

评述与展望

Reviews and Progress

兰科植物花色形成与变异分子机理

王有国¹, 李枝林¹, 孙慧晶¹, 郭红¹, 张广辉²

1. 云南农业大学园林园艺学院, 昆明, 650201;

2. 云南农业大学龙润普洱茶学院, 昆明, 650201

✉ 通讯作者: zgh73107310@163.com; ✉ 作者

分子植物育种, 2011 年, 第 9 卷, 第 80 篇 doi: 10.5376/mpb.cn.2011.09.0080

收稿日期: 2010 年 04 月 11 日

接受日期: 2011 年 06 月 01 日

发表日期: 2011 年 06 月 22 日

这是一篇采用 Creative Commons Attribution License 进行授权的开放获取论文。只要对本原作有恰当的引用, 版权所有人允许并同意第三方无条件的使用与传播。

引用格式:

王有国等, 2011, 兰科植物花色形成与变异分子机理, 分子植物育种 Vol.9 No.80 (doi: 10.5376/mpb.cn.2011.09.0080)

摘要 兰科是开花植物中的第二大科, 花色变异丰富。兰科植物花色素主要包含花青素苷和类胡萝卜素。近年兰科植物花色形成分子机理研究主要集中于花青素苷生物合成途径中结构基因和转录因子的克隆与功能分析, 对类胡萝卜素生物合成与调控, 环境因子对花色变异的影响等则少有涉及。云南省丰富的野生兰花资源是研究兰科植物花色形成与变异的优良材料。课题组在收集云南野生兰花资源过程中发现, 多数兰花种类缺乏红色系。本文作者提出, 超表达花青素苷生物合成途径中的转录因子, 是培育红色系兰花新品种的有效途径之一, 并讨论了存在的问题和解决方法进行。

关键词 兰科植物; 花色; 花青素苷; 类胡萝卜素; 转录因子; 超表达

Molecular Mechanism of Flower Color Formation and Variation in Orchidaceae

Wang Youguo¹, Li Zhilin¹, Sun Huijing¹, Guo Hong¹, Zhang Guanghui²

1. College of horticulture and landscape, Yunnan Agricultural University, Kunming, 650210, P.R. China

2. Longrun pu-erh tea college, Yunnan Agricultural University, 650210, P.R. China

✉ Corresponding author, zgh73107310@163.com; ✉ Authors

Abstract As the second largest family of flower plants, orchid family (Orchidaceae) has plentiful color variation. Their flower pigments mainly included anthocyanins and carotenoids. The studies on molecular mechanism of flower color formation concentrated on the cloning and functional analysis of structure genes and transcriptional factors involved in anthocyanins biosynthesis, only a few on carotenoids biosynthesis and the effects of environmental factors on flower color. There are many wild orchid species only distributed in Yunnan Province which is good materials for studying flower formation and variation. Our group's investigations revealed that most orchid species lack of red color lines. In this paper, the authors suggested that overexpression transcriptional factors involved anthocyanins biosynthesis will be an efficient way to create new flower color varieties.

Keywords Orchidaceae; Flower color; Anthocyanins; Carotenoids; Transcriptional factors; overexpression

研究背景

兰科(Orchidaceae)植物统称兰花, 是开花植物中第二大科。兰花的花色变化非常丰富, 是研究花着色机理的理想对象(朱根发和郭振飞, 2004)。云南省有丰富的野生兰花资源, 共有兰科植物135属、764种和16个变种以及众多变异类型, 是我国乃至世界的兰花资源宝库(关文灵等, 2006)。本文总结了兰科植物花色研究进展, 主要包括花色素组成及其合成与调控的分子机理。

1 兰科植物花色素组成

植物的花色通常是由花青素苷(anthocyanins)和/或类胡萝卜素(carotenoids)的组合而决定的。兰科植物花色表现出同样的趋势, 黄色到橙色由类胡萝卜素决定, 橙色到红色由花青素苷和类胡萝卜素组合决定, 红色到紫色由花青素苷决定(Thammasiri et al., 1986; Matsui and Nakamura, 1988; Matsui et al., 1994; Tatsuzawa et al., 2010)。文心兰(*Oncidium Gower Ramsey*)的花瓣和萼片(黄色带有红色斑点)

