

植物叶片花青素的光破坏防御机制研究进展*

王良再 胡彦波 张会慧 许楠 张秀丽 孙广玉**

(东北林业大学生命科学学院, 哈尔滨 150040)

摘要 植物花青素广泛分布在植物的根、茎、叶、花和果实等器官中,是植物形态建成过程中或响应逆境而产生的一种次生代谢物质.植物叶片中的花青素具有特殊的化学结构和光谱特性,在光破坏防御机制方面发挥了重要的作用,已经成为植物光合生理生态的研究热点.本文综述了近年来植物叶片花青素与光合作用的研究进展,从叶片花青素的分布、光谱特性及其与光合色素的关系等方面说明花青素对植物光合作用的影响,重点介绍了叶片花青素通过光吸收、抗氧化剂和渗透调节等在植物光破坏防御机制方面的作用,展望了今后的主要研究方向

关键词 花青素 光抑制 光破坏防御

文章编号 1001-9332(2012)03-0835-07 **中图分类号** Q945.1 **文献标识码** A

Photoprotective mechanisms of leaf anthocyanins: Research progress. WANG Liang-zai, HU Yan-bo, ZHANG Hui-hui, XU Nan, ZHANG Xiu-li, SUN Guang-yu (*College of Life Science, Northeast Forestry University, Harbin 150040, China*). -*Chin. J. Appl. Ecol.*, 2012, 23(3): 835–841.

Abstract: Anthocyanin is widely distributed in plant organs such as root, stem, leaf, flower and fruit, being a kind of secondary metabolites generated in plant morphogenesis or for stress response. Leaf anthocyanin has special chemical structure and spectral properties, playing important roles in plant photoprotection, and becomes a hotspot in plant photosynthetic physiological ecology. This paper summarized the recent research progress in the effects of leaf anthocyanin on plant photosynthesis, including the distribution of leaf anthocyanin, its spectral properties, and its relationships with photosynthetic pigments, with the focus on the potential mechanisms of anthocyanins photoprotection, including light absorption, antioxidation, and osmotic regulation. The further research directions on the effects of leaf anthocyanin on photoprotection were proposed.

Key words: anthocyanin; photoinhibition; photoprotection

花青素是一种具有多重生理功能的植物次生代谢物^[1],它的合成和积累受到光环境(光质、光强)、温度、植物营养状况(糖类、水分、激素、金属离子)和真菌等因素的影响^[2-3],在植物花瓣、果实、茎和叶等器官中均有分布.植物叶片中积累的花青素常见于幼小叶片、扩展中的叶片和衰老叶片.花青素虽不是光合色素,但两者之间存在一定的消长规律^[4],与叶绿体的发育关系密切,此外,花青素能调节叶绿素分子对光量子的吸收^[5],对照射到叶片上的光具有过滤^[6]、衰减^[7]和反射作用^[8],因此,花青素与植物光合作用有着密切的关系^[4].未完全展开

叶片的光合机构、气孔功能尚未完善,对照射光的利用水平较低,自然强光条件下易造成光能过剩;展开叶片光合机构虽已完善,光能利用水平相对较高,但在低温、干旱、盐碱等胁迫条件下光合作用会出现可逆或不可逆的抑制,同样会引起光能过剩.光能过剩会产生大量的活性氧自由基,破坏植物叶片的光合机构,造成光氧化甚至光破坏^[9].植物在长期的自然选择中形成了一系列的光破坏防御机制,例如,植物通过避光运动(缩小和加厚叶片、叶片卷曲、轻度萎蔫或叶绿体的移动等)^[4]、LHC II捕光蛋白的可逆降解、光合电子传递载体和光合酶含量及活化水平的提高以及增加热耗散等有效防护来减少或避免光能过剩对光合机构造成的伤害.研究发现:花青素在幼小叶片或者受胁迫的叶片中含量较高;它能有效消除光合电子传递系统产生的活性氧自由基,减缓

* 国家自然科学基金项目(30771746,31070307)、中央高校基本科研业务费专项资金项目(DL10BB24,DL11BA14)和黑龙江省自然科学基金重点项目(ZD201105)资助.

** 通讯作者. E-mail: sungy@vip.sina.com

2011-07-25 收稿,2011-12-13 接受.

可见光^[10-11]和紫外光^[12]引起的光抑制、光损害^[13-16];暗示花青素在植物光破坏防御中起到重要作用.花青素的光破坏防御作用已成为植物光合生理生态研究的热点问题之一,并取得了一些研究进展.然而,已有的综述文章多关注于花青素的合成代谢^[1,17-18]、提取纯化^[19]、理化性质^[20-21]、生物活性以及开发利用^[3,22]等方面.本文从生理功能角度,总结了花青素与植物光合作用的研究进展,综述了其在植物光破坏防御中的功能作用.

