Fu M *et al.* (2021)
Notulae Botanicae Horti Agrobotanici Cluj-Napoca
Volume 49, Issue 2, Article number 12071
DOI:10.15835/nbha49212071
Review Article

Advance in mechanism of plant leaf colour mutation

Mingyue FU[1], Shuiyuan CHENG[2], Feng XU[1,2]*, Zexiong CHEN[3], Zhongbing LIU[4], Weiwei ZHANG[1], Jiarui ZHENG[1], Ling WANG[1]

[1] *Yangtze University, Jingzhou 434025, Hubei, China; fumingyue1214@163.com; xufeng198@126.com (*corresponding author); wwzhangchn@163.com; Zhengjiarui1222@163.com; wangling085@163.com*
[2] *Wuhan Polytechnic University, National R&D for Se-rich Agricultural Products Processing Technology, Wuhan 430023, China; s_y_cheng@sina.com*
[3] *Chongqing University of Arts and Sciences, College of Landscape Architecture and Life Science, Chongqing 402160, China; chenzexiong1979@163.com*
[4] *Wuhan University of Bioengineering, School of Horticulture and Landscape, Wuhan 430415, China; 418953176@qq.com*

Abstract

As a common mutation trait in plants, leaf colour mutation is related to the degree of chlorophyll and anthocyanin changes and the destruction of chloroplast structure. This study summarizes the latest research progress in leaf colour mutation mechanism, including the metabolic basis of plant leaf colour mutation, leaf colour mutation caused by gene mutation in the chlorophyll metabolism pathway, leaf colour mutation caused by blocked chloroplast development, leaf colour mutation controlled by key transcription factors and non-coding RNAs, leaf colour mutation caused by environmental factors, and leaf colour mutation due to the involvement of the mevalonate pathway. These results will lay a theoretical foundation for leaf colour development, leaf colour improvement, and molecular breeding for leaf colour among tree species.

Keywords: chlorophyll; chloroplast; leaf colour mutation; light; mutant; MEP pathway; temperature

Introduction

Leaf is an important organ for photosynthesis and gas exchange in plants (Meng *et al.*, 2018). As a key visible feature of leaves, leaf colour is a reliable marker for plant breeding (Akhter *et al.*, 2018). The leaves of most plants in the normal growth period are green, which results from chlorophyll (Chl) enrichment (Yang *et al.*, 2015). With the increasing demand for a living environment, the number of green-leaved tree species cannot meet the needs of landscape engineering. To improve the ornamental effect of landscape plants, trees with colourful-leaves are widely used in gardening, e.g., *Cercis canadensis* with purple leaf (Roberts *et al.*, 2015), *Lagerstroemia indica* with yellow leaf (Li *et al.*, 2015), and *Prunus cerasifera* with purple leaf (Gu *et al.*, 2015). The leaf colours of these trees are all caused by mutations. As a common mutation trait in plants, leaf colour mutation is a vital source of germplasm resources for colourful leaf plants. Previous studies have shown that 208 leaf colour mutants exist in *Oryza sativa* (Deng *et al.*, 2014). Leaf mutants of *Cucumis sativus* (Ding *et al.*, 2019), *Glycine max* (Liu *et al.*, 2020), *Ginkgo biloba* (Liu *et al.*, 2016a; Li *et al.*, 2018a), *Triticum aestivum* (Rong *et al.*, 2018), and *Anthurium andraeanum* (Wang *et al.*, 2018a) also exist. Most of these mutants have

Received: 09 Sep 2020. Received in revised form: 10 Jun 2021. Accepted: 10 Jun 2021. Published online: 18 Jun 2021.
From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

diverse phenotypes, including virescent, yellow-green, dark-green, stay-green, albino, stripe, spot, zebra, and yellow (Yoo *et al.*, 2009; Park *et al.*, 2007). Some leaf colour mutations have a red or purple phenotype, which is related to the synthesis and accumulation of anthocyanins (Wei *et al.*, 2016). For example, two types of purple tea ('Ziyan' and 'Zijuan') are leaf colour variations caused by excessive anthocyanin accumulation (Jiang *et al.*, 2013; Lai *et al.*, 2016; Wei *et al.*, 2019).

