

土壤水分亏缺下棉花叶片光破坏防御机制研究进展

易小平, 张亚黎, 姚贺盛, 张旺锋*

石河子大学新疆生产建设兵团绿洲生态农业重点实验室, 新疆石河子832003

摘要: 干旱是影响植物生长发育和产量形成的重要环境因素。为了适应干旱环境, 植物形成了一系列保护光合机构免受损伤的光破坏防御机制。棉花(*Gossypium* spp.)抗旱性较强, 即使在中度土壤水分亏缺条件下光合机构也未产生慢性光抑制现象。本文简要地综述了土壤水分亏缺对棉花叶片碳同化能力的影响, 以及水分亏缺条件下棉花叶片的光抑制情况; 阐明了水分亏缺下棉花叶片的光破坏防御机制, 并对大田棉花适应土壤水分亏缺的研究提出了展望。

关键词: 水分亏缺; 棉花; 光抑制; 光保护

水分亏缺是限制作物生长发育和产量形成的最主要的非生物胁迫因子(Boyer 1982; Flexas等2006; Parent等2015)。水分亏缺条件下, 植物CO₂同化能力下降, 光合色素吸收的光能就会超过碳同化的利用能力, 进而导致过剩光能的产生(Kornyeyev等2005; Sanda等2011)。如果这些过剩光能不能及时有效地耗散, 光合电子链将过度还原, 将电子传递给氧或者邻近分子导致活性氧(reactive oxygen species, ROS)或有毒自由基的产生, 对光合机构产生光氧化伤害(Asada 1999; Krieger-Liszkay等2008; Deng等2014)。为了避免光合机构遭受潜在的氧化胁迫, 植物启动了许多光破坏防御机制以维持光能吸收与利用之间的平衡关系。一方面, 植物可通过形态特征的变化来避免过剩光能的吸收, 比如叶片运动(Pastenes等2005; Zhang等2010; Carmo-Silva等2012)和叶绿体运动(Kasahara等2002); 同时, 植物也通过相应的代谢过程来耗散过剩的光能, 如热耗散(Demmig-Adams和Adams 1996; Song等2011)、光呼吸(Osmond 1981; Foyer等2009; Huang等2014)、水水循环(Asada 1999; Miyake和Yokota 2000; Yi等2014)、环式电子传递(Heber和Walker 1992; Huang等2012, 2015)、光破坏的修复(Chow和Aro 2005; Takahashi和Badger 2011)等。

棉花(*Gossypium* spp.)是起源于热带亚热带的一种纤维和油料作物, 广泛种植于70多个国家, 主要有中国、美国、印度、乌兹别克斯坦、埃及等, 其中中国是世界上最大的棉花生产国和消费国。美国农业部统计数据 displays, 2015年世界棉花产量为1.014亿包(每包重量约为217.7 kg), 棉花消费1.096亿包, 其中, 中国棉花产量达到0.238亿包, 消费0.32亿包, 分别占世界棉花总产量和总消费量的

23.5%和29.2%。棉花是抗旱性较强的作物(Turner等1986; Petersen等1992; Kitao和Lei 2007; Yi等2016b), 即使在中度水分亏缺条件下也未导致慢性光抑制的发生(Yi等2014, 2016a, 2016b)。大量研究表明水分亏缺条件下棉花叶片启动了多种光破坏防御机制, 有效避免了光合机构光抑制的发生(Björkman和Schäfer 1989; Massacci等2008; 张亚黎等2008; Yi等2014; Singh等2014, 2015)。基于此, 本文主要综述了棉花田间条件下叶片适应土壤水分亏缺的光破坏防御机制。

1 水分亏缺对棉花叶片碳同化能力的影响

光合作用是决定作物产量形成的重要生理过程, 但对水分亏缺较为敏感。植物叶片的光合速率随土壤相对含水量以及叶片水势的降低而下降(Lawlor 2002)。研究表明, 在棉花叶片水势为-0.85 MPa时, 叶片的最大光合速率约为42 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; 当叶片水势为-1.77 MPa时, 光饱和速率约为18 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Yi等2016a)。水分亏缺导致光合速率降低的原因主要有两个方面: 一是水分亏缺导致气孔关闭, CO₂供应受限(Cornic和Massacci 1996; Flexas等2006; Chaves等2009); 二是叶肉细胞CO₂扩散阻力增大, 光合酶类物质活性下降, 1,5-二磷酸核酮糖(ribulose-1,5-bisphosphate, RuBP)再生受阻等(Lawlor和Cornic 2002)。大量研究表明, 土壤水分亏缺显著降低了棉花叶片的气孔导度(Wullschlegel和Oosterhuis 1990; Inamullah和Isoda 2005a; Kitao和Lei 2007; Chastain等2014; Yi等2014, 2016a,

收稿 2016-09-30 修定 2017-01-08

资助 国家自然科学基金(31260295和U1203283)。

* 通讯作者(E-mail: zwf_shzu@163.com; zhwf_agr@shzu.edu.cn)。

2016b), 但田间棉花叶片气孔导度对土壤水分亏缺的响应没有其他物种或者温室棉花那么敏感, 即使在低叶片水势条件下, 棉花叶片的气孔也未完全关闭(Jordan和Ritchie 1971; Ackerson等1977)。Hu等(2013a)研究表明, 中度水分亏缺条件下棉花叶片的1,5-二磷酸核酮糖羧化/加氧酶(ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBisCO)总量和活性显著降低。Carmo-Silva等(2012)研究报告田间棉花植株同时受热和水分胁迫时, CO₂浓度的降低以及RuBisCO的失活限制了棉花叶片的光合作用。此外, Ennahli和Earl (2005)研究表明中度和重度水分亏缺条件下, 棉花叶片RuBisCO的羧化速率以及羧化位点的CO₂浓度显著降低, 这说明中度和重度水分亏缺条件下棉花叶片的光合作用同时受到气孔和非气孔限制(Pallas等1967; Turner等1986; Genty等1987; Faver等1996; Lacape等1998; Leidi等1999)。目前研究者一致认为气孔和非气孔限制对光合作用的影响取决于水分亏缺的程度(Flexas和Medrano 2002a; Lawlor和Cornic 2002; Chaves等2002)。

2 水分亏缺对棉花叶片光抑制的影响

光是绿色植物进行光合作用的必要能源, 光不足则植物不能顺利进行光合作用, 然而当植物光合色素吸收过剩的光能时又会发生光合效率和光合功能的降低, 这种现象称为光抑制(Powles 1984; Takahashi和Badger 2011)。强光是导致光抑制发生的直接因素, 干旱等逆境环境可通过减少植物对光能的利用、降低植物光饱和点而加剧光抑制(Lawlor 1995; Flexas和Medrano 2002a; Ma等2006)。一般认为光系统II (photosystem II, PSII)是光抑制发生的原初位点和主要作用部位(Aro等1993a; Anderson等1998; Takahashi和Badger 2011)。PSII的光抑制包括慢性光抑制和动态光抑制(Osmond 1994), 前者可导致PSII最大光化学量子效率(F_v/F_m)下降, 与PSII反应中心D1蛋白的净损失有关, 后者为可快速修复的PSII量子效率(Φ_{PSII})的光保护性下调。前人研究结果表明, 水分亏缺条件下, 棉花叶片光合电子传递速率(electron transport rate, ETR)和 Φ_{PSII} 有轻微的上调(Pettigrew 2004; Kitao和Lei 2007; Massacci等2008; Zhang等2011), 也有研究表明ETR和 Φ_{PSII} 稳定不变(张亚黎等2008;