1 花青素在叶片中的分布

植物叶片的花青素主要存在于表皮细胞的液泡中^[23],一些植物如玉米(*Zea mays*)等叶片的花青素主要分布在叶片上表皮细胞的液泡中^[24-25],而另一些植物如欧洲榛(*Corylus avellana*)叶片中的花青素在上、下表皮细胞的液泡中均有分布^[23];此外,花青素在植物叶片的腺毛中也有分布^[26].叶片花青素的分布随着季节更迭(温度和光的变化)而变化显著^[27-28].叶片花青素还随植物生长发育而发生改变.一般情况下,幼嫩叶片花青素含量较多,而成熟叶片的花青素含量较少^[4].在春夏两季,植物叶片处于持续生长阶段,尤其是幼小叶片的结构并不完善,叶绿体不成熟,光合酶类质量低、数量少,气孔功能尚未完善,因此,气孔是限制叶片 CO₂ 吸收和影响光合作用的主要原因.处于生长阶段的植物叶片尤其是幼叶极易受到强光破坏.植物会频繁地改变生理生化功能和叶片结构来减少对光的吸收,保护其光合机构.当植物叶片可用的光破坏防御措施均被利用(如叶黄素循环、水水循环、C₂ 光呼吸循环和叶绿体运动的回避反应等),植物叶片会产生花青素,形成一个类似保护伞的状态,从而达到抵制强光的目的;在夏末秋初,大多数植物叶片已经成熟,叶片结构和光合机构已经完善,光强对植物叶片的威胁减小或消失,而植物叶片中的花青素分解^[29-31].这说明随着叶片的生长发育,花青素呈一定的季节变化^[32].

2 花青素的光谱学特性

植物叶片花青素对光的吸收波长范围在 200 ~ 600 nm,有特征性的吸收峰,峰值因植物叶片花青素结构不同而变化.叶片花青素的两个吸收波长范围,一个在波长为 465 ~ 560 nm 的可见光区,另一个在波长为 270 ~ 280 nm 的紫外光区^[20].花青素会影响叶绿体吸收光能的数量和质量^[33].红色花青素主要

吸收绿光和紫外光,对蓝光吸收较少,不能吸收红光^[34].花青素结构与吸收光谱相关联,若结构中存在 3-羟基,最大吸收峰则向红外光方向位移,如天竺葵(*Pelargonium hortorum*)叶片的花青素最大吸收峰为 520 nm,接近红外光;如果 B 环上存在相邻的羟基,最大吸收峰位置也向红外光方向位移,如矢车菊(*Centaurea cyanus*)叶片花青素最大吸收峰为 535 nm,翠雀(*Delphinium grandiflorum*)叶片花青素为 546 nm;如果花青素结构中的 6-端存在羟基,那么最大吸收峰向紫外光方向位移,如 6-羟基矢车菊花青素最大吸收峰为 518 nm;如果存在 8-羟基,最大吸收峰向红外位移,也可能向紫外位移;如果 B 环存在甲氧基,最大吸收峰位置将向紫外稍做位移;如果 B 环中只有一个羟基, A 环中存在甲氧基使最大吸收峰向紫外位移^[21].

3 花青素苷合成与环境因子的调控

花青素是植物次生代谢产物中类黄酮一类的物质,其合成途径是苯基丙酸类合成途径的分支^[4,35-36].光环境(光强、光质和光周期)是影响花青素合成的重要调节因子.唐杏姣和戴思兰^[18]综述了光对花青素苷合成途径中相关结构基因和调节基因的调控作用,强光、蓝光、紫外光(UV-A、UV-B)等显著诱导花青素苷合成相关基因表达,增加叶片内花青素的积累;而弱光或黑暗、红光等会抑制花青素的合成和积累.此外,光与温度、水分、pH、糖类物质、营养状况等因素协同处理对植物花青素合成的影响较为复杂^[37],即可能产生加和作用抑或抵消作用.姜卫兵等^[3]综述了光强及温度、水分、pH 等环境因子对花青素合成的影响,结果表明,高温强光会降低红叶桃(*Amygdalus persica*)叶片中花青素含量,而使紫叶李(*Prunus cerasifera*)的花青素含量升高;蓝光与蔗糖对花青素合成具有加和作用,蔗糖含量显著影响花青素的积累水平.

4 花青素与光合色素的关系

一般情况下,植物幼叶花青素含量较高,成熟叶片花青素含量相对降低,老叶中花青素含量又升高^[20].Saure^[38]认为,花青素是在叶绿素开始降解时形成的,叶绿素的降解物可能对花青素的形成起到活化作用.研究还发现,叶片光合机构完善较快的植物叶片,花青素降解也较早,暗示光合色素的完善与花青素消失之间存在某种联系^[4].Hughes 等^[39]以北美枫香(*Liquidambar styraciflua*)、红花槭(*Acer*

rubrum) 和加拿大紫荆 (*Cercis canadensis*) 为试验材料, 研究花青素和光合色素之间的消长规律, 结果表明, 随着胡萝卜素/叶绿素比率的降低, 叶片花青素含量相应减少, 可能是通过非光化学猝灭以达到光破坏防御的需要, 当每单位面积的叶绿素含量约为成熟叶片的 44%、单位体积含量达 58% 和单位面积上总类胡萝卜素含量达 49% 时, 花青素则消失, 说明叶片花青素与叶绿体和叶片的发育进程存在耦合关系, 在叶片光能吸收和利用没有达到平衡之前, 花青素起到了保护光合组织的作用^[39]. Mehlenbacher 和 Thompson^[40] 利用缺失叶绿素的欧洲榛变种进行试验, 结果表明, 在田间条件下, 缺失叶绿素和花青素的幼苗死亡, 而缺失叶绿素、含有花青素的幼苗正常生长. 这说明叶片花青素产生与叶绿素的变化密切相关.