同时含有花青素苷和类胡萝卜素, 类胡萝卜素主要是莖菜黄质(violaxanthin)的全反和9-顺异构体, 花青素苷主要是矢车菊素(cyanidin)及其甲基衍生物芍药花素(peonidin) (Hieber et al., 2006)。其它兰科植物的花青素苷也主要是矢车菊素, 其次是天竺葵素(pelargonidin)或芍药花素(Kuehnle et al., 1997; Fossen and Øvstedal, 2003; Tatsuzawa et al., 2010)。植物花色素的生物合成途径与分子调节机理已比较清楚(Tanaka et al., 2008), 为研究兰科植物花色变异提供了可能。

2 兰科植物花青素苷的生物合成与分子调控机理

花青素苷属于类黄酮(flavonoids)化合物, 是决定植物花色的最常见色素, 贡献颜色范围从黄色到橙色到红色乃至紫色。花青素苷的生物合成途径主要受到结构基因、转录因子和环境条件的调控。一些兰科植物参与花青素苷生物合成的酶的基因已经得到克隆, 并对其表达与花色关系有所了解, 但已有研究主要集中于蝴蝶兰和文心兰, 兰科其它种类则很少涉及。

2.1 兰科植物花青素苷生物合成中的结构基因

兰科植物的查耳酮合成酶(CHS)基因由一个小的多基因家族编码, 其在花器官的各部位和红色的幼叶均有表达, 萼片表达水平最高, 花尚未着色的发育初期表达水平最高(Mudalige-Jayawickrama et al., 2005; Liew et al., 1998a; Han et al., 2005; Pitakdantham et al., 2010; Han et al., 2006)。

二氢黄酮醇4-还原酶(DFR)是将二氢黄酮醇转变为花色素的第一个酶, 在不同花色形成中起着关键作用, 不同物种DFR对底物选择性不同, 合成不同的花色素, 呈现各异的花色。石斛兰(*Dendrobium*)缺乏橙色与蓝色, 这与石斛兰花色形成过程中DFR的活性密切相关。兰科植物DFR基因多数为单拷贝(Liew et al., 1998b), 少数为多拷贝(Hieber et al., 2006)。兰属植物DFR不能有效还原DHK(二氢山奈酚, dihydrokaempferol), 导致天竺葵素缺乏(Johnson et al., 1999)而使其缺乏橙色, 这可能是由于DFR和类黄酮-3'-羟化酶(F3'H)竞争相同底物DHK的结果(Mudalige-Jayawickrama et al., 2005)。

蓝色和紫色花通常含有飞燕草素(delphinidin),

类黄酮-3',5'-羟化酶(F3'5'H)是生物合成飞燕草素的关键酶。蝴蝶兰*F3'5'H*基因的表达与花发育时期和花色密切相关, 在完全开放的时期和紫色花中表达水平最高, 而在黄色和白色花中水平很低, 叶片和根中无表达(Wang et al., 2006), 蝴蝶兰*F3'5'H*基因瞬间表达于花瓣, 其颜色由粉红转为洋红(Su and Hsu, 2003)。

UDP-葡萄糖: 类黄酮3-O-糖基转移酶(UFGT)是形成稳定的花色素苷所必需的。红色和白色蝴蝶兰品种*CHS*, *CHI*(查耳酮异构酶基因)和*ANS*(花青素合成酶基因)表达水平没有差别, 但*UFGT*基因仅在红花中有强烈表达, 因此*UFGT*基因与红花形成高度相关(Chen et al., 2011)。

2.2 转录因子对兰科植物花青素苷生物合成的调控

花青素苷生物合成途径中结构基因的时空表达由3种转录因子及其相互作用而决定, 分别是R2R3-Myb, Myc 基因家族的bHLH (basic helix-loop-helix)和WD40-型转录因子(Tanaka et al., 2008)。Wu(2003)等最早从石斛属(*Dendrobium*)中分离出21个R2R3-Myb基因(Wu et al., 2003)。