Snider等2013, 2014; Chastain等2014; Yi等2016a)或者ETR和 Φ_{PSII} 降低的(Ennahli和Earl 2005; Inamullah和Isoda 2005b; Carmo-Silva等2012; Yi等2016a)。水分亏缺导致棉花叶片ETR和 Φ_{PSII} 稳定不变、轻微上升或者下降与水分亏缺强度、不同生长环境以及不同材料等密切相关。正常条件下, 植物叶片的 F_v/F_m 变化较小, 基本维持在0.83 (Björkman和Demmig 1987; 张守仁1999)。前人研究表明植物叶片的 F_v/F_m 较稳定, 一定水分亏缺范围内不受叶片水分状况的影响, 但重度或长期水分亏缺极易导致植物叶片发生慢性光抑制, 例如, 非灌溉葡萄(*Vitis vinifera*)叶片的 F_v/F_m 维持在0.72~0.78之间(Flexas等1998)。小麦(*Triticum aestivum*)叶片PSII光化学活性和蛋白代谢未受轻度水分亏缺的影响, 但当叶片水势下降到-1.8 MPa时, PSII反应中心的D1和D2蛋白发生降解(He等1995)。然而, 大量研究表明, 棉花叶片PSII活性对水分亏缺不敏感(Genty等1987; Kitao和Lei 2007; 张亚黎等2008; Massacci等2008; Zhang等2010; Chastain等2014; Snider等2015; Yi等2014, 2016a, 2016b)。张亚黎等(2008)研究发现不同水分亏缺条件下, 棉花叶片的 F_v/F_m 无明显变化, 维持在0.83~0.84之间。Yi等(2014, 2016a)研究发现中度水分亏缺条件下(叶片水势约为-2.0 MPa), 棉花叶片的 F_v/F_m 也未下降, 维持在0.85左右。水分亏缺及复水后, 棉花叶片PSII和光系统I (photosystem I, PSI)活性未受到水分亏缺的影响(Yi等2016b)。此外, Zhang等(2010)研究了大田棉花在极度干旱条件下(叶片水势约为-4.0 MPa)的日变化, 结果表明即使在高温(最高温度达34°C)和高光强(水平最高光强达1 880 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)的环境条件下, 极度干旱棉花叶片的 F_v/F_m 在白天也只是呈现暂时性下调, 傍晚和夜间又可完全恢复。以上研究结果表明, 土壤水分亏缺不易导致棉花叶片PSII发生不可修复的慢性光抑制。

3 水分亏缺条件下棉花叶片的光破坏防御机制

水分亏缺导致棉花叶片碳同化能力降低, 减少了叶片对吸收光能的利用, 这可能会导致过剩激发能增加和ROS代谢增强。如过剩激发能未及时通过各种耗能途径耗散出去, 光合反应中心就会处于过激发状态, 这极有可能导致光抑制的产生。但如上所述, 水分亏缺并未导致棉花叶片PSII

发生不可修复的慢性光抑制。大量研究表明, 棉花叶片具有较强的光破坏防御能力以适应水分亏缺, 包括通过形态特征及叶片角度的改变来减少对光能的吸收(Wilson等1987; Pettigrew 2004; Parida等2007; 张亚黎等2008; Zhang等2010; Carmo-Silva等2012)、过剩光能的热耗散(Björkman和Schäfer 1989; Yi等2016a)、通过光化学途径(光呼吸、Mehler反应和环式电子传递)进行的光保护性调节(Massacci等2008; Chastain等2014; Yi等2014, 2016a; Singh等2014, 2015)、ROS代谢(Burke等1985; Mahan和Wanjura 2005; Korniyev等2003; Yi等2016a)以及光氧化伤害的修复(Hu等2013b)。

3.1 叶片运动

多种植物叶片能够随着太阳入射光线的改变而运动, 这种现象称为“向日性运动”(Ehleringer和Forseth 1980)。通常, 叶片运动包括向日性运动、偏向日性运动和萎焉运动三种类型。向日性运动是为了捕获更多的光能, 而偏向日性运动和萎焉运动是为了减少对光能的捕获, 避免吸收过剩光能。前人研究表明叶片向日性运动受生长环境的影响, 如: 光照强度、温度、水分、养分等(Shackel和Hall 1979; Oosterhuis等1985; Fu和Ehleringer 1989; Kao和Forseth 1991, 1992)。正常生长条件下, 棉花叶片一天中均呈现向日性运动(Lang 1973; Miller 1975), 豆科作物叶片在日进程中呈现偏向日性运动(川嶋良一1969; Oosterhuis等1985; Berg和Heuchelin 1990)。水分亏缺条件下, 植物叶片呈现偏向日性运动或萎焉运动, 这有利于维持光能吸收与利用间的平衡(Kao和Forseth 1992; Isoda和Wang 2002; Inamullah和Isoda 2005a; Pastenes等2005; 张亚黎等2008; Zhang等2010; Carmo-Silva等2012)。Kao和Forseth (1992)研究表明, 阻断不同水氮供应条件下大豆叶片的偏向日性运动将加速光抑制。Pastenes等(2005)通过阻止水分亏缺条件下大豆叶片的偏向日性运动得到了相似的结果。此外, 耐旱性的蕨类植物在干旱条件下通过茎秆卷曲有效避免了光抑制的发生(Lebkuecher和Eickmeier 1991)。

棉花叶片依据其自身的水分状况呈现向日性运动和萎焉运动(Lang 1973; Ehleringer和Hammond 1987; 张亚黎等2008, 2010; Zhang等2010;

Carmo-Silva等2012), 但向日性运动只针对于陆地棉叶片, 海岛棉叶片的向日性运动较弱或完全没有(Lang 1973; Ehleringer和Hammond 1987; 张亚黎等2010)。Zhang等(2009)研究了固定(叶片无向日性运动)和未固定(叶片有向日性运动)陆地棉叶片光合特性的日变化, 结果发现未固定棉花叶片呈现更高的碳同化能力和水分利用效率, 但固定与未固定棉花叶片的 F_v/F_m 表现出相似的日变化规律, 这就表明棉花叶片具有很强的利用吸收光能的能力。事实证明陆地棉叶片可以通过相对较强的光化学途径来耗散激发能(张亚黎等2010; Zhang等2011)。Wang等(2004)研究表明水分亏缺条件下陆地棉叶片仍能保持一定程度的向日性运动。张亚黎等(2008)研究结果表明, 中午时分轻度水分亏缺条件下(田间持水量的60%), 陆地棉叶片的PSII活性与对照间无明显差异, 叶片仍具有向日性运动; 但中度水分亏缺条件下(田间持水量的45%), PSII光化学效率降低, 光抑制程度加强, 叶片出现暂时萎焉下垂运动, 向日性运动消失。水分亏缺条件下陆地棉叶片萎焉运动保护了水分亏缺棉花叶片免受光损害, 并且还能维持一定的碳同化能力(Zhang等2010)。Carmo-Silva等(2012)研究发现, 重度水分亏缺条件下, 海岛棉叶片在中午也出现暂时萎焉运动。综上所述, 正常生长条件和适度水分亏缺条件下, 陆地棉叶片呈现向日性运动, 吸收的光能可以通过较强的电子传递途径耗散; 中度和重度水分亏缺条件下, 陆地棉和海岛棉叶片均发生下垂萎焉运动, 这避免了棉花叶片吸收过多的光能, 有效防止了光抑制的发生。

3.2 热耗散

光能过剩时, 植物叶片通过增加热耗散有效地耗散了部分过剩光能(Demmig-Adams 1990; Horton等1996; Ahn等2008), 通常用非光化学淬灭(non-photochemical quenching, NPQ)来度量热耗散的程度。其中, 依赖叶黄素循环(xanthophyll cycle)的热耗散被认为是保护光合机构免受过剩光能破坏的主要途径。叶黄素循环是指参与该循环的三个组分紫黄质、环氧玉米黄质和玉米黄质依照光能过剩情况而相互转变的过程(Demmig-Adams和Adams 1996, 2006)。Flexas和Medrano (2002b)统

计发现正常生长条件和饱和光强下,植物叶片吸收光能的54%~72%用于热耗散;在中度和重度水分亏缺条件下,通过热耗散途径耗散的能量高达叶片所吸收光能的70%~92%。Björkman和Schäfer (1989)研究发现正常生长条件下,棉花叶片吸收光能的44%用于光合电子传递,剩下的56%以热能的形式耗散;中度和重度水分亏缺条件下,棉花叶片吸收的光能70%~82%用于热耗散。棉花叶片热耗散的日变化与叶片接受光强的日变化趋势一致,中午时分棉花叶片吸收的光能过剩时,热耗散能有效耗散过剩光能保护光合机构(Kornyeyev等2005; Zhang等2009; 张亚黎等2010)。张亚黎等(2008)和Zhang等(2010)研究发现水分亏缺条件下棉花叶片的热耗散能力在下午14:00~18:00明显高于正常水分条件下棉花叶片的热耗散能力。此外,Massacci等(2008)研究发现高光强下,中度水分亏缺显著增强了棉花叶片的热耗散能力。但也有相反的研究结果,认为水分亏缺并未导致棉花叶片热耗散能力的增强(Genty等1987; Zhang等2011; Yi等2016a)。Inamullah和Isoda (2005b)研究发现水分亏缺条件下,棉花叶片的光化学反射指数(photochemical reflectance index, PRI)无显著变化,表明水分亏缺条件下依赖于叶黄素循环的热耗散能力并未增强。此外,张亚黎等(2010)和Yi等(2016a)研究发现正常条件下,海岛棉比陆地棉具有更强的热耗散能力。这表明不同棉花材料以及试验环境条件,比如温度、光强可能导致棉花叶片热耗散对水分亏缺的不同响应。