5 植物叶片花青素的光破坏防御机制

5.1 花青素对植物光合作用的影响

叶片花青素会影响植物的光合作用, 这是由花青素的光谱特性和化学结构决定的. 一方面, 花青素吸收光谱与光合色素吸收光谱相似, 可调控叶片光合色素对光能的吸收; 另一方面, 花青素具有强大的抗氧化能力, 可猝灭氧自由基^[41]. Burger 和 Edwards^[42] 研究发现, 彩叶草 (*Coleus scutellarioides*) 积累花青素的红色叶片光合放氧能力低于正常的绿色叶片; Dodd 等^[43] 在 *Syzygium* 和 Gould 等^[44] 在 *Quintinia serrata* 中也得到相似的结果. 叶片花青素可吸收可见光来减少光能的吸收, 减轻光能捕获、CO₂ 同化和碳水化合物利用之间的不平衡, 形成光氧化伤害^[45]. 实际上, 花青素减少叶片光能吸收和猝灭氧自由基这两方面的作用也是植物光破坏防御的一种自卫功能的需要. Hughes 等^[46] 对 10 种常绿阔叶树的研究证实, 相对于绿色叶片, 含有花青素的红色叶片始终保持较高的 PS II 最大捕光效率 (F_v/F_m), 由于 F_v/F_m 与非光化学猝灭相关, 因此, 红色叶片的树种较少依靠持续的叶黄素介导的光破坏防御, 而是更多的依赖花青素的光破坏防御功能. 另外, 黄酮类化合物和单一酚类化合物也能成为氧自由基清除剂^[47]. 而 Lee 等^[48] 对 89 种木本植物黎明前的叶片 PSII 光化学效率进行测定, 没有发现花青素光破坏防御功能的证据.

对于常绿树木叶片的碳同化系统, 秋季较低的温度抑制了卡尔文循环的生化过程, 但对光能的捕获没有明显影响. 秋冬季节的树木叶片暴露于高光

强和低温条件下, 会导致光能的能量过剩^[49], 转移到分子氧的能量和电子增加, 形成过多的氧自由基, 增加了易受光氧化伤害的几率. 因此秋冬季节叶片的花青素可适当减轻光能过剩的危害^[4, 49]. 陈静等^[50] 对野生型 (WT) 和光敏素双突变体 (*phyB1phyB2*) 番茄幼苗进行光处理, 发现合成花青素的 WT 叶片 F_v/F_m 的下降程度低于不能合成花青素的 *phyB1phyB2*, 得出花青素对低温弱光逆境处理番茄叶片的光合机构具有保护作用. 这种保护作用极可能与花青素对可见光和紫外光的吸收和屏蔽作用有关. 另外, 花青素的积累降低了叶片的含氮量^[5]. 研究发现, 糖槭 (*Acer saccharum*) 叶片开始衰老时, 叶片花青素含量逐渐增加, 而叶片氮含量逐渐降低^[51]. 叶片氮含量与光合能力密切相关, 红色叶片较低的氮水平与低的电子传递率存在某种联系^[52]. 因此, 花青素的积累降低了植物叶片的光合能力^[53].

5.2 花青素和光抑制

光是植物光合作用的能量基础. 但是, 当光资源超过光合机构利用的量时, 植物光合能力将下降, 出现光合作用的光抑制^[54]. 在植物生长过程中, 通常植物幼叶和扩展的叶片容易受到光抑制. 植物幼叶叶绿素含量较低, 叶片气孔功能尚不完善、碳同化能力较低, 低温、霜冻和干旱等胁迫处理会造成幼叶光能过剩, 引起光抑制^[55]. 而幼叶花青素含量较高, 可以有效减轻光抑制. Krol 等^[56] 将北美短叶松 (*Pinus banksiana*) 幼苗从温室 20 °C 移栽到田间 5 °C 时, 叶片花青素含量增加了两倍, 同时幼苗对光抑制的忍耐能力增强. 营养胁迫会诱导桉树 (*Eucalyptus nitens*) 幼苗的光抑制, 而营养缺乏时叶片会通过产生花青素来减轻光抑制^[57]. 因此, 植物叶片花青素的合成和降解与植物光抑制紧密相连, 尤其对由温室移栽到大田的移栽植物更为重要.