蝴蝶兰(*Phalaenopsis amabilis*)白色花瓣中同时表达玉米(*Zea mays*) Myc Lc 和 Myb C1 可激活花青素苷的合成, 而单独表达其中任何一个则不能激活, 说明其花青素苷的生物合成需要上述两种转录因子(Griesbach and Klein, 1993), 这种激活作用也与植物基因启动子有关(Ma and Pooler, 2008)。白花蝴蝶兰(*P. amabilis*) DFR 表达水平很低, 紫花蝴蝶兰(*P. schilieriana*) DFR 表达水平很高, 二者均表达 Myc 和 Wd 基因, 但 Myb 基因只表达在后者中有表达, 说明缺乏 Myb 基因使白花蝴蝶兰丧失 DFR 活性, 致使不能合成花青素苷(Ma and Pooler, 2009)。在文心兰的黄色唇瓣中瞬间表达 *OgMYB1*, 可以通过激活 CHI 和 DPR 基因的转录, 而诱导产生红色(Chiou and Yeh, 2008)。最新的研究表明, 玉米花青素转录因子 Leaf color, Colorless 1 和金鱼草(*Anthurium andraeanum*) AaMYB1 均可以激活墨兰(*Cymbidium*)花青素苷的合成(Albert et al., 2010)。

2.3 环境因子对植物花青素苷合成的调控

环境因子调控花青素苷生物合成途径中的结构基因与转录因子的表达, 从而影响花青素苷种类

与含量(胡可等, 2010)。影响花青素苷合成的环境因子包括光照、温度、糖、水份、氮或磷等(Weiss, 2000; Rajendran et al., 1992)。光照强度和光质均影响花青素苷的合成和植物花、果实和叶片等的呈色。光信号通过激活花青素苷合成途径上相关基因的表达直接或间接地调控花青素苷的合成与积累(唐杏姣和戴思兰, 2011)。强光促进结构基因和调节基因的表达, 促使花青素苷积累; 而黑暗或弱光下调基因的表达, 产生白花或浅色花(胡可等, 2010), 如拟南芥(*Arabidopsis thaliana*)、矮牵牛(*Petunia hybrida*)、葡萄(*Vitis vinifera*)和百合(*Lilium spp.*)等(Cominelli et al., 2008; Albert et al., 2009; Matus et al., 2009; Nakatsuka et al., 2009)。UV-B是大多数植物花青素苷呈色所必需的(Dong et al., 1998), UV-A和低强度的UV-B可以诱导花青素苷生物合成相关基因的表达, 从而诱导花青素苷的积累(Guo et al., 2008), 科特兰(*Cattleya*)和惠兰(*Cymbidium*)叶片叶绿素、类胡萝卜素和类黄酮的含量均受到紫外辐射的影响(Zhao et al., 2003)。

温度升高时花青素苷合成速率减慢, 降解速率加快导致其积累减少(Shaked-Sachray et al., 2002), 如长叶车前(*Plantago lanceolata*), 葡萄和菊花(*Chrysanthemum morifolium*)均是如此(Stiles et al., 2007; Mori et al., 2007; Poudel et al., 2009; Nozaki et al., 2006; Huh et al., 2008)。缺氮、缺磷或二者同时缺少导致花青素苷含量增加(Rajendran et al., 1992; Lillo et al., 2008)。外源NH₄⁺抑制非洲菊(*Gerbera hybrida*)花瓣色素的积累(Huang et al., 2008), 而外源腐胺能够有效促进苹果花青素苷的积累(田义等, 2009)。综上所述, 花青素苷的生物合成受到多种环境因子的调控, 但哪个起主导作用及其作用途径尚不清楚。同时, 相关研究主要集中于拟南芥和矮牵牛等少数模式植物上, 环境因子对兰科植物花色的影响和调控机理等尚未有报道。

3 兰科植物类胡萝卜素的生物合成与分子调控机理

类胡萝卜素是一类积累于非光合质体中的脂溶性色素, 多数植物的主要是黄色的莖菜黄素(Tanaka et al., 2008), 包括兰科植物中的文心兰(Hieber et al., 2006; Chiou et al., 2010)。研究发现, 黄花的文心兰品种Gower Ramsy积累莖菜黄素新黄