3.3 光化学途径的光破坏防御作用

正常生长条件下,大部分光合机构的光合电子流用于驱动光化学反应,将吸收的光能转化成活跃的化学能储存在ATP、NADPH和还原型铁氧还蛋白(reduced ferredoxin, Fd_{red})中。而分配到光化学反应上的激发能主要用于光合碳还原、光呼吸碳氧化、氧的还原(Mehler反应)、氮代谢等。大量研究表明,当水分亏缺导致棉花叶片碳同化能力下降时,过剩的激发能可以通过其他的电子传递途径得以耗散,包括光呼吸(Massacci等2008; Chastain等2014; Yi等2014, 2016a)、Mehler反应(Yi等2014, 2016a)、环式电子传递(Singh等2014, 2015)等。

3.3.1 光呼吸

卡尔文循环中, RuBisCO催化RuBP的羧化作用产生卡尔文循环的中间产物3-磷酸甘油。但是,在CO₂受到限制的条件下, RuBisCO催化RuBP的加氧作用,生成2-磷酸甘油(Ogren和Bowes 1971),再经过光呼吸碳循环生成3-磷酸甘油。Flexas和Medrano (2002b)统计发现在正常生长条件和饱和光强下,植物叶片吸收光能的20%~30%用于碳还原,10%~20%用于光呼吸作用,表明光呼吸是除碳同化以外的重要电子库。Björkman和Schäfer (1989)研究发现正常生长条件下的棉花,大约25%的吸收光能用于碳同化,19%的吸收光能用于光呼吸。CO₂受到限制时,光呼吸能够维持一定的线性电子传递和光能利用率,对光合器官起保护作用,避免产生光破坏。Chastain等(2014)和Yi等(2014)利用气体交换和叶绿素荧光相结合的方法,研究了土壤水分亏缺对棉花叶片光合生理代谢的影响,结果表明当水分亏缺导致气孔导度和胞间二氧化碳浓度下降时,碳同化过程首先受到限制,光呼吸能力随之增强。Flexas和Medrano (2002b)统计发现轻度水分亏缺条件下,植物叶片的光呼吸速率增强,而中度和重度水分亏缺条件下,光呼吸能力减弱。这主要是因为RuBisCO催化的是一个竞争反应,羧化与加氧速率的相对比例主要依赖于CO₂和O₂的相对浓度,轻度水分亏缺条件下,气孔关闭导致细胞间CO₂浓度降低, O₂的浓度就相对增加,此时主要以O₂为底物,电子传递给氧用于RuBisCO的加氧作用,光呼吸增强;中度和重度水分亏缺条件下, RuBisCO活性受到抑制,羧化和加氧速率均降低,因此,降低了碳同化和光呼吸作用。Massacci等(2008)研究了棉花叶片对水分亏缺的适应机制,结果表明在水分亏缺的初始阶段光呼吸能力增强。Yi等(2016a)也利用气体交换和叶绿素荧光相结合的方法,研究了陆地棉和海岛棉适应水分亏缺的光破坏防御机制,结果表明轻度水分亏缺条件下,陆地棉和海岛棉叶片光呼吸能力增强,而中度水分亏缺下的光呼吸能力弱于轻度水分亏缺下的光呼吸能力。事实上,利用气体交换和叶绿素荧光相结合的方法报道的结果一致表明轻度水分亏缺下植物叶片的光呼吸增强,而中度和重度水分亏缺下光呼吸减弱,但利用气体交换方法报道水分

亏缺条件下光呼吸能力增强均是基于光呼吸相对值的变化(光呼吸速率与光合速率之比) (Lawlor 1976; Björkman和Schäfer 1989; Flexas等2002), 光呼吸的绝对值降低(Gerbaud和André 1980; Biehler和Fock 1996; Zhang等2011)。不同试验方法可能导致不同的试验结果, 如何消除不同试验方法间的差异, 准确测量光呼吸仍需深入研究。

3.3.2 Mehler反应

Mehler反应即来自水中的电子经PSII和PSI, 在PSI端传给大气中的分子氧形成超氧阴离子($O_2^{\cdot-}$)的电子传递过程(Mehler 1951)。大量研究表明正常供水条件下, Mehler反应所占总光合电子传递的比例较小(Björkman和Schäfer 1989; Biehler和Fock 1996; Osmond等1997; Badger等2000; Flexas等1999, 2002)。但在水分亏缺条件下, 当电子过剩时, Mehler反应以分子氧为电子受体, 可以分流一部分线性电子, 防止光合电子传递链的过度还原(Biehler和Fock 1996; Yi等2014)。Biehler和Fock (1996)利用 $^{16}O_2/^{18}O_2$ 同位素示踪和质谱技术测定了水分亏缺下小麦叶片 O_2 的交换情况, 结果显示当水势在-3.0~-0.7 MPa范围内, O_2 的总吸收量随水分亏缺程度的加重而增加, 当叶片水势为-2.6 MPa时, 乙醇酸合成速率(光呼吸绝对速率)降低, 这就表明当小麦叶片水势为-2.6 MPa时, 传递给 O_2 的电子流的增加主要是Mehler反应而非光呼吸, 大约有29.1%的光合电子用于Mehler反应。Yi等(2014)利用Miyake和Yokota (2000)同步测量气体交换和叶绿素荧光的方法计算了电子流分配情况, 结果显示棉花叶片水势为-1.0 MPa时, 用于Mehler反应的电子流占总电子流的4.3%; 当叶片水势为-1.3 MPa时, 用于Mehler反应的电子流占总电子流的8.3%; 当叶片水势为-2.1 MPa时, 用于Mehler反应的电子流占总电子流的15.2%, 表明随着水分亏缺程度的加重, Mehler反应的活性逐渐增强。但Björkman和Schäfer (1989)研究结果发现随水分亏缺程度的加重, 用于光呼吸和Mehler反应的总电子流在逐渐减少, 表明Mehler反应在棉花叶片耗散过剩电子中的贡献较小甚至没有。类似的研究结果在番茄(*Solanum lycopersicum*) (Haupt-Herting和Fock 2002)、葡萄(Flexas等1999, 2002)、菜豆(*Phaseolus vulgaris*)和玉米(*Zea mays*) (Driever和Baker 2011)中也有报道,

认为Mehler反应作为电子库的作用并不重要。至于水分亏缺下, Mehler反应在棉花叶片中的光破坏防御作用还需进一步研究。此外, 值得注意的是Mehler反应活性的增强必定会导致超氧化物、 H_2O_2 以及羟基自由基的产生, 所以Mehler反应必须伴随着抗氧化酶系统的协同运转才能起到有效的保护作用。

3.3.3 环式电子传递

环式电子传递主要是指PSI侧处于还原态的电子通过NADPH或Fd返回光合电子链, 进而传递到质体醌(plastoquinone, PQ)库或细胞色素 b_6/f 的电子传递过程(Heber和Walker 1992; Breyton等2006; Joliot和Joliot 2006; Johnson 2011)。围绕PSI的环式电子传递(cyclic electron flux around PSI, CEF-PSI)通过促进跨类囊体膜质子梯度的建立, 驱动了ATP合成酶合成ATP, 激活了PSII处的热耗散, 稳定了放氧复合体(Arnou等1967; Heber和Walker 1992; Golding和Johnson 2003; Miyake等2004; Munekage等2004; Shikanai 2007; Takahashi等2009; Kou等2013; Huang等2016b)。此外, CEF-PSI能够缓解PSI受体端的过度还原, 有效防止了PSI受到光损伤, 对PSI起到重要的光保护作用(Munekage等2002; Huang等2013, 2016a; Kono等2014; Tikkanen等2015)。大量研究表明当植物遭受干旱胁迫时, CEF-PSI在光破坏防御中具有重要的作用(Katona等1992; Golding和Johnson 2003; Munné-Bosch等2005; Gao等2011; Gao和Wang 2012; Huang等2012, 2013; Kou等2013; Singh等2014, 2015)。Huang等(2012)利用荧光和P700技术研究了蛛毛苣苔(*Paraboea sinensis*) CEF-PSI在干旱胁迫下的光破坏防御作用, 结果显示蛛毛苣苔在遭遇干旱胁迫后CEF-PSI可上调至线性电子传递的3倍以上, 有效防止了光抑制的发生。Singh等(2014)利用同样的方法研究了室内盆栽棉花叶片CEF-PSI对水分亏缺的响应, 结果发现正常生长棉花叶片的CEF/ETR(II)约为0.3, 轻度水分亏缺下该比值约为0.8, 而重度水分亏缺该比值高达1.8左右, 这表明盆栽棉花叶片的CEF在轻度和重度水分亏缺下均被激发, 能有效耗散过剩电子, 对PSII和PSI起到重要的光保护作用。最近, 我们用Kou等(2013)提出的一种准确量化CEF-PSI的方法测量了室内盆栽棉花