5.3 花青素的光过滤、光衰减和光反射作用

5.3.1 光过滤和光衰减作用

强光条件下, 叶片花青素具有过滤光 (light-filtering) 和衰减光 (attenuation) 功能, 通过吸收入射强光中的蓝绿光来保护叶片表皮细胞免受伤害^[58-59]. Pietrini 等^[6] 研究表明, 玉米须中花青素可以拦截 43% 的入射光 (PAR), 降低了用于 CO₂ 固定的表观量子产额和 PS II 非循环电子传递的分配比例. Manetas 等^[60] 研究了栎树 (*Quercus coccifera*) 两个变种中红色和非红色叶片花青素的光过滤作用, 与薄叶片和不含花青素的叶片相比, 红色幼叶中叶绿素 a/b 比值较低, 且具有更完

善的强光过滤系统,叶黄素循环周期也较低。

Hughes 和 Smith^[7]将含有花青素的 *Galax urceolata* 叶片上表面和下表面暴露于强光下,结果发现,两种类型叶片的 F_v/F_m 均高于不含花青素的绿色叶片,说明含有花青素的叶片可通过光衰减作用减轻叶片的光抑制。Merzlyak 等^[61]研究了挪威槭 (*Acer platanoides*)、栒子 (*Cotoneaster alauica*)、欧洲榛、红瑞木 (*Cornus alba*) 和五叶地锦 (*Parthenocissus quinquefolia*) 叶片在不同发育阶段的光学特性和色素组成,发现个体发育早期的环境胁迫或者秋天低温都会造成叶片光合机构的破坏,在植物组织中出现叶绿素的降解物和其他一些有效的内生光敏剂,诱导植物细胞的光毒性作用,而液泡中的花青素积累具有“解毒”作用。枫叶秋海棠 (*Begonia heracleifolia*) 是一种耐阴的林下植物,其叶片上表面有呈现红色的花青素。当林窗或林隙间的强光照射在叶片时,它通过红光散射到叶片内部经过衰减为绿光而具有光破坏防御的功能。对于林下的木本植物(如秋海棠属植物),通过衰减透过含有花青素的叶片上表面进入叶组织内的分散绿光而保护光合机构。

5.3.2 光反射作用 Lee 等^[8]在研究热带雨林植物叶片花青素时提出叶片花青素的光反射作用假说,即在热带雨林弱光下生长的叶片,花青素会反射从上表面透射的红色光而被叶绿素再次吸收,弱光下的叶片花青素起到了光增强器 (enhancer) 的作用。但是, Hughes 等^[62]研究耐阴的枫叶秋海棠叶片花青素时发现,不含花青素的绿色叶片下表皮比含有花青素的叶片更能反射上表皮吸收的光,而且叶片下表皮红色的存在并没有导致叶肉组织吸收更多的红光,光合速率也没有增加。

叶片蜡质化同样具有光反射作用,而且叶片蜡质化与花青素积累之间关系较为密切。在叶片伸展或扩展过程中,叶片积累较多的花青素,而叶片蜡质较少;在成熟叶片中,花青素含量较低,却形成了较多的蜡质。Barker 等^[63]认为,这是植物叶片发育过程中的光破坏防御策略,即伸展叶片依赖于花青素减弱过剩光能,而成熟叶片则依赖蜡质来反射光,以减少过多光能的危害^[64]。

5.4 抗氧化剂的作用

植物代谢过程中电子传递系统产生活性氧 (reactive oxygen species, ROS)^[4]。光能过剩会导致活性氧产量激增,威胁光合机构,及时有效地清除 ROS 是植物防止光合机构遭到破坏的光破坏防御机制之一。在叶绿体中,抗氧化酶和非酶促的抗氧化

剂可有效地清除 ROS。非酶促的抗氧化剂通常是一些小分子,如亲水的 AsA 和谷胱甘肽、亲脂的 α -维生素 E 和类胡萝卜素等。此外,酚类化合物和类黄酮化合物也能清除 ROS。研究发现,叶片花青素同样具有抗氧化剂作用^[4]。但是,花青素的抗氧化剂作用以及在保护组织免受 ROS 损害方面尚有争论^[65]。花青素能够直接消除 ROS,然而这些试验却是在离体条件下或者采用人工合成的活性氧自由基 (1,1-二苯基-2-三硝基苯肼, DPPH) 进行的,花青素消除自由基作用是间接证据^[66-67]。如果叶片花青素具有抗氧化功能,那么能够穿透叶绿体膜和液泡膜的 ROS (如 H_2O_2) 就能被液泡中的花青素有效的中和^[68-70]。Neil 等^[71]发现, *Elatostema rugosum* 叶片提取物的抗氧化能力明显高于绿色植物,而且花青素的抗氧化功能明显高于低分子量的抗氧化剂。刘超^[72]通过研究紫甘薯 (*Ipomoea batatas*) 花青素的体外抗氧化活性发现,紫甘薯花青素的还原力和清除羟自由基能力较强,并且随着浓度的增加而增加,抗氧化能力与抗坏血酸相当,显著高于 α -生育酚和人工合成的抗氧化剂 BHA。也有研究发现, *Quintinia serrata* 叶片以及枫树幼叶和衰老叶片中的花青素并不具有抗氧化能力^[73-74]。田间条件下, *Mahonia repens* 和 *Eucalyptus nitens* 叶片花青素的季节变化与叶片的抗氧化能力并不相关^[75-76]。

5.5 渗透调节物质的作用

花青素苷是存在于植物表皮细胞液泡中的水溶性物质。在低温、干旱、紫外线、营养缺乏等胁迫时,植物叶片会迅速积累花青素而起到渗透调节物质的作用,提高植物抵御逆境的能力^[37]。植物在低温^[77]、干旱^[78-79]条件下叶片花青素的积累,对叶片渗透势的降低起到一定的作用。植物液泡中可合成或积累可溶性物质作为渗透调节物质来降低冰点,而表皮细胞液泡中花色素作为可溶性物质可以防止表皮细胞受到冻害,尤其是可以防止叶表面形成冰核物质,从而保护落叶植物免受早秋霜冻的危害^[32]。将低温下生长的桉树幼苗暴露在高光下,叶片花青素的积累量是微不足道的,没有起到渗透调节物质的作用^[80]。