Leaf colour mutation is also known as Chl deficiency. The leaf colour mutation often directly or indirectly involves the synthesis of pigments and the development of chloroplasts, which change pigment content and ratio, thereby causing leaf colour mutation. Meanwhile, because Chl is the main photosynthesis pigment, Chl deficiency affects the photosynthetic efficiency of plants. Therefore, leaf colour mutations are widely used in basic research, such as photosynthesis, photomorphogenesis, Chl biosynthesis, development of chloroplast, and gene function identification (Stern *et al.*, 2004). And leaf colour mutation as ideal materials for mutation breeding. Additionally, leaf colour mutant genes can be used as effective molecular markers for molecular breeding and identification of hybrid offspring (Qin *et al.*, 2015). In nature, leaf colour mutants originate from a wide range of sources, e.g., spontaneous (Hou *et al.*, 2009), transposon insertion (Hayashi-Tsugane *et al.*, 2014), T-DNA insertion (Chao *et al.*, 2014), and ethyl methane sulfonste (EMS) induced mutations (Zhu *et al.*, 2016), making mutation breeding convenient. For instance, the chemical mutagen EMS has been widely used in the breeding of wheat and rice (Wang *et al.*, 2009a; Ansari *et al.*, 2012). Although the types of leaf colour mutations differ, their genetic patterns can be divided into two categories. The characteristics of most leaf colour mutants are controlled by nuclear genes, that is, the characteristics of leaf colour mutants are controlled by recessive or dominant nuclear alleles (Ma *et al.*, 2017; Zhang *et al.*, 2017a). Among the reported mutants, the virescent mutant of *Gossypium hirsutum*, and the albino mutant of *T. aestivum* are all controlled by cytoplasmic inheritance (Hou *et al.*, 2009; Jiang *et al.*, 2011). The inheritance of some mutants shows a pattern of nuclear-cytoplasmic interaction (La *et al.*, 2007).

Leaf colour mutation involves changes in the types and contents of Chl, carotenoid, and anthocyanin in the leaves. It is regulated by the cooperation of internal genetic factors and the external environment. Meanwhile, it is also affected by the microstructure of cells and the levels of physiological and biochemical metabolism. With the development of high-throughput sequencing technology, a great breakthrough has been made in leaf colour mutation research, i.e., the yields of rice derived from a desirable mutation of the *OsSGR* (*stay-green*) gene were increased (Shin *et al.*, 2020). The interaction of FLNs (Fructokinase-like protein 1) and TRXz (THIOREDOXINZ) affects the development of chloroplasts, resulting in the formation of albino rice leaves (He *et al.*, 2018). In addition, research methods for developing leaf colour mutants were designed from traditional physiological and biochemical assays to screen and identify leaf colour regulatory genes through big data-based methods, such as high-throughput sequencing and multi-omics joint analysis. Based on results of previous studies, this study reviews the formation mechanism and metabolic basis of leaf colour mutation in plants.

Metabolic Basis of Leaf Colour Mutation

The diversity of plant pigment is composed of Chl, anthocyanin, carotenoid, and betaine (Mol *et al.*, 1998), and the precise temporal and spatial changes of these pigments lead to specific colouring patterns (Albert *et al.*, 2014). The first three pigments are widespread in plants, whereas betaine only exists in Caryophyllales (Clement and Mabry, 1996). Among these pigments, Chl is responsible for producing a single green leaf phenotype, whereas carotenoid and anthocyanin are widely distributed in plants, contributing phenotypes that orange in colour from orange to blue (Tanaka *et al.*, 2008). Leaf colour mutation always involves the changes of these pigments. For example, cyanidin is the key contributor of red leaves in *Acer rubrum*, the content of which is thrice that in normal green leaves (Chen *et al.*, 2019). Chl and carotenoid contents significantly decreased to 1/28 and 1/4 of those in normal green leaves, respectively, in the golden leaves of *Ulmus pumila*

(Zhang *et al.*, 2017b). In *Brassica oleracea*, the content of anthocyanin in purple leaves is 2.5 times that in ordinary green leaves (Jin *et al.*, 2018).

Leaf colour mutation is a complex physiological process involving the effects of various substances. Considering the accuracy of mass spectrometry in identifying compounds, metabolome has become an important technique in plant research. A large number of compounds involved in plant leaf colour mutation have been identified through metabolome. Li *et al.* (2019a) compared the content of secondary metabolites in albino leaves of *Camellia sinensis* to that of normal green leaves through metabolic screening. Further analysis showed that the contents of total amino acids, L-theanine, and glutamic acid increased significantly, whereas the contents of alkaloid, catechin, and polyphenols decreased significantly. These substances contributed to formation of albino leaves in *C. sinensis*. Similarly, a decrease in total amino acids and L-theanine of 'ZH2', a leaf colour mutant of *C. sinensis*, was also observed (Wang *et al.*, 2014). By comparing the metabolites in purple and green leaves of *Tetrastigma hemsleyanum*, the purple leaves were found to have accumulated a larger number of anthocyanins and flavone-glycosides than green leaves. Moreover, the contents of pelargonidin and dihydrokaempferol in purple leaves were significantly higher than in green leaves, indicating that these substances contribute to the purple colour of *T. hemsleyanum* leaves (Yan *et al.*, 2020).