质(neoxanthin), 橙花品种Sunist除二者外还含有β-胡萝卜素(β-carotene), 白花品种White Jade则不含类胡萝卜素类化合物(Hieber et al., 2006)。进一步的研究表明, 由于橙花品种中β-羟化酶基因(β-hydroxylase, HYB)和玉米黄质环氧酶基因(zeaxanthin epoxidase, ZEP)转录水平低于其在红花品种的转录水平, 导致莖菜黄素和新黄质含量减少, β-胡萝卜素含量增加, 而表现出橙色; 白花品种则是由于9-顺式-环氧类胡萝卜素双加氧酶(9-cis-epoxycarotenoid dioxygenase, NCED)基因和类胡萝卜素裂解双加氧酶(carotenoids cleavage dioxygenase, CCD)基因表达水平高, 导致降解为无色的脱辅基类胡萝卜素(apocarotenoid) (Chiou et al., 2010)。类胡萝卜素生物合成途径中各酶及其编码基因的成功分离, 为鉴定其关键的调节步骤提供了基础, 但其分子调节机理仍然缺乏了解(Tanaka et al., 2008), 环境因子对类胡萝卜素的合成与呈色影响等也少有研究。最新的研究表明, 一些光信号因子如HY5和COP1对番茄果实类胡萝卜素的生物合成有相反的调节作用(Liu et al., 2004; Davuluri et al., 2005)。

4 问题与展望

兰科植物的花色素组成主要是花青素苷和类胡萝卜素。近年来花青素苷的生物合成与调控分子机理研究很多, 对一些环境因子如光的调控机理等也了解比较深入(唐杏姣和戴思兰, 2011), 但是研究多数集中于模式植物, 兰科植物涉及较少, 特别是国兰的种类。云南有丰富的兰花资源和多变的地理环境, 一些稀有的兰花种类, 如莲瓣兰(*Cymbidium Lianpan*)等其花色很少有报道。课题组在收集野生资源过程中发现, 兰花生长地的环境条件, 如海拔、紫外辐射、温度等对其花色有显著影响, 这些环境因子也是形成云南兰花变异众多的原因。因为云南特有兰花资源幼苗稀少、价格高昂, 对研究工作造成很大的影响, 同时一些环境因子如海拔高度对花色变异的影响因为很难创造模拟条件, 研究难度很大。因此, 必需首先将云南特有兰花资源进行花色初步分类, 然后重点研究各类花色组成和调控分子机理, 特别转录因子对花色的调控以及环境条件对转录因子表达的影响。

同时, 课题组在研究中也发现, 多数兰科植物缺乏红色、蓝色和紫色。兰花缺乏红色系和紫色系是结构基因和转录因子共同作用的结果。前人的研究表明, 瞬时表达花青素苷生物合成途径的转录因子, 能够促进兰花花色改变而产生红色(Griesbach and Klein, 1993; Chiou and Yeh, 2008; Ma and Pooler, 2009; Albert et al., 2010), 而且在模式作物上的研究也表明, 超表达花青素苷转录因子不但能够改变植物花色(Lloyd et al., 1992), 而且能够改变营养器官如叶片的颜色(Golesbrough et al., 1996; Elomaa et al., 2003; Ray et al., 2003)。因此, 超表达花青素苷转录因子是兰花花色育种的有效途径之一。

近年兰科植物的离体培养(Chugh et al., 2009)和遗传转化均取得较大进展, 但依然落后于其他草本植物, 多数研究仍集中于转化体系建立(Zhang et al., 2010; Shrestha et al., 2007; Semiarti et al., 2010; Sjahail and Mii, 2006)。壳聚糖(chitosan)能够促进石斛兰属原球茎(protocorn-like body)的增殖、芽分化和幼苗发育(Pornpienpakdee et al., 2010), 而且能够促进其种子萌发(Kananont et al., 2010)。最新研究发现, 蝴蝶兰原球茎在添加番茄提取物的培养基上预培养, 能够促进抗性芽的再生, 转化频率高达10%~14%(Semiarti et al., 2011)。这些研究为兰花花色分子育种, 特别是培育红色、蓝色和紫色兰花提供了可能。

作者贡献

王有国和张广辉完成文献检索和初稿的写作, 孙慧晶和郭红参与了论文的写作和修改。李枝林审阅了全文。全体都阅读并同意最终的文本。

致谢

本研究工作得到云南省科技厅重点产业创新工程项目(项目编号: 2009BB013)和云南教育厅科学研究基金(项目编号: 09Y0195)资助。

参考文献

Albert N.W., Arathoon S., Collette V.E., Schwinn K.E., Jameson P.E., Lewis D.H., Zhang H.B., and Davies K.M., 2010, Activation of anthocyanin synthesis in *Cymbidium* orchids: variability between known regulators, *Plant Cell Tissue and Organ Culture*, 100(3): 355-360

Albert N.W., Lewis D.H., Zhang H., Irving L.J., Jameson P.E., and Davies K.M., 2009, Light-induced vegetative anthocyanin pigmentation in *Petunia*, *J. Exp. Bot.*, 60(7): 2191-2202