6 结语和展望

植物叶片花青素的积累常见于植物幼叶、扩展叶片和衰老脱落的叶片。营养缺乏、紫外辐射、低温、干旱和霜冻等环境因子会诱导叶片花青素的合成和积累,而这些逆境因素往往会造成叶片吸收光能过

剩。叶片花青素的积累可通过其光学和物理化学特性来减少光能的吸收或防御过剩光能的危害,起到了光破坏防御作用。叶片花青素的光破坏防御作用包括:吸收可见光以衰减入射光能;作为抗氧化剂有效地清除 ROS;液泡中可溶性渗透调节物质。另外,叶片花青素可吸收紫外光来减轻紫外线对植物的伤害。

花青素在叶片形成过程中发挥着重要的保护和防御作用。但是其生理作用尚存在一定的争议,需要进一步探讨。首先,叶片花青素与光合色素的关系问题,是花青素的合成促进了叶绿素的降解,还是叶绿素的降解诱导了花青素的合成,涉及到花青素合成的信号物质和信号转导途径,那么叶绿素的降解物或叶绿素合成前体是不是花青素的信号分子?其次,叶片花青素源于光合产物,也就是说,植物的糖代谢调节着花青素的合成,尤其在逆境条件下,花青素合成必然影响到光合作用的库源关系^[80]。虽然花青素积累通过调节库源平衡可以减轻光抑制,防止光破坏,但是必然影响到光合产物的形成。如何调节和控制花青素形成的阈值,需要在化学计量学(stoichiometry)方面深入探讨。再次,从植物生理生态方面进一步研究花青素的作用,如叶片花青素对肥料的反应比较敏感,花青素可作为指示指标来指导植物品种的肥料运筹。总之,花青素在植物光破坏防御中发挥着重要作用,需要进一步研究以发挥它的最大功能。

参考文献

- [1] Shi S-C (石少川), Gao Y-K (高亦珂), Zhang X-H (张秀海), *et al.* Progress on plant genes involved in biosynthetic pathway of anthocyanins. *Bulletin of Botanical Research* (植物研究), 2011, **31**(5): 633-640 (in Chinese)
- [2] Steyn WJ, Wand SJE, Holcroft DM, *et al.* Anthocyanins in vegetative tissues: A proposed unified function in photoprotection. *New Phytologist*, 2002, **155**: 349-361
- [3] Jiang W-B (姜卫兵), Xu L-L (徐莉莉), Weng M-L (翁忙玲), *et al.* Effects of environmental factors and exogenous chemicals on anthocyanins in plants: A review. *Ecology and Environmental Sciences* (生态环境学报), 2009, **18**(4): 1546-1552 (in Chinese)
- [4] Nicole M. The Photoprotective Role of Anthocyanin Pigment in Leaf Tissues. PhD Thesis. America: Wake Forest University, 2009
- [5] Kytridis VP, Karageorgou P, Levizou E, *et al.* Intraspecific variation in transient accumulation of leaf anthocyanins in *Cistus creticus* during winter: Evidence that anthocyanins may compensate for an inherent photosynthetic and photoprotective inferiority of the red-leaf phe-