In addition to the effect of pigments on leaf colour formation, starch and sugar also affect leaf colour changes. During leaf development in *Acer saccharum*, the concentration of starch, glucose, and fructose were positively correlated with the expression of leaf colour, and the red colour of leaves were significantly affected by the content of sucrose and fructose (Schaberg *et al.*, 2003). Murakami et al. (2008) found that girding in *A. saccharum* can significantly increase the content of sugar in leaves and accelerate the accumulation of anthocyanin. A comparative analysis of the metabolites of the three types of albino leaves in *C. sinensis* showed that the content of sugar (mainly sorbitol and erythrose) in albino leaves was significantly higher than in green leaves (Li *et al.*, 2018b). Flavones and flavonols are important parts of flavonoids in plants, and the changes in their content also affect the expression of plant leaf colour (Martens *et al.*, 2010). In *G. biloba*, the accumulation of flavonols and flavones promotes the expression of yellow leaves (Shi *et al.*, 2012). However, for *Camellia nitidissima*, flavonols are the main component of golden leaves (Zhou *et al.*, 2013a). The abovementioned studies showed that leaf colour mutation involves the interaction of multiple compounds. Moreover, the content and morphological changes of these compounds constitute a tight regulatory network for leaf colour mutation.

Leaf Colour Mutation Caused by Gene Mutation of Chlorophyll Metabolism

Chl is a major component of green leaves. Since the Chl biosynthesis pathway was first reported by Beale, a large number of genes related to Chl biosynthesis have been identified (Beale *et al.*, 2005; Deng *et al.*, 2014). In *Arabidopsis thaliana*, the synthesis of Chl starts from glutamyl-tRNA, and Chl finally forms through the action of 15 enzymes encoded by 27 genes (Meier *et al.*, 2011). If any step in this process is hindered, then leaf colour mutation may occur. Previous studies showed that the mutation of genes related to Chl synthesis, such as *CHLI/CHLD/CHLH*, *HemA*, *CHLG*, *CAO*, and *DVR*, is one of the common sources of leaf colour mutation (Figure 1). The three subunits coded by *CHLI/CHLD/CHLH* are the functional basis of Mg^{2+} chelatase, which is a key protein complex for Chl synthesis, and the lack of any subunit destroys Chl synthesis (Hansson *et al.*, 2002). In *O. sativa*, varied yellow-green leaf mutants are the results of the gene mutation of *CHLI/CHLD/CHLH*, such as *chlorina-1*, *chlorina-9*, *chlorina-2*, *ygl3*, *ygl7*, and *ygl98* (Jung *et al.*, 2003; Zhang *et al.*, 2006; Sun *et al.*, 2011; Tian *et al.*, 2013; Deng *et al.*, 2014). Interestingly, the mutation in different subunits also causes a variety of different mutant phenotypes. For example, the gene mutation of *OsCHLD* in mutant *chlorina-1* led to the yellow-green leaf phenotype at the seedling stage, whereas the gene mutation of *OsCHLI* in mutant *ell* led to the yellow leaf phenotype at the seedling stage. However, the seedlings died after the trefoil stage (Zhang *et al.*, 2006, 2015). Studies on mutant *ygl1* found that *YGL1* encodes Chl synthase

(CHLG), thereby causing leaf colour mutation (Wu *et al.*, 2007). Similarly, the mutant *ygl3* showed a yellow-green phenotype, reduced plant height, and decreased grain yield (Zhang *et al.*, 2006). Furthermore, the 9-bp deletion in the *OsDVR* sequence caused leaf colour mutation in mutant *824ys* (Wang *et al.*, 2010). *OsCAO1* and *OsCAO2* encode chlorophyllide an oxygenase, which catalyses the conversion of Chl a to Chl b (Figure1). Moreover, *OsCAO1* was induced by light, whereas *OsCAO2* was expressed in the dark, and the *OsCAO* knockout mutation led to the expression of leaf color mutation (Lee *et al.*, 2005). *HEMA* gene encodes glutamyl-tRNA reductase (GluTR), which is a key catalytic enzyme for Chl synthesis. *HEMA* gene is regulated by light, and the expression of HEMA antisense RNA inhibits the formation of δ-aminolevulinic acid (ALA), thereby leading to the expression of Chl in *A. thaliana* (Kumar and Soll, 2000).

