发现相比其他光质处理, 红蓝复合光的光合色素水平更高。

2.3 光质对植物光系统性能的影响

光合作用过程分为光反应和暗反应, 其中光反应阶段主要有光系统I (PSI)和光系统II (PSII)两部分构成, PSI在PSII之前, 但电子的传递是首先从PSII开始的。PSII作为植株叶片光合作用的首个位点, 其性能的强弱直接决定了光能的利用率和叶片的光合效率。PSII是植物细胞中一定量亚基组成的复合体, 高等植物的PSII反应中心主要包括*psb A*基因编码蛋白、*psb D*基因编码蛋白、*psb E/F*基因编码蛋白、*psb B*基因编码蛋白、*psb C*基因编码蛋白等蛋白质。PSI通过光合作用的电子传递链和PSII密切结合在一起, 不仅参与非环式的电子传递, 还能促进PSI周围的环式电子传递链的形成

和PSI-PSII的假环式电子的传递。

相关研究表明, 光质影响PSII的活性进而影响植物的光合作用(Xu等2020; Oguchi等2021; Kumiko等2020; Pashkovskiy等2018; 周成波等2017)。Hamdani等(2019)用不同光质的光源培养水稻, 发现蓝光诱导使植株光合的F_v/F_m显著降低, P700后P700$^+$的还原速率降低, 完全被氧化, 同时蓝光诱导NPQ的初始速度越大, NPQ也越高, 对应于NPQ的qE分量, PSII的最大量子产额较低; 相比之下, 水稻长期红光处理下PSII降低, NPQ升高, F_v/F_m无变化。Gao等(2020)用不同光质光源培养洋葱(*Allium fistulosum*)发现, 蓝光的非光化学淬灭系数(NPQ)最高, 同时光系统II (PSII)在暗适应下的最大光化学效率(F_v/F_m)、PSII在光适应下的最大光化学效率(F_v'/F_m')、光化学淬灭系数(q_P)、实际光化学效率(Φ_{PSII})、表观电子传递率(ETR)等叶绿素荧光特性蓝光也均高于其他单色光源的处理, 且蓝光处理叶片的叶绿体超结构发育也最完整。Li等(2020)研究表明蓝光有效改善杜氏藻类光合作用下的初始斜率和最大氧气产生速率的辐照度曲线, 同时降低了补偿辐照度和暗呼吸速率, 蓝光是其光系统PSII的适宜光源, 促进藻类细胞快速分裂生长。相比白光, 红光处理的黄瓜幼苗在定植后生长缓慢, 光合效率降低, 净光合速率(P_n)、PSII有效光化学效率(Φ_{II})显著降低, 而PSII处调节性(Φ_{NPQ})和非调节性(Φ_{NO})能量耗散的量子产量显著升高(苗妍秀等2019)。Paradiso等(2019)在马铃薯、Yousef等(2021)在番茄、Fang等(2021)在大豆和Tian等(2019)在茶叶(*Camellia sinensis*)上的试验, 也报道了光质调节植物光系统性能的相关研究成果。

2.4 光质对植物光合速率的影响

光合作用是植物进行各项生命活动的基础, 光合作用提供植株生命活动所需要的能量和生长发育需要的有机化合物。在太阳全辐射的光谱中, 只有可见光范围的辐射才可以给植株提供光合作用有效的光波; 用不同波段的单色光源培养植物, 植株叶片的光合作用速率不同。通过分析植物光合作用的光谱, 植物的光合作用在蓝光区(440 nm)和红光区(波峰为620 nm)达到峰值, 且红光波峰高度位置约是蓝光波峰高度的1.4倍。因此红蓝光质对植物生长发育、生理活动以及叶片光合速率的影响已经成为国内外专家学者研究的重要内容。

光质通过植株叶片气孔导度、光合色素形成、叶片生理发育等方面来影响植物的光合作用(Zhang等2018; Ghedifa等2021; Liu等2019; Yang等2017; Kang等2022)。Cao等(2013)用不同光质光源培养黄瓜, 研究其光合参数、水分利用效率以及叶绿体超微结构所受影响, 发现单色蓝光和红蓝组合光处理下黄瓜叶片的净光合速率普遍高于其他处理; 处理第10天, 蓝光下植株的净光合速率明显最高, 是白光的1.27倍; 处理第20天, 红蓝(8:2)组合光处理的植株净光合速率最高, 是白光的1.57倍。Hu等(2016)用不同光质光源培养桑树(*Morus alba*), 发现蓝光处理的植株株高和叶面积最小, 红光处理的植株的叶绿素a/b、可溶性蛋白含量、蔗糖和淀粉含量以及叶片氮含量最低, 而红蓝光处理的植株叶片的气孔导度(G_s)、PSII的实际光化学效率(Φ_{PSII})、净光合速率(P_n)等均高于单色光的处理。Di等(2021)研究不同光质对茄子生长发育的影响中, 发现叶绿素a、叶绿素b和类胡萝卜素含量在红光处理下均显著增加, 而蓝光处理下则显著降低; 相反, 单色红光处理抑制了植株的株高、叶片发育和光合特性, 蓝光则提高了植株的光合特性。He等(2020)在油茶(*Camellia oleifera*)、Yang等(2018)在番茄、Esmaeilizadeh等(2021)在草莓、董飞等(2018)在番茄和Miliauskienė等(2021)在生菜上的试验, 也报道了光质调节植物光合效率的相关研究成果。