叶片在不同水分条件下的CEF-PSI, 结果也显示CEF-PSI随水分亏缺程度的加重而增强(论文待发表)。此外, Singh等(2015)比较了海岛棉和陆地棉叶片CEF-PSI对水分亏缺的响应, 结果显示水分亏缺均激发了海岛棉和陆地棉的CEF-PSI, 总体上海岛棉的CEF-PSI能力比陆地棉的低, 水分亏缺下海岛棉叶片的CEF-PSI是正常水分条件下的1.5~2倍。然而, 我们在大田水分亏缺条件下的初步研究表明, 棉花叶片的CEF-PSI只有在中度水分亏缺下才得以启动, 且与陆地棉相比, 海岛棉具有更强的CEF-PSI能力(论文待发表)。CEF-PSI的激发为CO₂的固定提供了额外的ATP (Rumeau等2007; Shikanai 2014; Yamori等2016; Yamori和Shikanai 2016)。CEF-PSI缺失的烟草(*Nicotiana tabacum*)突变体在空气湿度低的条件下生长受到限制(Horvath等2000)。Yamori等(2016)研究发现在自然波动的光照条件下, CEF-PSI的调控可以优化水稻(*Oryza sativa*)光合作用和生长发育过程。此外, CEF-PSI介导合成的ATP也有可能用于PSII光损伤的修复。Allakhverdiev等(2005)研究证实了PSII的光损伤速度受ATP合成的影响。Gao和Wang (2012)研究表明CEF-PSI的增强促进了严重失水条斑紫菜(*Porphyra yezoensis*)的修复。中午高光条件下CEF-PSI的激发有效避免了PSII和PSI发生光抑制, 下午低光条件下CEF-PSI通过合成额外ATP对PSII的修复非常重要(Huang等2016a)。目前大多利用荧光技术测定通过PSII的线性电子流ETR(II)以及用P700测定通过PSI的电子流ETR(I), 用两者之差来表示CEF-PSI的大小, 由于光化光和测量光不能穿过整个叶片, 导致光合机构接受的光较弱, 光化学淬灭(photochemical quenching, q_p)小于实际值, 这就低估了ETR(II), 进而高估了植物叶片的环式电子流。因此, 如何准确量化CEF-PSI还需进一步研究。

3.4 ROS清除系统

正常生长条件下, 植物体内ROS的产生与清除处于动态平衡状态, 光合机构不会遭到破坏, 但逆境胁迫导致光能过剩时, 植物体内ROS产生和清除间的平衡就会受到破坏, 导致ROS大量积累(Mittler 2002)。ROS对光合机构具有很强的氧化能力, 对许多细胞组分, 如脂类、蛋白质以及核酸

等有破坏作用(Monk等1987; Sharma等2012)。为了避免ROS对光合机构造成伤害, 植物在长期的进化过程中形成了一套完整的抗氧化系统, 包括超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)、过氧化氢酶(catalase, CAT)、抗坏血酸过氧化物酶(ascorbate peroxidase, APX)、谷胱甘肽还原酶(glutathione reductase, GR)等在内的酶促抗氧化系统和类胡萝卜素(carotenoid, Car)、抗坏血酸(ascorbic acid, AsA)、谷胱甘肽(reduced glutathione, GSH)、甘露醇、类黄酮等非酶促抗氧化系统, 酶促和非酶促抗氧化系统的相互配合能有效清除O₂⁻和H₂O₂, 解除ROS的毒害作用(Smirnoff 1993; Alscher等1997)。

水分亏缺可能会诱导植物产生氧化胁迫, 同时也触发抗氧化防御系统(Smirnoff 1993)。比如, 水分亏缺导致水稻叶片发生氧化胁迫, 表现为脂质过氧化、叶绿素漂白、抗氧化剂(AsA、GSH、Car等)含量降低, SOD活性以及AsA-GSH循环增强(Yong和Jin 1999)。水分亏缺条件下, 小麦和棉花叶片GR活性增强(Burke等1985)。Mahan和Wanjura (2005)研究了土壤水分亏缺下大田棉花叶片抗氧化系统的光保护作用, 结果显示水分亏缺导致棉花叶片的AsA含量以及APX的活性增加, 水分亏缺未导致棉花叶片丙二醛(malondialdehyde, MDA)含量的增加, 这表明土壤水分亏缺条件下棉花叶片的抗氧化能力能够保护其自身不受氧化胁迫的伤害。Kornyeyev等(2003)研究发现低温条件下(10°C), 过量表达APX的棉花突变株能提高其抗氧化系统能力, 进而增强棉花耐低温能力。Badawi等(2004)研究发现, 过量表达烟草叶绿体中的APX能够增加其对盐和干旱胁迫的适应能力。Yi等(2014, 2016b)研究发现土壤水分亏缺导致棉花叶片的O₂⁻产生速率和H₂O₂含量增加, 其清除酶SOD、POD和APX活性随之增强。Yi等(2016a)比较研究了陆地棉和海岛棉叶片抗氧化系统对土壤水分亏缺的响应, 结果发现水分亏缺提高了陆地棉叶片的SOD和APX活性, 而海岛棉叶片的抗氧化酶活性对水分亏缺不敏感, 这表明水分亏缺条件下陆地棉具有更强的ROS清除能力。但也有相反的研究报道, 认为水分亏缺降低了棉花叶片的SOD和GR活性(Kawakami等2010)。Reddy等(2004)认为水分胁迫

下植物抗氧化能力增强、减弱或对水分不敏感主要是由于水分亏缺的强度、植物种类以及植物的生长发育阶段不同导致的。

3.5 光损坏的修复

环境胁迫条件下, 尽管植物有多种光破坏防御机制, 但光合器官的损坏是光合作用不可避免的一个结果, 并且PSI和PSII反应中心都会受到光的氧化损伤, 单线态氧能够破坏PSII反应中心(Chow和Aro 2005; Krieger-Liszkay等2008), O_2^- 对PSI反应中心具有很强的破坏作用(Sonoike 2006)。PSII在弱光条件下的修复速度很快, 几个小时内便可完全修复(He和Chow 2003; Zhang和Scheller 2004; Huang等2010b), 这主要是由于D1蛋白的迅速周转、受损PSII亚基的快速修复以及重新构建具有功能性的PSII (Aro等1993b)。PSI的修复在大麦(*Hordeum vulgare*)和拟南芥(*Arabidopsis thaliana*)中是一个非常缓慢的过程, 通常需要一个星期才能完全修复(Teicher等2000; Zhang和Scheller 2004), PSI的慢速修复主要是由于所有PSI核心亚基同时降解, 受损的复合体几乎没有可再使用的(Zhang和Scheller 2004)。光抑制的发生是光损伤与修复过程失调的结果(Allahverdiev等2005), 只有损伤速率超过修复速率时才会发生净光抑制, 也就是慢性光抑制(Takahashi和Badger 2011)。因此, 为了避免慢性光抑制的产生, 植物的修复速率一定要快于损伤速率。Aro等(1993b)研究表明, 在不同生长光强下, 维持豌豆(*Pisum sativum*)叶片D1蛋白合成速率与降解速率间的平衡可避免慢性光抑制的发生。如上文所述土壤水分亏缺并未导致大田棉花叶片发生慢性光抑制, 据此推测棉花叶片的修复速率快于损伤速率, 有效避免了光抑制的发生。Lee等(2001)和Kato等(2002)研究报道高光下生长的植物具有较高的修复速率, 这表明高光下生长的植物维持了一个较高的D1周转速率。Oguchi等(2008)研究发现了类似的规律, 即高光下生长的菠菜(*Spinacia oleracea*)其修复系数要高于低光下生长的菠菜的修复系数。Hu等(2013b)研究发现, 棉花叶片的修复系数随光强的增加而稳定上升, 叶片未受到氧化胁迫。大田条件下生长的棉花经常伴随着高光, 这或许是导致棉花叶片修复速率较快的原因之一。此外, PSII的修复速率还

依赖于PSI受损的程度, PSI受损较轻的前提下, PSII的修复很快, 但如果PSI受损严重, PSII的损坏将不能修复(Huang等2010a, b)。Yi等(2016b)研究发现水分亏缺并未导致棉花叶片PSII和PSI发生慢性光抑制, 这表明棉花叶片PSI的稳定性保证了PSII的快速修复。