- notype. *Journal of Plant Physiology*, 2008, **165**: 952-959
- [6] Pietrini F, Iannelli MA, Massacci A. Anthocyanin accumulation in the illuminated surface of maize leaves enhances protection from photo-inhibitory risks at low temperature, without further limitation to photosynthesis. *Plant, Cell and Environment*, 2002, **25**: 1251-1259
- [7] Hughes NM, Smith WK. Attenuation of incident light in *Galax urceolata* (Diapensiaceae): Concerted concerted influence of adaxial and abaxial anthocyanic layers on photoprotection. *American Journal of Botany*, 2007, **94**: 784-790
- [8] Lee DW, Lowry JB, Stone BC. Abaxial anthocyanin layer in leaves of tropical rainforest plants: Enhancer of light capture in deep shade. *Biotropica*, 1979, **11**: 70-77
- [9] Liakopoulos G, Nikolopoulos D, Klouvatou A, *et al.* The photoprotective role of epidermal anthocyanins and surface pubescence in young leaves of grapevine (*Vitis vinifera*). *Annals of Botany*, 2006, **98**: 257-265
- [10] Baker ME. Genealogy of regulation of human sex and adrenal function, prostaglandin action, snapdragon and petunia flower colors, antibiotics, and nitrogen fixation: Functional diversity from two ancestral dehydrogenases. *Steroids*, 1991, **56**: 354-361
- [11] Leyva A, Linag X, Pintor-Toro JA, *et al.* Cis-element combinations determine phenylalanine ammonia-lyase gene tissue-specific expression patterns. *Plant Cell*, 1992, **4**: 263-271
- [12] Zhao D-X (赵德修), Li M-Y (李茂寅), Xing J-M (邢建民), *et al.* Effects of light on cell growth and flavonoids biosynthesis in callus cultures of *Saussurea medusa* Maxim. *Acta Phytophysiological Sinica* (植物生理学报), 1999, **25**(2): 127-132 (in Chinese)
- [13] Steyn WJ, Wand SJE, Holcroft DM, *et al.* Anthocyanins in vegetative tissues: A proposed unified function in photoprotection. *New Phytologist*, 2002, **155**: 349-361
- [14] Close C, Beadle CL. The ecophysiology of foliar anthocyanins. *Botanical Review*, 2003, **69**: 49-161
- [15] Gould KS. Nature's Swiss army knife: The diverse protective roles of anthocyanins in leaves. *Journal of Biomedicine and Biotechnology*, 2004, **5**: 314-320
- [16] Manetas Y. Why some leaves are anthocyanic and why most anthocyanic leaves are red. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 2006, **201**: 163-177
- [17] Cheng H-Y (程海燕), Li D-H (李德红). Progress in effects of light, saccharide and hormones on the anthocyanin synthesis and accumulation in plants. *Subtropical Plant Science* (亚热带植物科学), 2010, **39**(3): 82-86 (in Chinese)
- [18] Tang X-J (唐杏姣), Dai S-L (戴思兰). Light regulation of anthocyanin synthesis and coloration. *Molecular Plant Breeding* (分子植物育种), 2011, **9**: 1284-1290 (in Chinese)
- [19] Wang Z-J (王振江), Xiao G-S (肖更生), Liu X-M (刘学铭), *et al.* Research and application of mulberry anthocyanins. *Acta Sericologica Sinica* (蚕业科学), 2006, **32**(1): 90-94 (in Chinese)
- [20] Liu L-W (刘邻渭), Huang X-Y (黄晓钰). Compre-