Chen W.H., Hsu C.Y., Cheng H.Y., Chang H., Chen H.H., and Ger M.J., 2011, Downregulation of putative UDP-glucose:

Flavonoid 3-O-glucosyltransferase gene alters flower coloring in *Phalaenopsis*, *Plant Cell Reports*, 30(6): 1007-1017

Chiou C.Y., and Yeh K.W., 2008, Differential expression of *MYB* gene (*OgMYB1*) determines color patterning in floral tissue of *Oncidium* Gower Ramsey, *Plant Mol Biol*, 66(4): 379-388

Chiou C.Y., Pan H.A., Chuang Y.N., and Yeh K.W., 2010, Differential expression of carotenoid-related genes determines diversified carotenoid coloration in floral tissues of *Oncidium* cultivars, *Planta*, 232(4): 937-48

Chugh S., Guha S., and Rao I.U., 2009, Micropropagation of orchids: A review on the potential of different explants, *Scientia Horticulturae*, 122(4): 507-520

Cominelli E., Gusmaroli G., Allegra D., Galbiati M., Wade H.K., Jenkins G.I., and Tonelli C., 2008, Expression analysis of anthocyanin regulatory genes in response to different light qualities in *Arabidopsis thaliana*, *J. Plant Physiol.*, 165(8): 886-894

Weiss D., 2000, Regulation of flower pigmentation and growth: multiple pathways control anthocyanin synthesis in expanding petals, *Physiol Plant*, 110(2): 152-157

Davuluri G.R., van Tuinen A., Fraser P.D., Manfredonia A., Newman R., Burgess D., Brummell D.A., King S.R., Palys J., Uhliq J., Bramley P.M., Pennings H.M., and Bowler C., 2005, Fruit-specific RNAi-mediated suppression of *DET1* enhances carotenoid and flavonoid content in tomatoes, *Nat. Biotechnol.*, 23(7): 890-895

Dong Y.H., Beuning L., Davies K., Mitra D., Morris B., and Kootstra A., 1998, Expression of pigmentation genes and photo-regulation of anthocyanin biosynthesis in developing Royal Gala apple flowers, *Aust. J. Plant Physiol*, 25(2): 245-252

Elomaa P., Uimari A., Mehto M., Albert V.A., Laitien R.A., and Teeri T.H., 2003, Activation of anthocyanin biosynthesis in *Gerbera hybrida* (Asteraceae) suggests conserved protein-protein and protein-promoter interactions between the anciently diverged monocots and eudicots, *Plant Physiology*, 133(4): 1831-1842

Fossen T., and Øvstedal D.O., 2003, Anthocyanins from flowers of the orchids *Dracula chimaera* and *D. cordobae*, *Phytochemistry*, 63(7): 783-787

Golesbrough A P, Tong Y., and Yoder J I., 1996, *Lc* as a non-destructive visual reporter and transposition excision marker gene for tomato, *The Plant Journal*, 9(6): 927-933