4 展望

综上所述, 水分亏缺导致棉花叶片碳同化能力下降, 但光合系统较稳定, 这就导致棉花叶片吸收的光能超过了碳同化的利用能力, 造成光能过剩。棉花是抗旱性较强的作物, 为了避免过剩光能对光合器官造成光氧化胁迫, 棉花也形成了一套完整的光破坏防御系统(包括叶片运动、热耗散、交替电子传递、ROS清除、光破坏修复等), 这些防御系统相互协调, 共同起到对棉花的光保护作用, 其中通过交替电子传递进行的光保护性调节是棉花最为重要的光破坏防御机制。对于棉花叶片光破坏防御机制的研究目前还存在不足, 一是测量方法, 大部分研究结果是基于荧光技术, 由于荧光只能检测叶片表层的信号, 测量结果不能真实反映整个叶片组织的变化; 二是试验材料, 科学家们热衷于借助突变株与抑制剂来研究一些机理上的科学问题, 目前棉花在光破坏防御方面的突变株还较少。此外, 我们已经明确了土壤水分亏缺下田间棉花叶片的修复速率较快, 但导致棉花叶片修复速率较快的机制尚不清楚。CEF在植物抗逆过程中的光破坏防御作用是当前研究的一个热点, CEF通过促进跨膜质子梯度的建立, 激发ATP合成酶合成ATP, 这或许为棉花叶片的快速修复提供了ATP, 但CEF在田间棉花叶片适应土壤水分亏缺的光破坏防御作用及CEF与其他光破坏防御途径间的关系还需进一步深入研究。

参考文献

- Ackerson RC, Krieg DR, Haring CL, Chang N (1977). Effects of plant water status on stomatal activity, photosynthesis, and nitrate reductase activity of field grown cotton. *Crop Sci*, 17: 81–84
- Ahn TK, Avenson TJ, Ballottari M, Cheng YC, Niyogi KK, Bassi R, Fleming GR (2008). Architecture of a charge-transfer state regulating light harvesting in a plant antenna protein. *Science*, 320: 794–797
- Allakhverdiev SI, Nishiyama Y, Takahashi S, Miyairi S, Suzuki I, Murata N (2005). Systematic analysis of the relation of electron transport and ATP synthesis to the photodamage and repair of

- photosystem II in synechocystis. *Plant Physiol*, 137: 263–273
- Alscher RG, Donahue JL, Cramer CL (1997). Reactive oxygen species and antioxidants: relationships in green cells. *Physiol Plant*, 100: 224–233
- Anderson JM, Park YI, Chow WS (1998). Unifying model for the photoinactivation of photosystem II *in vivo* under steady-state photosynthesis. *Photosynth Res*, 56: 1–13
- Arnon DI, Tsujimoto HY, Mcswain BD (1967). Ferredoxin and photosynthetic phosphorylation. *Nature*, 214: 562–566
- Aro EM, Mccaffery S, Anderson JM (1993b). Photoinhibition and D1 protein degradation in peas acclimated to different growth irradiances. *Plant Physiol*, 103: 835–843
- Aro EM, Virgin I, Andersson B (1993a). Photoinhibition of photosystem II. Inactivation, protein damage and turnover. *Biochim Biophys Acta*, 1143: 113–134
- Asada K (1999). The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. *Annu Rev Plant Physiol Plant Mol Biol*, 50: 601–639
- Badawi GH, Kawano N, Yamauchi Y, Shimada E, Sasaki R, Kubo A, Tanaka K (2004). Over-expression of ascorbate peroxidase in tobacco chloroplasts enhances the tolerance to salt stress and water deficit. *Physiol Plant*, 121: 231–238
- Badger MR, von Caemmerer S, Ruuska S, Nakano H (2000). Electron flow to oxygen in higher plants and algae: rates and control of direct photoreduction (Mehler reaction) and rubisco oxygenase. *Philos Trans R Soc B-Biol Sci*, 355: 1433–1446
- Berg VS, Heuchelin S (1990). Leaf orientation of soybean seedlings. I. Effect of water potential and photosynthetic photon flux density on paraheliotropism. *Crop Sci*, 30: 631–638
- Biehler K, Fock H (1996). Evidence for the contribution of the Mehler-peroxidase reaction in dissipating excess electrons in drought-stressed wheat. *Plant Physiol*, 112: 265–272
- Björkman O, Demmig B (1987). Photon yield of O₂ evolution and chlorophyll fluorescence at 77 K among vascular plants of diverse origins. *Planta*, 170: 489–504
- Björkman O, Schäfer C (1989). A gas exchange–fluorescence analysis of photosynthetic performance of a cotton crop under high-irradiance stress. *Philos Trans R Soc B-Biol Sci*, 323: 309–311
- Boyer JS (1982). Plant productivity and environment. *Science*, 218: 443–448
- Breyton C, Nandha B, Johnson GN, Joliot P, Finazzi G (2006). Redox modulation of cyclic electron flow around photosystem I in C3 plants. *Biochemistry*, 45: 13465–13475
- Burke JJ, Gamble PE, Hatfield JL, Quisenberry JE (1985). Plant morphological and biochemical responses to field water deficits. *Plant Physiol*, 79: 415–419
- Carmo-Silva AE, Gore MA, Andrade-Sanchez P, French AN, Hunsaker DJ, Salvucci ME (2012). Decreased CO₂ availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. *Environ Exp Bot*, 83: 1–11
- Chastain DR, Snider JL, Collins GD, Perry CD, Whitaker J, Byrd SA (2014). Water deficit in field-grown *Gossypium hirsutum* primarily limits net photosynthesis by decreasing stomatal conductance, increasing photorespiration, and increasing the ratio of dark respiration to gross photosynthesis. *J Plant Physiol*, 171: 1576–1585
- Chaves MM, Flexas J, Pinheiro C (2009). Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann Bot*, 103: 551–560
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho I, Faria T, Pinheiro C (2002). How plants cope with water stress in the field. *Photosynthesis and growth*. *Ann Bot*, 89: 907–916
- Chow WS, Aro EM (2005). Photoinactivation and mechanisms of recovery. In: Wydrzynski T, Satoh K, Freeman JA (eds). *Photosystem II. The Light-Driven Water: Plastoquinone Oxidoreductase*. Dordrecht: Springer Netherlands, 627–648
- Cornic G, Massacci A (1996). Leaf photosynthesis under drought stress. In: Baker NR (ed). *Photosynthesis and the Environment*. Berlin: Kluwer Academic Publishers, 347–366
- Demmig-Adams B (1990). Carotenoids and photoprotection in plants: a role for the xanthophyll zeaxanthin. *Biochim Biophys Acta*, 1020: 1–24
- Demmig-Adams B, Adams III WW (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends Plant Sci*, 1: 21–26
- Demmig-Adams B, Adams III WW (2006). Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytol*, 172: 11–21
- Deng B, Jin X, Yang Y, Lin Z, Zhang Y (2014). The regulatory role of riboflavin the drought tolerance of tobacco plants depends on ROS production. *Plant Growth Regul*, 72: 269–277
- Driever SM, Baker NR (2011). The water–water cycle in leaves is not a major alternative electron sink for dissipation of excess energy when CO₂ assimilation is restricted. *Plant Cell Environ*, 34: 837–846
- Ehleringer J, Forseth I (1980). Solar tracking by plants. *Science*, 210: 1094–1098
- Ehleringer JR, Hammond SD (1987). Solar tracking and photosynthesis in cotton leaves. *Agric For Meteorol*, 39: 25–35
- Ennahli S, Earl HJ (2005). Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. *Crop Sci*, 45: 2374–2382
- Faver KL, Gerik TJ, Thaxton PM, El-Zik KM (1996). Late season water stress in cotton: II. Leaf gas exchange and assimilation capacity. *Crop Sci*, 36: 922–928
- Flexas J, Bota J, Escalona JM, Sampol B, Medrano H (2002). Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Funct Plant Biol*, 29 (4): 461–471
- Flexas J, Bota J, Galmés J, Medrano H, Ribas-Carbó M (2006). Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. *Physiol Plant*, 127: 343–352
- Flexas J, Escalona JM, Medrano H (1998). Down-regulation of photosynthesis by drought under field conditions in grapevine leaves. *Aust J Plant Physiol*, 25: 893–900
- Flexas J, Escalona JM, Medrano H (1999). Water stress induces dif-