3 光质对植物碳氮代谢的影响

在植物生长发育的过程中碳氮代谢是最基本(也是最重要)的生理代谢活动之一, 碳氮代谢会直接影响到植物的生长发育情况, 决定其产量及果实的品质。碳代谢主要包括光合产物的固定、碳水化合物运输转化和积累等植物生理活动, 氮代谢主要包括植物氨基酸和蛋白质的合成。植物的碳氮代谢的生理变化能调节植株叶片的光合作用, 同时影响植物根系对矿质元素的吸收以及相关蛋白质和酶的合成。氮代谢活动依赖于碳代谢提供的能量和碳源, 与此同时氮代谢又给碳代谢提供活动所需要的光合色素及相关酶。这两种代谢活

动需要共同的还原力以及碳骨架。碳氮代谢相互协调、相互促进, 有着密切的关系, 共同调控植物的生长发育。光质影响植物碳氮代谢的循环、相关酶的活性以及基因的表达(孙娜等2016; 凌丹丹等2021; 高松等2020)。

3.1 光质对植物碳代谢影响

糖类化合物是植物体内重要的有机代谢物质, 其作为植物光合作用产物是维持植物生命活动的主要能量物质, 糖类化合物含量越高越有利于植物的分蘖和发根。糖类化合物含量的高低是植物体内“源－库－源”协调情况的直接反应, 可以作为植物碳代谢的主要标志之一。光质影响植物光合产物(糖类化合物)的积累(Zhou等2020; Ren等2021; Tarakanov等2022)。

相关研究中, 红光可以促进植物体内果糖、葡萄糖、蔗糖、淀粉等碳水化合物的积累(Zheng等2019; Zhang等2018), 蓝光等其他光质也同样对植物体内的碳代谢具有显著影响(Lukeš等2019; Dickinson等2019)。不同光质对植物的碳代谢的影响, 因植物种类不同而有一定的差异。Hu等(2019)用不同光质发光二极管(LED)和紫外线(UV)照射甜橙(*Citrus sinensis*) 6 d后, 发现LED和UV照射不仅加速了橙子的成熟, 而且使其可溶性糖、有机酸和类胡萝卜素含量发生了显著变化。紫外线处理的果实总可溶性糖、果糖和葡萄糖含量显著增加, 除UVB外, 其他光均能显著诱导总有机酸积累; 红光处理在诱导类胡萝卜素积累方面有显著促进作用, 包括总类胡萝卜素、异黄酮、叶黄素、植物荧光素、β-胡萝卜素等物质。Zhou等(2013)利用连续LED光照种植生菜, 发现红蓝复合光质相比其他光质处理生菜的硝酸盐含量下降、可溶性糖含量增加更为显著; 而Liu等(2018)用不同光质培养生菜发现, 黄光处理生菜的可溶性糖含量显著高于其他光质处理。Wang等(2018)在夜间用不同光质光源对刺梨进行补光, 发现蓝光处理有利于促进次生代谢产物(总黄酮、总多酚等)的产生和积累, 黄光处理能显著提高可溶性糖和多糖含量。Peng等(2020)用不同颜色透明塑料薄膜培养草莓, 研究其品质影响, 发现红色薄膜有利于草莓还原糖、蔗糖、总糖、花青素、可溶性蛋白和总可滴定酸度等物质的积累, 可以生产出高香气草莓。Dong等(2019)研究表明在红蓝(3:1)光质培养下, 番茄果实的可溶性糖、总可溶性固形物、葡萄糖、果糖和蔗糖含量最高。

3.2 光质对植物氮代谢影响

氮代谢是植物生长发育过程中重要的生理活动, 植物通过氮同化作用吸收氮素, 以供生长发育之用。植物主要通过根系吸收利用土壤中的氮素(主要是硝态氮和铵态氮), 因此根系的发育状况直接影响植物氮代谢活动。光质可以通过影响根系的生长情况来间接调节植物的氮代谢活动, 也会直接参与植物氮代谢其他方面, 影响氮代谢相关生理活动产物(如: 硝态氮、可溶性蛋白、游离氨基酸等)的含量以及相关氮代谢酶(如谷氨酰胺合成酶、硝酸还原酶、亚硝酸还原酶等)的活性。