Griesbach R.J., and Klein T.M., 1993, In situ genetic

- complementation of a flower color mutant in *Doritis pulcherrima* (Orchidaceae), *Lindleyana*, 8: 223-226
- Guan W.L., Li Z.L., Yu C.X., Wang Y.Y., and Cheng L.X., 2006, Report on the diversity and introduction and domestication of wild orchid resources in Yunnan (Southwest China *Journal of Agricultural Sciences*), 19(4): 688-691 (关文灵, 李枝林, 余朝秀, 王玉英, 程利霞, 2006, 云南野生兰花资源的多样性及其引种驯化, *西南农业学报*, 19(4): 688-691)
- Guo J., Han W., and Wang M.H., 2008, Ultraviolet and environmental stresses involved in the induction and regulation of anthocyanin biosynthesis: A review, *Afr. J. Biotechnology*, 7(25): 4966-4972
- Han Y.Y., Ming F., Wang W., Wang J.W., Ye M.M., and Shen D.L., 2006, Molecular evolution and functional specialization of chalcone synthase superfamily from *phalaenopsis* orchid, *Genetica*, 128(1-3): 429-438
- Han Y.Y., Ming F., Wang J.W., Ye M.M., and Shen D., 2005, A novel chalcone synthase gene from *Phalaenopsis* orchid that alters floral morphology in tobacco plants, *Plant Mol Biol Reporter*, 23(2): 193-193
- Hieber A.D., Mudalige-Jayawickrama R.G., and Kuehnle A.R., 2006, Color genes in the orchid *Oncidium* Gower Ramsey: Identification, expression, and potential genetic instability in an interspecific cross, *Planta*, 223(3): 521-31
- Hu K., Han K.T., and Dai S.L., 2010, Regulation of plant anthocyanin synthesis and pigmentation by environmental factors, *Zhiwu Xuebao* (Chinese Bulletin of Botany), 45(3): 307-317 (胡可, 韩科厅, 戴思兰, 2010, 环境因子调控植物花青素合成及呈色的机理, *植物学报*, 45(3): 307-317)
- Huang Z., Liang M., Peng J., Xing T., and Wang X., 2008, Exogenous ammonium inhibits petal pigmentation and expansion in *Gerbera hybrida*, *Physiol Plant*, 133(2): 254-265
- Huh E.J., Shin H.K., Choi S.Y., Kwon O.G., and Lee Y.R., 2008, Thermosusceptible developmental stage in anthocyanin accumulation and color response to high temperature in red chrysanthemum cultivars, *Korean J. Hortic. Sci. Technol.*, 26(4): 357-361
- Johnson E.T., Yi H., Shin B., Oh B.J., Cheong H., and Choi G., 1999, *Cymbidium* hybrida dihydroflavonol 4-reductase does not efficiently reduce dihydrokaempferol to produce orange pelargonidin-type anthocyanins, *Plant J.*, 19(1): 81-85
- Kananont N., Pichyangkura R., Chanprame S., Chadchawan S., and Limpanavech P., 2010, Chitosan specificity for the *in vitro* seed germination of two *Dendrobium* orchids (Asparagales: Orchidaceae), *Scientia Horticulturae*, 124(2): 239-247
- Kuehnle A.R., Lewis D.H., Markham K.R., Mitchell K.A., Davies K.M., and Jordan B.R., 1997, Floral flavonoids and pH in *Dendrobium* orchid species and hybrids, *Euphytica*, 95(2): 187-194
- Liew C.F., Goh C.J., Loh C.S., and Lim S.H., 1998a, Cloning and characterization of full-length cDNAs clones encoding chalcone synthase from the orchid *Bromheadia finlay* Soniana, *Plant Physiology and Biochemistry*, 36(9): 647-656
- Liew C.F., Loh C.S., Goh C.J., and Lim S.H., 1998b, The isolation, molecular characterization and expression of dihydroflavonol 4-reductase cDNA in the orchid, *Bromheadia finlaysoniana*, *Plant Sci.*, 135(2): 161-169
- Lillo C., Lea U.S., and Ruoff P., 2008, Nutrient depletion as a key factor for manipulating gene expression and product formation in different branches of the flavonoid pathway, *Plant Cell Environ*, 31(5): 587-601
- Liu Y., Roof S., Ye Z., Barry C., van Tuinen A., Vrebalov J., Bowler C., and Giovannoni J., 2004, Manipulation of light signal transduction as a means of modifying fruit nutritional quality in tomato, *Proc. Natl. Acad. Sci. USA.*, 101(26): 9897-9902
- Lloyd A.M., Walbot V., and Davis R.W., 1992, Arabidopsis and Nicotiana anthocyanin production activated by maize regulators R and C1, *Science*, 258(5089): 1773-1775
- Ma H., and Pooler M., 2008, Ratio of *Myc* and *Myb* transcription factors regulates anthocyanin production in orchid flowers, *J. Amer. Soc. Hort. Sci.*, 133(1): 133-138
- Ma H., and Pooler M., 2009, Anthocyanin regulatory/structural gene expression in *Phalaenopsis*, *J Amer Soc Hort Sri*, 134(1): 88-96
- Matsui S., and Nakamura M., 1998, Distribution of flower pigments in perianth of *Cattleya* and allied genera I. species, *J. Japan Soc. Hort. Sci.*, 57(2): 222-232
- Matsui, S., 1994, Floral carotenoids in species and hybrids of the Laeliinae, *Lindleyana*, 9: 213-217
- Matus J.T., Loyola R., Vega A., Pena-Neira A., Bordeu E., Arce-Johnson P., and Alcalde J.A., 2009, Post-veraison sunlight exposure induces MYB-mediated transcriptional regulation of anthocyanin and flavonol synthesis in berry skins of *Vitis vinifera*, *J. Exp. Bot.*, 60(3): 853-867
- Mori K., Goto-Yamamoto N., Kitayama M., and Hashizume K.,