- ferent levels of photosynthesis and electron transport rate regulation in grapevines. *Plant Cell Environ*, 22: 39–48
- Flexas J, Medrano H (2002a). Drought-inhibition of photosynthesis in C_3 plants: stomatal and non-stomatal limitations revisited. *Ann Bot*, 89: 183–189
- Flexas J, Medrano H (2002b). Energy dissipation in C_3 plants under drought. *Funct Plant Biol*, 29: 1209–1215
- Foyer CH, Bloom AJ, Queval G, Noctor G (2009). Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. *Annu Rev Plant Biol*, 60: 455–484
- Fu QA, Ehleringer JR (1989). Heliotropic leaf movements in common beans controlled by air temperature. *Plant Physiol*, 91: 1162–1167
- Gao S, Shen S, Wang G, Niu J, Lin A, Pan G (2011). PSI-driven cyclic electron flow allows intertidal macro-algae *Ulva* sp. (Chlorophyta) to survive in desiccated conditions. *Plant Cell Physiol*, 52: 885–893
- Gao S, Wang GC (2012). The enhancement of cyclic electron flow around photosystem I improves the recovery of severely desiccated *Porphyra yezoensis* (Bangiales, Rhodophyta). *J Exp Bot*, 63: 4349–4358
- Genty B, Briantais JM, Da Silva JBV (1987). Effects of drought on primary photosynthetic processes of cotton leaves. *Plant Physiol*, 83: 360–364
- Gerbaud A, André M (1980). Effect of CO_2 , O_2 , and light on photosynthesis and photorespiration in wheat. *Plant Physiol*, 66: 1032–1036
- Golding AJ, Johnson GN (2003). Down-regulation of linear and activation of cyclic electron transport during drought. *Planta*, 218: 107–114
- Haupt-Herting S, Fock HP (2002). Oxygen exchange in relation to carbon assimilation in water-stressed leaves during photosynthesis. *Ann Bot*, 89: 851–859
- He J, Chow WS (2003). The rate coefficient of repair of photosystem II after photoinactivation. *Physiol Plant*, 118: 297–304
- He JX, Wang J, Liang HG (1995). Effects of water stress on photochemical function and protein metabolism of photosystem II in wheat leaves. *Physiol Plant*, 93: 771–777
- Heber U, Walker D (1992). Concerning a dual function of coupled cyclic electron transport in leaves. *Plant Physiol*, 100: 1621–1626
- Horton P, Ruban AV, Walters RG (1996). Regulation of light harvesting in green plants. *Annu Rev Plant Physiol Plant Mol Biol*, 47: 655–684
- Horváth EM, Peter SO, Joët T, Rumeau D, Cournac L, Horváth GV, Kavanagh TA, Schäfer C, Peltier G, Medgyesy P (2000). Targeted inactivation of the plastid *ndhB* gene in tobacco results in an enhanced sensitivity of photosynthesis to moderate stomatal closure. *Plant Physiol*, 123: 1337–1349
- Hu YY, Fan DY, Losciale P, Chow WS, Zhang WF (2013b). Whole-tissue determination of the rate coefficients of photoinactivation and repair of photosystem II in cotton leaf discs based on flash-induced P700 redox kinetics. *Photosynth Res*, 117: 517–528
- Hu YY, Zhang YL, Yi XP, Zhan DX, Luo HH, Chow WS, Zhang WF (2013a). The relative contribution of non-foliar organs of cotton to yield and related physiological characteristics under water deficit. *J Integr Agric*, 13: 975–989
- Huang W, Fu PL, Jiang YJ, Zhang JL, Zhang SB, Hu H, Cao KF (2013). Differences in the responses of photosystem I and photosystem II of three tree species *Cleistanthus sumatranus*, *Celtis philippensis* and *Pistacia weinmannifolia* exposed to a prolonged drought in a tropical limestone forest. *Tree Physiol*, 33: 211–220
- Huang W, Yang SJ, Zhang SB, Zhang JL, Cao KF (2012). Cyclic electron flow plays an important role in photoprotection for the resurrection plant *Paraboea rufescens* under drought stress. *Planta*, 235: 819–828
- Huang W, Yang YJ, Hu H, Cao KF, Zhang SB (2016a). Sustained diurnal stimulation of cyclic electron flow in two tropical tree species *Erythrophleum guineense* and *Khaya ivorensis*. *Front Plant Sci*, 7: 1068
- Huang W, Yang YJ, Hu H, Zhang SB (2015). Different roles of cyclic electron flow around photosystem I under sub-saturating and saturating light intensities in tobacco leaves. *Front Plant Sci*, 6: 923
- Huang W, Yang YJ, Hu H, Zhang SB, Cao KF (2016b). Evidence for the role of cyclic electron flow in photoprotection for oxygen-evolving complex. *J plant Physiol*, 194: 54–60
- Huang W, Zhang SB, Cao KF (2010a). Stimulation of cyclic electron flow during recovery after chilling-induced photoinhibition of PSII. *Plant Cell Physiol*, 51: 1922–1928
- Huang W, Zhang SB, Cao KF (2010b). The different effects of chilling stress under moderate illumination on photosystem II compared with photosystem I and subsequent recovery in tropical tree species. *Photosynth Res*, 103: 175–182
- Huang W, Zhang SB, Hu Hong (2014). Sun leaves up-regulate the photorespiratory pathway to maintain a high rate of CO_2 assimilation in tobacco. *Front Plant Sci*, 5: 688
- Inamullah, Isoda A (2005a). Adaptive responses of soybean and cotton to water stress I. Transpiration changes in relation to stomatal area and stomatal conductance. *Plant Prod Sci*, 8: 16–26
- Inamullah, Isoda A (2005b). Adaptive responses of soybean and cotton to water stress. II. Changes in CO_2 assimilation rate, chlorophyll fluorescence and photochemical reflectance index in relation to leaf temperature. *Plant Prod Sci*, 8: 131–138
- Isoda A, Wang PW (2002). Leaf temperature and transpiration of field grown cotton and soybean under arid and humid conditions. *Plant Prod Sci*, 5: 224–228
- Johnson GN (2011). Physiology of PSI cyclic electron transport in higher plants. *Biochim Biophys Acta*, 1807: 384–389
- Joliot P, Joliot A (2006). Cyclic electron flow in C_3 plants. *Biochim Biophys Acta*, 1757: 362–368
- Jordan WR, Ritchie JT (1971). Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. *Plant Physiol*, 48: 783–788
- Kao WY, Forseth IN (1991). The effects of nitrogen, light and water availability on tropic leaf movements in soybean (*Glycine max*). *Plant Cell Environ*, 14: 287–293
- Kao WY, Forseth IN (1992). Diurnal leaf movement, chlorophyll fluorescence and carbon assimilation in soybean grown under