- hensive Experiments of Food Chemistry. Beijing: China Agriculture Press, 1998: 116–121 (in Chinese)
- [21] Lü F-M (吕福梅). Study on the Characteristics of Anthocyanin and Photosynthesis in the Leaves of Four Species Leaf-colored Plants of *Prunus*. PhD Thesis. Tai'an: Shandong Agricultural University, 2005 (in Chinese)
- [22] Guo F-D (郭凤丹), Wang X-Z (王效忠), Liu X-Y (刘学英), *et al.* Metabolic regulation of plants anthocyanin. *Chinese Bulletin of Life Sciences* (生命科学), 2011, **23**(10): 938–944 (in Chinese)
- [23] Merzlyak MN, Chivkunova OB, Solovchenko AE, *et al.* Light absorption by anthocyanins in juvenile, stressed, and senescing leaves. *Journal of Experimental Botany*, 2008, **59**: 3903–3911
- [24] Pietrini F, Iannelli MA, Massacci A. Anthocyanin accumulation in the illuminated surface of maize leaves enhances protection from photo-inhibitory risks at low temperature, without further limitation to photosynthesis. *Plant, Cell and Environment*, 2002, **25**: 1251–1259
- [25] Steyn WJ, Wand SJE, Holcroft DM, *et al.* Anthocyanins in vegetative tissues: A proposed unified function in photoprotection. *New Phytologist*, 2002, **155**: 349–361
- [26] Ntefidou M, Manetas Y. 1996. Optical properties of hairs during the early growth stages of leaf development in *Platanus orientalis*. *Australian Journal of Plant Physiology*, 1996, **23**: 535–538
- [27] Hughes NM, Neufeld HS, Burkey KO. Functional role of anthocyanins in high-light winter leaves of the evergreen herb *Galax urceolata*. *New Phytologist*, 2005, **168**: 575–587
- [28] Hughes NM, Smith WK. Attenuation of incident light in *Galax urceolata* (Diapensiaceae): Concerted influence of adaxial and abaxial anthocyanic layers on photoprotection. *American Journal of Botany*, 2007, **94**: 784–790
- [29] Asada K. The water-water cycle as alternative photon and electron sink. *Philosophical Transactions of the Royal Society B: Biological Science*, 2000, **355**: 1419–1431
- [30] Williams WE, Gorton HL, Witiak SM. Chloroplast movements in the field. *Plant, Cell and Environment*, 2003, **26**: 2005–2014
- [31] Pastenes C, Pimentel P, Lillo J. Leaf movements and photoinhibition in relation to water stress in field-grown beans. *Journal of Experimental Botany*, 2005, **56**: 425–433
- [32] Sun M-X (孙明霞), Wang B-Z (王宝增), Fan H (范海), *et al.* Anthocyanins of leaves and their environmental significance in plant stress responses. *Plant Physiology Communications* (植物生理学通讯), 2003, **39**(6): 688–694 (in Chinese)
- [33] Krol M, Gray GR, Hurry VM, *et al.* Low-temperature stress and photoperiod affect an increased tolerance to photoinhibition in *Pinus banksiana* seedlings. *Canadian Journal of Botany*, 1995, **73**: 1119–1127
- [34] McClure JW. Physiology and functions of flavonoids// Harborne JB, Mabry TJ, Mabry H, eds. The Flavonoids. London: Chapman & Hall Ltd, 1975: 970–1055
- [35] Wang M-L (王美玲). Study on Photosynthetic Characteristics of Purple Cabbage. PhD Thesis. Tai'an: Shandong Agricultural University, 2008 (in Chinese)
- [36] Davies KM, Schwinn KE. Transcriptional regulation of secondary metabolism. *Functional Plant Biology*, 2003, **30**: 913–925
- [37] Hu K (胡可), Han K-T (韩科厅), Dai S-L (戴思兰). Regulation of plant anthocyanin synthesis and pigmentation by environmental factors. *Chinese Bulletin of Botany* (植物学报), 2010, **45**(3): 307–317 (in Chinese)
- [38] Saure MC. External control of anthocyanin formation in apple. *Scientia Horticulturae*, 1990, **42**: 181–218
- [39] Hughes NM, Morley CB, Smith WK. Coordination of anthocyanin decline and photosynthetic maturation in juvenile leaves of three deciduous tree species. *New Phytologist*, 2007, **175**: 675–685
- [40] Mehlenbacher SA, Thompson MM. Inheritance of a chlorophyll deficiency in hazelnut. *HortScience*, 1991, **26**: 1414–1416
- [41] Wang H, Cao GH, Prior RL. Oxygen radical absorbing capacity of anthocyanins. *Journal of Agricultural and Food Chemistry*, 1997, **45**: 304–309
- [42] Burger J, Edwards GE. Photosynthetic efficiency and photodamage by UV and visible radiation, in red versus green leaf coleus varieties. *Plant and Cell Physiology*, 1996, **37**: 395–399
- [43] Dodd IC, Critchley C, Woodall GS, *et al.* Photoinhibition in differently coloured juvenile leaves of species. *Journal of Experimental Botany*, 1998, **49**: 1437–1445
- [44] Gould KS, Markham KR, Smith RH, *et al.* Functional role of anthocyanins in the leaves of *Quintinia serrata* A. Cunn. *Journal of Experimental Botany*, 2000, **51**: 1107–1115
- [45] Steyn WJ, Wand SJE, Holcroft DM. Anthocyanins in vegetative tissues: A proposed unified function in photoprotection. *New Phytologist*, 2002, **155**: 349–361
- [46] Hughes NM, Morley CB, Smith WK. Seasonal photosynthesis and anthocyanin production in 10 broadleaf evergreen species. *Functional Plant Biology*, 2007, **34**: 1072–1079
- [47] Yiannis M. Why some leaves are anthocyanins and why most anthocyanin leaves are red? *Science Direct*, **201**: 163–177
- [48] Lee DW, O'Keefe J, Holbrook NM, *et al.* Pigment dynamics and autumn leaf senescence in a New England deciduous forest, eastern USA. *Ecological Research*, 2003, **18**: 677–694
- [49] Hiiner NPA, Oquist G, Sarhan F. Energy balance and acclimation to light and cold. *Trends in Plant Science*, 1998, **3**: 224–230
- [50] Chen J (陈静), Chen Q-L (陈启林), Cheng Z-H (程智慧), *et al.* Protective effect of anthocyanin on photosynthetic apparatus of omato (*L. esculentum* Mill.) seedling leaves exposed to low temperature and low irradiance. *Scientia Agricultura Sinica* (中国农业科学), 2007, **40**(4): 788–793 (in Chinese)
- [51] Schaberg PG, Van den Berg AK, Murakami PF, *et al.* Factors influencing red expression in autumn foliage of sugar maple trees. *Tree Physiology*, 2003, **23**: 325–333
- [52] Hikosaka K. Interspecific difference in the photosynthe-