- 2007, Loss of anthocyanins in red-wine grape under high temperature, *J. Exp. Bot.*, 58(8): 1935-1945
- Mudalige-Jayawickrama R.G., Champagne M.M., Hieber A.D., and Kuehnle A.R., 2005, Cloning and characterization of two anthocyanin biosynthetic genes from *Dendrobium* orchid, *J. Am. Soc. Hort. Sci.*, 130: 611-618
- Nakatsuka A., Yamagishi M., Nakano M., Tasaki K., and Kobayashi N., 2009, Light-induced expression of basic helix-loop-helix genes involved in anthocyanin biosynthesis in flowers and leaves of Asiatic hybrid lily, *Sci. Hortic*, 121(1): 84-91
- Nozaki K., Takamura T., and Fukai S., 2006, Effects of high temperature on flower colour and anthocyanin content in pink flower genotypes of greenhouse chrysanthemum (*Chrysanthemum morifolium* Ramat.), *J. Hort. Sci. Biotechnol*, 81(4): 728-734
- Pitakdantham W., Sutabutra T., Chiemsombat P., and Pitaksutheepong C., 2010, Isolation and characterization of chalcone synthase gene isolated from *Dendrobium* Sonia Earsakul, *Pakistan Journal of Biological Sciences*, 13(20): 1000-1005
- Pornpienpakdee P., Singhasurasak R., Chaiyasap P., Pichyangkura R., Bunjongrat R., Chadchawan S., and Limpanavech P., 2010, Improving the micropropagation efficiency of hybrid *Dendrobium* orchids with chitosan, *Scientia Horticulturae*, 124(4): 490-499
- Pornpienpakdee P., Singhasurasak R., Chaiyasap P., Pichyangkura R., Bunjongrat R., Chadchawan S., and Limpanavech P., 2010, Improving the micropropagation efficiency of hybrid *Dendrobium* orchids with chitosan, *Scientia Horticulturae*, 124(4): 490-499
- Poudel P.R., Mochioka R., Beppu K., and Kataoka I., 2009, Influence of temperature on berry composition of interspecific hybrid wine grape 'Kadainou R-1' (*Vitis ficifolia* var. ganebu x *V. vinifera* 'Muscat of Alexandria'), *J. Jpn. Soc. Hort. Sci.*, 78(2): 169-174
- Rajendran L., Ravishankar G.A., Venkataraman L.V., and Prathiba K.R., 1992, Anthocyanin production in callus cultures of *Daucus carota* as influenced by nutrient stress and osmoticum, *Biotechnol Lett*, 14(8): 707-712
- Ray H., Yu M., Auser P., Blahut-Beatty L., McKersie B., Bowley S., Westcott N., Coulman B., Lloyd A., and Gruber M.Y., 2003, Expression of anthocyanins and proanthocyanidins after transformation of alfalfa with maize *LC*, *Plant Physiol*, 132(3): 1448-1463
- Semiarti E., Indrianto A., Suyono E.A., Nurwulan R.L., Restiani R., Machida Y., Machida C., 2010, Genetic transformation of the Indonesian black orchid (*Coelogyne pandurata* Lindley) through *Agrobacterium tumefaciens* for micropropagation, *Proceedings of Nagoya International Orchid Congress, Japan*, 16-20
- Semiarti E., Indrianto A., Purwantoro A., Martiwi I.N. A., Feroniasanti Y.M.L., Nadifah F., Mercuriani I.S., Dwiyani R., Kojima S., Machida Y., Machida C., 2011, Establishment of high-frequency genetic transformation method of Indonesian orchid species mediated by *Agrobacterium tumefaciens*, *Proceedings of Nagoya International Orchid Congress, Japan*, 32-39
- Shaked-Sachray L., Weiss D., Reuveni M., Nissim-Levi A., and Oren-Shamir M., 2002, Increased anthocyanin accumulation in aster flowers at elevated temperatures due to magnesium treatment, *Physiol Plant*, 114(4): 559-565
- Shrestha B.R., Poh Chin D.P., Tokuhara K., Masahiro M.M., 2007, Efficient production of transgenic plants of *Vanda* through sonication-assisted *Agrobacterium*-mediated transformation of protocorm-like bodies, *Plant Biotechnology*, 24: 429-434
- Sjahail R., and Mitt M., 2006, High-efficiency *Agrobacterium*-mediated transformation of *Phalaenopsis* using meropenem, a novel antibiotic to eliminate *Agrobacterium*, *Journal of Horticultural Science & Biotechnology*, 81(3): 458-464
- Stiles E.A., Cech N.B., Dee S.M., and Lacey E.P., 2007, Temperature-sensitive anthocyanin production in flowers of *Plantago lanceolata*, *Physiol Plant*, 129(4): 756-765
- Su V., and Hsu B.D., 2003, Cloning and expression of a putative cytochrome P450 gene that influences the colour of *Phalaenopsis* flowers, *Biotechnol Lett*, 25(22): 1933-1939
- Tanaka Y., Sasaki N., and Ohmiya A., 2008, Biosynthesis of plant pigments: Anthocyanins, betalains and carotenoids, *The Plant Journal*, 54(4): 733-749
- Tang X.J., and Dai S.L., 2011, Light regulation of anthocyanin synthesis and coloration, *Fenzi Zhiwu Yuzhong (Plant Molecular Breeding)*, 9: 1284-1290 (唐杏姣, 戴思兰, 2011, 光调控花青素苷合成及呈色的机理, 分子植物育种, 9: 1284-1290)
- Tatsuzawa F., Ichihara K., Shinoda K., and Miyoshi K., 2010, Flower colours and pigments in *Disa* hybrid (Orchidaceae), *South African Journal of Botany*, 76(1): 49-53
- Thammasiri K., Tang C.S., Yamamoto H.Y., and Kamemoto H.,