- different nitrogen and water availabilities. *Plant Cell Environ*, 15: 703–710
- Kasahara M, Kagawa T, Oikawa K, Suetsugu N, Miyao M, Wada M (2002). Chloroplast avoidance movement reduces photodamage in plants. *Nature*, 420: 829–832
- Kato MC, Hikosaka K, Hirose T (2002). Photoinactivation and recovery of photosystem II in *Chenopodium album* leaves grown at different levels of irradiance and nitrogen availability. *Funct Plant Biol*, 29: 787–795
- Katona E, Neimanis S, Schönknecht G, Heber U (1992). Photosystem I-dependent cyclic electron transport is important in controlling Photosystem II activity in leaves under conditions of water stress. *Photosynth Res*, 34: 449–464
- Kawakami EM, Oosterhuis DM, Snider JL (2010). Physiological effects of 1-methylcyclopropene on well-watered and water-stressed cotton plants. *J Plant Growth Regul*, 29: 280–288
- Kawashima R (1969). Studies on the leaf orientation-adjusting movement in soybean plants: I. The leaf orientation-adjusting movement and light intensity on leaf surface. *Jpn J Crop Sci*, 38: 718–729 (in Japanese with English abstract) [川嶋良一(1969). 大豆の葉の調位運動に関する研究: 第1報 調位運動と葉面受光. 日本作物學會紀事, 38: 718–729]
- Kitao M, Lei TT (2007). Circumvention of over-excitation of PSII by maintaining electron transport rate in leaves of four cotton genotypes developed under long-term drought. *Plant Biol*, 9: 69–76
- Kono M, Noguchi K, Terashima I (2014). Roles of the cyclic electron flow around PSI (CEF-PSI) and O₂-dependent alternative pathways in regulation of the photosynthetic electron flow in short-term fluctuating light in *Arabidopsis thaliana*. *Plant Cell Physiol*, 55: 990–1004
- Kornyeyev D, Logan BA, Allen RD, Holaday AS (2003). Effect of chloroplastic overproduction of ascorbate peroxidase on photosynthesis and photoprotection in cotton leaves subjected to low temperature photoinhibition. *Plant Sci*, 165: 1033–1041
- Kornyeyev D, Logan BA, Allen RD, Holaday AS (2005). Field-grown cotton plants with elevated activity of chloroplastic glutathione reductase exhibit no significant alteration of diurnal or seasonal patterns of excitation energy partitioning and CO₂ fixation. *Field Crop Res*, 94: 165–175
- Kou JC, Takahashi S, Oguchi R, Fan DY, Badger MR, Chow WS (2013). Estimation of the steady-state cyclic electron flux around PSI in spinach leaf discs in white light, CO₂-enriched air and other varied conditions. *Funct Plant Biol*, 40: 1018–1028
- Krieger-Liszak A, Fufezan C, Trebst A (2008). Singlet oxygen production in photosystem II and related protection mechanism. *Photosynth Res*, 98: 551–564
- Lacape MJ, Wery J, Annerose DJM (1998). Relationships between plant and soil water status in five field-grown cotton (*Gossypium hirsutum* L.) cultivars. *Field Crop Res*, 57: 29–43
- Lang ARG (1973). Leaf orientation of a cotton plant. *Agric Meteorol*, 11: 37–51
- Lawlor DW (1976). Water stress induced changes in photosynthesis, photorespiration, respiration and CO₂ compensation concentration of wheat. *Photosynthetica*, 10: 378–387
- Lawlor DW (1995). The effects of water deficit on photosynthesis. In: Smirnov M (ed). *Environment and Plant Metabolism: Flexibility and Acclimation*. Oxford: BIOS Scientific, 129–160
- Lawlor DW (2002). Limitation to photosynthesis in water-stressed leaves: stomata vs. metabolism and the role of ATP. *Ann Bot*, 89: 871–885
- Lawlor DW, Cornic G (2002). Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ*, 25: 275–294
- Lebkuecher JG, Eickmeier WG (1991). Reduced photoinhibition with stem curling in the resurrection plant *Selaginella lepidophylla*. *Oecologia*, 88: 597–604
- Lee HY, Hong YN, Chow WS (2001). Photoinactivation of photosystem II complexes and photoprotection by non-functional neighbours in *Capsicum annuum* L. leaves. *Planta*, 212: 332–342
- Leidi EO, López M, Gorham J, Gutiérrez JC (1999). Variation in carbon isotope discrimination and other traits related to drought tolerance in upland cotton cultivars under dryland conditions. *Field Crop Res*, 61: 109–123
- Ma QQ, Wang W, Li YH, Li DQ, Zou Q (2006). Alleviation of photoinhibition in drought-stressed wheat (*Triticum aestivum*) by foliar-applied glycinebetaine. *J Plant Physiol*, 163: 165–175
- Mahan JR, Wanjura DF (2005). Seasonal patterns of glutathione and ascorbate metabolism in field-grown cotton under water stress. *Crop Sci*, 45: 193–201
- Massacci A, Nabiev SM, Pietrosanti L, Nematov SK, Chernikova TN, Thor K, Leipner J (2008). Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum*) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. *Plant Physiol Biochem*, 46: 189–195
- Mehler AH (1951). Studies on reactions of illuminated chloroplasts. II. Stimulation and inhibition of the reaction with molecular oxygen. *Arch Biochem Biophys*, 34: 339–351
- Miller CS (1975). Short interval leaf movements of cotton. *Plant Physiol*, 55: 562–566
- Mittler R (2002). Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci*, 7: 405–410
- Miyake C, Shinzaki Y, Miyata M, Tomizawa KI (2004). Enhancement of cyclic electron flow around PSI at high light and its contribution to the induction of non-photochemical quenching of chl fluorescence in intact leaves of tobacco plants. *Plant Cell Physiol*, 45: 1426–1433
- Miyake C, Yokota A (2000). Determination of the rate of photoreduction of O₂ in the water-water cycle in watermelon leaves and enhancement of the rate by limitation of photosynthesis. *Plant Cell Physiol*, 41: 335–343
- Monk LS, Fagerstedt KV, Crawford RMM (1987). Superoxide dismutase as an anaerobic polypeptide: a key factor in recovery from oxygen deprivation in *Iris pseudacorus*? *Plant Physiol*, 85: 1016–1020
- Munekage Y, Hashimoto M, Miyake C, Tomizawa KI, Endo T, Tasaka M, Shikanai T (2004). Cyclic electron flow around photosystem I is essential for photosynthesis. *Nature*, 429: 579–582

- Munekage Y, Hojo M, Meurer J, Endo T, Tasaka M, Shikanai T (2002). *PGR5* is involved in cyclic electron flow around photosystem I and is essential for photoprotection in *Arabidopsis*. *Cell*, 110: 361–371
- Munné-Bosch S, Shikanai T, Asada K (2005). Enhanced ferredoxin-dependent cyclic electron flow around photosystem I and α -tocopherol quinone accumulation in water-stressed *ndhB*-inactivated tobacco mutants. *Planta*, 222: 502–511
- Ogren WL, Bowes G (1971). Ribulose diphosphate carboxylase regulates soybean photorespiration. *Nature*, 230: 159–160
- Oguchi R, Jia HS, Barber J, Chow WS (2008). Recovery of photoactivated photosystem II in leaves: retardation due to restricted mobility of photosystem II in the thylakoid membrane. *Photosynth Res*, 98: 621–629
- Oosterhuis DM, Walker S, Eastham J (1985). Soybean leaflet movements as an indicator of crop water stress. *Crop Sci*, 25: 1101–1106
- Osmond B, Badger M, Maxwell K, Björkman O, Leegood R (1997). Too many photons: photorespiration, photoinhibition and photooxidation. *Trends Plant Sci*, 2: 119–121
- Osmond CB (1981). Photorespiration and photoinhibition: some implications for the energetics of photosynthesis. *Biochim Biophys Acta*, 639: 77–98
- Osmond CB (1994). What is photoinhibition? Some insights from comparison of shade and sun plants. In: Baker NR, Bowyer JR (eds). *Photoinhibition of Photosynthesis: from Molecular Mechanisms to the Field*. Oxford: BIOS Scientific, 1–24
- Pallas Jr JE, Michel BE, Harris DG (1967). Photosynthesis, transpiration, leaf temperature, and stomatal activity of cotton plants under varying water potentials. *Plant Physiol*, 42: 76–88
- Parent B, Shahinnia F, Maphosa L, Berger B, Rabie H, Chalmers K, Kovalchuk A, Langridge P, Fleury D (2015). Combining field performance with controlled environment plant imaging to identify the genetic control of growth and transpiration underlying yield response to water-deficit stress in wheat. *J Exp Bot*, 66: 5481–5492
- Parida AK, Dagaonkar VS, Phalak MS, Umalkar GV, Aurangabadkar LP (2007). Alterations in photosynthetic pigments, protein and osmotic components in cotton genotypes subjected to short-term drought stress followed by recovery. *Plant Biotechnol Rep*, 1: 37–48
- Pastenes C, Pimentel P, Lillo J (2005). Leaf movement and photoinhibition in relation to water stress in field-grown beans. *J Exp Bot*, 56: 425–433
- Petersen KL, Fuchs M, Moreshet S, Cohen Y, Sinoquet H (1992). Computing transpiration of sunlit and shaded cotton foliage under variable water stress. *Agron J*, 84: 91–97
- Pettigrew WT (2004). Physiological consequences of moisture deficit stress in cotton. *Crop Sci*, 44: 1265–1272
- Powles SB (1984). Photoinhibition of photosynthesis induced by visible light. *Ann Rev Plant Physiol*, 35: 15–44
- Reddy AR, Chaitanya KV, Vivekanandan M (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in high-er plants. *J Plant Physiol*, 161: 1189–1202
- Rumeau D, Peltier G, Cournac L (2007). Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. *Plant Cell Environ*, 30: 1041–1051
- Sanda S, Yoshida K, Kuwano M, Kawamura T, Munekage YN, Akashi K, Yokota A (2011). Response of the photosynthetic electron transport system to excess light energy caused by water deficit in wild watermelon. *Physiol Plant*, 142: 247–264
- Shackel KA, Hall AE (1979). Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. *Aust J Plant Physiol*, 6: 265–276
- Sharma P, Jha AB, Dubey RS, Pessarakli M (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J Bot*, doi: 10.1155/2012/217037
- Shikanai T (2007). Cyclic electron transport around photosystem I: genetic approaches. *Ann Rev Plant Biol*, 58: 199–217
- Shikanai T (2014). Central role of cyclic electron transport around photosystem I in the regulation of photosynthesis. *Curr Opin Biotech*, 26: 25–30
- Singh R, Naskar J, Pathre UV, Shirke PA (2014). Reflectance and cyclic electron flow as an indicator of drought stress in cotton (*Gossypium hirsutum*). *Photochem Photobiol*, 90: 544–551
- Singh R, Pandey N, Naskar J, Shirke PA (2015). Physiological performance and differential expression profiling of genes associated with drought tolerance in contrasting varieties of two *Gossypium* species. *Protoplasma*, 252: 423–438
- Smirnoff N (1993). The role of active oxygen in the response of plants to water deficit and desiccation. *New Phytol*, 125: 27–58
- Snider JL, Chastain DR, Meeks CD, Collins GD, Sorensen RB, Byrd SA, Perry CD (2015). Predawn respiration rates during flowering are highly predictive of yield response in *Gossypium hirsutum* when yield variability is water-induced. *J Plant Physiol*, 183: 114–120
- Snider JL, Collins GD, Whitaker J, Perry CD, Chastain DR (2014). Electron transport through photosystem II is not limited by a wide range of water deficit conditions in field-grown *Gossypium hirsutum*. *J Agron Crop Sci*, 200: 77–82
- Snider JL, Oosterhuis DM, Collind GD, Pilon C, FitzSimons TR (2013). Field-acclimated *Gossypium hirsutum* cultivars exhibit genotypic and seasonal differences in photosystem II thermostability. *J Plant Physiol*, 170: 489–496
- Song XS, Shang ZW, Yin ZP, Ren J, Sun MC, Ma XL (2011). Mechanism of xanthophyll-cycle-mediated photoprotection in *Cerasus humilis* seedlings under water stress and subsequent recovery. *Photosynthetica*, 49: 523–530
- Sonoike K (2006). Photoinhibition and protection of photosystem I. In: Golbeck JH (ed). *Photosystem I. The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase*. The Netherlands: Springer, 657–668
- Takahashi S, Badger MR (2011). Photoprotection in plants: a new light on photosystem II damage. *Trends Plant Sci*, 16: 53–60
- Takahashi S, Milward SE, Fan DY, Chow WS, Badger MR (2009). How does cyclic electron flow alleviate photoinhibition in *Arabidopsis*? *Plant Physiol*, 149: 1560–1567