- sis-nitrogen relationship: Patterns, physiological causes and ecological importance. *Journal of Plant Research*, 2004, **117**: 481–94
- [53] van Heerden PDR, Tsimilli-Michael M, Kruger GHJ, *et al.* Dark chilling effects on soybean genotypes during vegetative development: Parallel studies of CO₂ assimilation, chlorophyll a fluorescence kinetics O-J-I-P and nitrogen fixation. *Physiologia Plantarum*, 2003, **117**: 476–491
- [54] Xu D-Q (许大全), Zhang Y-Z (张玉忠), Zhang R-X (张荣铎). Photoinhibition of photosynthesis in plants. *Plant Physiology Communications* (植物生理学通讯), 1992, **28**(4): 237–243 (in Chinese)
- [55] Jordan DN, Smith WK. Energy balance analysis of night-time leaf temperatures and frost formation in a sub-alpine environment. *Agricultural and Forest Meteorology*, 1994, **77**: 359–372
- [56] Krol M, Gray GR, Hurry VM, *et al.* Low temperature stress and photoperiod effect an increased tolerance to photoinhibition in *Pinus banksiana* seedlings. *Canadian Journal of Botany*, 1995, **73**: 1119–1127
- [57] Close DC, Davies NW, Beadle CL. Temporal variation of tannins (galloylglucoses), flavonols and anthocyanins in leaves of *Eucalyptus nitens* seedlings: Implications for light attenuation and antioxidant activities. *Australian Journal of Plant Physiology*, 2001, **28**: 269–278
- [58] Chalker-Scott L. Environmental significance of anthocyanins in plant stress responses. *Photochemistry and Photobiology*, 1999, **70**: 1–9
- [59] Gould KS. Nature's Swiss army knife: The diverse protective roles of anthocyanins in leaves. *Journal of Biomedicine and Biotechnology*, 2004, **5**: 314–320
- [60] Manetas Y, Petropoulou Y, Psaras GK, *et al.* Exposed red (anthocyanic) leaves of *Quercus coccifera* display shade characteristics. *Functional Plant Biology*, 2003, **30**: 265–270
- [61] Merzlyak MN, Chivkunova OB, Solovchenko AE, *et al.* Light absorption by anthocyanins in juvenile, stressed, and senescing leaves. *Journal of Experimental Botany*, 2008, **59**: 3903–3911
- [62] Hughes NM, Vogelmann TC, Smith WK. Optical effects of abaxial anthocyanin on absorption of red wavelengths by understorey species: Revisiting the backscatter hypothesis. *Journal of Experimental Botany*, 2008, **59**: 3435–3442
- [63] Barker DH, Seaton GGR, Robinson SA. Internal and external photoprotection in developing leaves of the CAM plant *Cotyledon orbiculata*. *Plant, Cell and Environment*, 1997, **20**: 617–624
- [64] Close DC, Beadle CL. The ecophysiology of foliar anthocyanin. *The Botanical Review*, 2003, **69**: 149–161
- [65] Manetas Y. Why some leaves are anthocyanic and why most anthocyanic leaves are red. *Flora*, 2006, **201**: 163–177
- [66] Yamasaki H, Uefuji H, Sakihama Y. Bleaching of the red anthocyanin induced by superoxide radical. *Archives of Biochemistry and Biophysics*, 1996, **332**: 183–186
- [67] Neill OS, Gould KS. Anthocyanins in leaves: Light attenuators or antioxidants? *Functional Plant Biology*, 2003, **30**: 865–873
- [68] Yamasaki H, Uefuji H, Sakihama Y. Bleaching of the red anthocyanin induced by superoxide radical. *Archives of Biochemistry and Biophysics*, 1996, **332**: 183–186
- [69] Gould KS, McKelvie J, Markham KR. Do anthocyanins function as antioxidants in leaves? Imaging of H₂O₂ in red and green leaves after mechanical injury. *Plant, Cell and Environment*, 2002, **25**: 1261–1269
- [70] Nagata T, Todoriki S, Masumizu T, *et al.* Levels of active oxygen species are controlled by ascorbic acid and anthocyanin in *Arabidopsis*. *Journal of Agricultural and Food Chemistry*, 2003, **51**: 2992–2999
- [71] Neil S, Gould KS, Kilmartin PA, *et al.* Antioxidant activities of red versus green leaves in *Elatostema rugosum*. *Plant, Cell and Environment*, 2002, **25**: 539–547
- [72] Liu C (刘超). The Study of the Extraction, Stability and Antioxidation of Anthocyanidin from Purple Sweet Potato. PhD Thesis. Hunan: Hunan Agricultural University, 2008 (in Chinese)
- [73] van Den Berg AK, Perkins T. Contribution of anthocyanins to the antioxidant capacity of juvenile and senescing sugar maple (*Acer saccharum*) leaves. *Functional Plant Biology*, 2007, **34**: 714–719
- [74] Neill SO, Gould KS, Kilmartin PA, *et al.* Antioxidant capacities of green and cyanic leaves in the sun species, *Quintinia serrata*. *Functional Plant Biology*, 2002, **29**: 1437–1443
- [75] Grace SC, Logan BA, Adams III WW. Seasonal differences in foliar content of chlorogenic acid, a phenylpropanoid antioxidant in *Mahonia repens*. *Plant, Cell and Environment*, 1998, **21**: 513–521
- [76] Close DC, Davies NW, Beadle CL. Temporal variation of tannins (galloylglucoses), flavonols and anthocyanins in leaves of *Eucalyptus nitens* seedlings: Implications for light attenuation and antioxidant activities. *Australian Journal of Plant Physiology*, 2001, **28**: 1–10
- [77] Foot JE, Caporn SJM, Lee JA, *et al.* The effect of long term ozone fumigation on the growth, physiology and frost sensitivity of *Calluna vulgaris*. *New Phytologist*, 1996, **133**: 503–511
- [78] Ronehi A, Farina G, Gozzo E, *et al.* Effects of a triazolic fungicide on maize plant metabolism: Modifications of transcript abundance in resistance-related pathways. *Plant Science*, 1997, **130**: 51–62
- [79] Wln HW, Farrant M. Protection mechanisms against excess light in the resurrection plants *Craterostigma wilmsii* and *Xerophyta viscosa*. *Plant Growth Regulator*, 1998, **24**: 203–210
- [80] Close DC, Beadle CL, Holz GK, *et al.* Effect of shade cloth tree shelters on cold-induced photoinhibition, foliar anthocyanin and growth of *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden seedlings during establishment. *Australian Journal of Botany*, 2002, **50**: 15–20

作者简介 王良再,男,1985年生,硕士研究生。主要从事植物生理生态研究。E-mail: wangliangzail1@126.com

责任编辑 李凤琴