Li等(2021)研究不同光质对叶用莴苣氮代谢的影响, 发现红蓝光质中添加绿光可显著提高生菜叶片亚硝酸盐含量, 原因是通过激活亚硝酸盐还原酶(NiR)基因表达和酶活性, 促进亚硝酸盐还原为铵态氮; 红蓝光质中添加紫光抑制了NR和NiR的基因表达和酶活性, 导致硝酸盐和铵的含量降低; 在氮同化方面, 添加绿光、紫色光和远红光可诱导Asp、Glu和Leu等氨基酸和总氨基酸的增加。Liang等(2022)、Zhang等(2018)、Bian等(2018)和Fu等(2017)在叶用莴苣上的研究也有相似的报道。Gao等(2020)在不同光质对水培菠菜生长研究中, 发现随着蓝光比例的增加, 菠菜维生素C含量提高, 硝态氮含量降低, 光能利用效率提高。Figueroa等(2014)在研究长花冠红藻时发现, 红、蓝光质均能提高硝酸还原酶和谷氨酰胺合成酶的活性, 且红光和蓝光对氮代谢的促进作用被远红光部分逆转(Demotes-Mainard等2016)。刘玉兵等(2020)在研究红蓝光的基础上, 研究了添加绿光、紫光、近远红光等不同光质对芹菜生长的影响, 发现不同处理均提高了芹菜叶柄的硝酸还原酶、谷氨酰胺合成酶和谷氨酸合酶活性, 进而促进氮素吸收以及转化, 增加了氮代谢产物积累及蛋白质的合成。凌丹丹等(2021)研究发现白光基础上增加红光和蓝光可以显著提高叶片全氮和可溶性蛋白含量, 但叶片游离氨基酸含量有明显降低, 叶片中氮代谢

相关酶活性(硝酸还原酶、谷氨酰胺合成酶、谷氨酸合成酶活性)有显著增加。而高松等(2020)的试验表明, 白光处理大葱(*Allium fistulosum*)叶片中不同形态氮含量(NO_3^--N、NH_4^+-N、可溶性蛋白、游离氨基酸含量)和氮代谢相关酶活性(硝酸还原酶、谷氨酰胺合成酶、谷氨酸合成酶活性)均显著高于各单色光(蓝光、红光、绿光和黄光)处理。

4 展望

光质影响着植物的生长、形态建成和生理代谢, 并与光照的其他因素(光强、光周期等)、环境参数(温度、水分、营养、氧气、二氧化碳等)以及栽培技术因素共同决定植物的生长发育。本综述中, 多项研究表明, 单色红光可以促进植株茎的伸长和活性代谢物的合成, 提高果实的营养品质。红光与近远红光有利于植株的形态建成、果实发育、光合作用和干物质的积累。红光和蓝光相互作用, 可以调节植物的生长发育, 提高光合作用效率。单色蓝光通过叶片诱导气孔开发和叶绿体形成, 促进植株的光合作用, 提高叶肉细胞的色素水平。

关于光质对植物形态建成的相关研究在近几年迅速增加, 尤其是发光二极管(LED)技术突破之后, 它可以根据不同作物的生长规律, 设置特定的光谱以及调节光照的强弱。目前, 植物对不同光质的研究中, 植株生长发育对某一光质的响应研究已经比较透彻, 但对于光质与其他因素耦合等方面的研究仍然比较薄弱。在充分利用好光质对植物研究已有成果的基础上, 借助现代生物科学、光谱学和信息科学等技术手段, 未来可在以下几个方面加强研究, 实现光质调节植物生长发育机制研究的突破。

第一, 加强光质与其他因素的耦合研究。植物在生长发育期间阶段性需要的最佳光谱, 以及此光谱下需要的光照强度、光周期、温度范围、矿质营养、水分管理、病虫害防治等方面, 都需要系统的研究。只有充分认识植物生长过程中各项环境因素的协同或拮抗作用, 科学合理调整这些因子, 才能更好调控植物的生长发育, 达到促进或抑制植物生长的目的。

第二, 加强调节自然光光谱的研究。研究者往往通过不同颜色的透明材料反射或吸收一部分特定波段的光波, 来调节自然光的光谱从而调节植物的生长。但在自然光基础上添加不同波段的光, 在植株生长的特定时期, 可以调节植物生长发育。比如番茄在苗期增加蓝光, 有利于培育壮苗; 在果实转色期增加远红光, 有利于番茄色素的形成。

第三, 加强光质增强植物抗逆性的研究。在植物生长发育中, 不可避免遇到低温、弱光、盐碱、干旱、重金属污染等逆境。光质不仅仅可以调剂植物的生长发育, 还可以增强植物的抗逆性, 因此研究光质对植物抗逆性的影响对植物生产具有重要意义。物种的进化往往伴随环境适应性的驯化与选择, 从进化角度寻找基因组中与光质增强抗逆相关的位点, 鉴定并驯化以获得新基因, 补充植物的光质抗逆基因资源, 可促进其分子机理研究及在抗逆性遗传改良方面的应用。

第四, 加强光质对大田作物影响的研究。光质的相关研究多是在封闭可控的环境中进行的, 研究的对象也多以园艺植物(蔬菜、花卉等)为主, 其他作物的研究多以苗期为主。可以从打破暗期、病虫害预防、提高作物抗逆性、改善果实品质等方面展开研究。

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