- 1986, Carotenoids and chlorophylls in yellow-flowered *Dendrobium* species, *Lindleyana*, 1: 215-218
- Tian Y., Wang Q., Zhang L.Y., Kang G.D., Yang L., Hao H.M., Yang Z.Y., and Cong P.H., 2009, Promotion effect of exogenous putrescine on anthocyanin accumulation in 'Red Fuji' apple fruits, *Zhiwu Xuebao* (Chinese Bulletin of Botany), 44: 310-316 (田义, 王强, 张利义, 康国栋, 杨玲, 郝红梅, 杨振英, 丛佩华, 2009, 外源腐胺促进苹果果皮花青苷积累的效应, *植物学报*, 44: 310-316)
- Wang J., Ming F., Han Y., and Shen D., 2006, Flavonoid-3', 5'-hydroxylase from *Phalaenopsis*: A novel member of cytochrome P450s, its cDNA cloning, endogenous expression and molecular modeling, *Biotechnology Letters*, 28(5): 327-334
- Wu X.M., Lim S.H., and Yang W.C., 2003, Characterization, expression and phylogenetic study of R2R3-MYB genes in orchid, *Plant Mol. Biol.*, 51(6): 959-972
- Zhang L., Chin D.P., Fukami M., Ichikawa H., Nakamura I., and Mii M., 2010, *Agrobacterium*-mediated genetic transformation of *Cattleya* with an *Odontoglossum ringspot* virus replicase gene sequence, *Plant Biotechnology*, 27(5): 421-426
- Zhao X.H., Li J.C., Matsui S., and Maezawa S., 2003, Effects of UV radiation on pigment contents and antioxidative enzyme activities in leaves of *Cattleya* and *Cymbidium* orchid plants, *J. Japan. Soc. Hort. Sci.*, 72(5): 446-450
- Zhu G.F., and Guo Z.F., 2004, Progress on molecular biology of main ornamental Orchidaceae, *Zhiwuxue Tongbao* (Chinese Bulletin of Botany), 21(4): 471-477 (朱根发, 郭振飞, 2004, 重要观赏兰科植物的分子生物学研究进展, *植物学通报*, 21(4): 471-477)



5thPublisher是一个致力于科学与文化传播的中文出版平台

在5thPublisher上发表论文, 任何人都可以免费在线取阅您的论文

- ※同行评审, 论文接受严格的高质量评审
- ※在线发表, 论文一经接受, 即刻在线发表
- ※开放取阅, 任何人都可免费取阅无限使用
- ※快捷搜索, 涵盖谷歌学术搜索与知名数据库
- ※论文版权, 作者拥有版权读者自动授权使用

在线投稿: <http://5th.sophiapublisher.com>