- Teicher HB, Möller BL, Scheller HV (2000). Photoinhibition of photosystem I in field-grown barley (*Hordeum vulgare* L.): induction, recovery and acclimation. *Photosynth Res*, 64: 53–61
- Tikkanen M, Rantala S, Aro EM (2015). Electron flow from PSII to PSI under high light is controlled by PGR5 but not by PSBS. *Front Plant Sci*, 6: 521
- Turner NC, Hearn AB, Begg JE, Constable GA (1986). Cotton (*Gossypium hirsutum* L.): physiological and morphological responses to water deficits and their relationship to yield. *Field Crop Res*, 14: 153–170
- Wang C, Isoda A, Li Z, Wang P (2004). Transpiration and leaf movement of cotton cultivars grown in the field under arid conditions. *Plant Prod Sci*, 7: 266–270
- Wilson RF, Burke JJ, Quisenberry JE (1987). Plant morphological and biochemical responses to field water deficits: II. Responses of leaf glycerolipid composition in cotton. *Plant Physiol*, 84: 251–254
- Wullschleger SD, Oosterhuis DM (1990). Photosynthetic and respiratory activity of fruiting forms within the cotton canopy. *Plant Physiol*, 94: 463–469
- Yamori W, Makino A, Shikanai T (2016). A physiological role of cyclic electron transport around photosystem I in sustaining photosynthesis under fluctuating light in rice. *Sci Rep*, 6: 20147
- Yamori W, Shikanai T (2016). Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. *Ann Rev Plant Biol*, 67: 81–106
- Yi XP, Zhang YL, Yao HS, Luo HH, Gou L, Chow WS, Zhang WF (2016a). Different strategies of acclimation of photosynthesis, electron transport and antioxidative activity in leaves of two cotton species to water deficit. *Funct Plant Biol*, 43: 448–460
- Yi XP, Zhang YL, Yao HS, Luo HH, Gou L, Chow WS, Zhang WF (2016b). Rapid recovery of photosynthetic rate following soil water deficit and re-watering in cotton plants (*Gossypium herbaceum* L.) is related to the stability of the photosystems. *J Plant Physiol*, 194: 23–34
- Yi XP, Zhang YL, Yao HS, Zhang XJ, Luo HH, Gou L, Zhang WF (2014). Alternative electron sinks are crucial for conferring photoprotection in field-grown cotton under water deficit during flowering and boll setting stages. *Funct Plant Biol*, 41: 737–747
- Yong CB, Jin J (1999). Water deficit –induced oxidative stress and antioxidative defenses in rice plants. *J Plant Physiol*, 155: 255–261
- Zhang S, Scheller HV (2004). Photoinhibition of photosystem I at chilling temperature and subsequent recovery in *Arabidopsis thaliana*. *Plant Cell Physiol*, 45: 1595–1602
- Zhang SR (1999). A discussion on chlorophyll fluorescence kinetics parameters and their significance. *Chin Bull Bot*, 16 (4): 444–448 (in Chinese with English abstract) [张守仁(1999). 叶绿素荧光动力学参数的意义及讨论. *植物学通报*, 16 (4): 444–448]
- Zhang YL, Hu YY, Luo HH, Chow WS, Zhang WF (2011). Two distinct strategies of cotton and soybean differing in leaf movement to perform photosynthesis under drought in the field. *Funct Plant Biol*, 38: 567–575
- Zhang YL, Luo HH, Zhang WF, Fan DY, He ZJ, Bai HD (2008). Effects of water deficit on photochemical activity and excitation energy dissipation of photosynthetic apparatus in cotton leaves during flowering and boll-setting stages. *Chinese J Plant Ecol*, 32 (3): 681–689 (in Chinese with English abstract) [张亚黎, 罗宏海, 张旺锋, 樊大勇, 何在菊, 白慧东(2008). 土壤水分亏缺对陆地棉花铃期叶片光化学活性和激发能耗散的影响. *植物生态学报*, 32 (3): 681–689]
- Zhang YL, Luo Y, Yao HS, Tian JS, Luo HH, Zhang WF. (2010). Mechanism for photoprotection of leaves at the bolling stage under field conditions in *Gossypium barbadense* and *G. hirsutum*. *Chin J Plant Ecol*, 34 (10): 1204–1212 (in Chinese with English abstract) [张亚黎, 罗毅, 姚贺盛, 田景山, 罗宏海, 张旺锋 (2010). 田间条件下海岛棉和陆地棉花铃期叶片光保护的机制. *植物生态学报*, 34 (10): 1204–1212]
- Zhang YL, Zhang HZ, Du MW, Li W, Luo HH, Chow WS, Zhang WF (2010). Leaf wilting movement can protect water-stressed cotton (*Gossypium hirsutum* L.) plants against photoinhibition of photosynthesis and maintain carbon assimilation in the field. *J Plant Biol*, 53: 52–60
- Zhang YL, Zhang HZ, Feng GY, Tian JS, Zhang WF (2009). Leaf diaheliotropic movement can improve carbon gain and water use efficiency and not intensify photoinhibition in upland cotton (*Gossypium hirsutum* L.). *Photosynthetica*, 47: 609–615

Research progress of the photoprotective mechanisms of cotton leaves under soil water deficit

YI Xiao-Ping, ZHANG Ya-Li, YAO He-Sheng, ZHANG Wang-Feng*

Key Laboratory of Oasis Eco-agriculture, Xinjiang Production and Construction Group-Shihezi University, Shihezi, Xinjiang 832003, China

Abstract: Drought is considered to be the most limiting environmental factor, limiting plant growth, development and yield. In order to adapt to drought environment, plants have evolved multiple photoprotective mechanisms to protect the photosynthetic apparatus from photodamage. Cotton is regarded as a drought tolerant crop, and drought does not lead to chronic photoinhibition of photosynthetic apparatus even moderate drought. This paper briefly reviews the following three aspects: effect of water deficit on photosynthesis; effect of water deficit on photoinhibition; possible photoprotective mechanisms under water deficit. Further research on the adaptation mechanism of field-grown cotton plants to water deficit has also been discussed.

Key words: water deficit; cotton; photoinhibition; photoprotection

Received 2016-09-30 Accepted 2017-01-08

This work was supported by the National Natural Science Foundation of China (Grant Nos. 31260295 and U1203283).

*Corresponding author (E-mail: zwf_shzu@163.com; zhwf_agr@shzu.edu.cn).