Chl and heme are two types of tetrapyrrole with a similar structure. They share a pathway from ALA to protoporphyrin IX (Figure 1) (Weller *et al.*, 1996). Heme is necessary for photosynthesis and respiration. However, excessive heme accumulation inhibits the activity of glutamyl-tRNA reductase and the synthesis of ALA, thereby affecting Chl biosynthesis (Terry *et al.*, 1999). Many leaf colour mutants caused by abnormal heme metabolism have been identified, including *A. thaliana* (Xie *et al.*, 2012), *O. sativa* (Xu *et al.*, 2012; Li *et al.*, 2014), *Pisum sativum* (Linley *et al.*, 2006), *Zea mays* (Shi *et al.*, 2013), and *Brassica pekinensis* (Zhang *et al.*, 2020). Studies on the yellow leaf colour mutant *pylm* showed that the single-base mutation of recessive nuclear genes (*PY1* and *PY2*), results in the dysfunction of *heme oxygenase-1* (*HO-1*) (Zhang *et al.*, 2020). The accumulation of excessive heme in leaves activates the feedback inhibition of Chl synthesis (Weller *et al.*, 1996), leading to the expression of the yellow leaf phenotype. This mutation mechanism was similar to that in the in rice mutant *yellow-green leaf 2* (Chen *et al.*, 2013). Furthermore, the functional defects of *HO1* increase heme levels and cause the abnormal development of chloroplast thylakoids. For example, the *HO1* mutation in the maize mutant *elm1* showed decreased thylakoid basal accumulation, declined HEMA activity, and reduced Chl content (Shi *et al.*, 2013). Studies in rice also showed that *HO1* defective mutation affects thylakoid development (Li *et al.*, 2014). Moreover, genes in the Chl degradation pathway, such as *NYC1*, *NOL*, and *SGR*, are important sources of leaf colour mutation (Ren *et al.*, 2007, 2010; Barry *et al.*, 2008; Borovsky and Paran, 2008; Horie *et al.*, 2009; Wang *et al.*, 2018b).

Leaf Colour Mutation Caused by Destroyed Chloroplast Structure

Chloroplast, as the synthesis site of Chl and carotenoid, is important for the formation of plant leaf colour. Transmission electron microscopy (TEM) analysis of the ultrastructure of leaf colour mutant varieties showed that most of the leaf colour mutants showed a destroyed chloroplast structure, degraded thylakoid lamella, and dissolved thylakoid granule (Gao *et al.*, 2020; Du *et al.*, 2020). The yellow leaves of *B. pekinensis* expressed the inhibited development of chloroplast, and showed immature starch grains. Furthermore, the chloroplast had no complete granule and clear thylakoid membrane, which blocked Chl synthesis (Xie *et al.*, 2018). In rice albino leaves, the chloroplast structure is destroyed. The chloroplast is filled with a large number of oval vesicles and has no thylakoid basal accumulation (Qiu *et al.*, 2018). These studies indicated that chloroplast development defect is the important cause of leaf colour mutation in plants.

Chloroplasts in higher plants are developed from proplastids, which fold into vesicles and then develop into thylakoid lamella (Waters and Langdale, 2009). A complete chloroplast usually consists of chloroplast membrane, thylakoid, and stroma. The number, size, morphology, and distribution of chloroplasts directly affect leaf colour. Therefore, the presence of dysfunctional chloroplasts always accompanies the lack of green colour in leaves (Yang *et al.*, 2015). Several genes related to chloroplast development and chloroplast division have been identified. Their functions in leaf colour formation have been clarified through a previous study on a variety of leaf colour mutants. *Golden2-like* (*GLK*) transcription factor (TF) is a vital member of the GARP family in plants. *GLK* is reportedly involved in multiple biological processes and plays an important role in chloroplast development (Powell *et al.*, 2012). The homologous genes of *GLK* have been identified from various plants, such as *A. thaliana* (Waters *et al.*, 2009), *Z. mays* (Rossini *et al.*, 2001), and birch (Gang *et al.*, 2019). Moreover, most *GLK* families include two members, i.e., *GLK1* and *GLK2*. Through the functional analysis of the *GLK* gene in *A. thaliana* and rice, the *GLK* gene was shown wo exhibit functional redundancy (Nguyen *et al.*, 2014; Wang *et al.*, 2013a). Moreover, a transgenic functional verification experiment showed that only *glk1glk2* double mutants expressed the virescent phenotype, and any overexpression of a *GLK* gene can restore the green phenotype of leaves (Fitter *et al.*, 2002). In the birch mutant *yl*, a 40 kb deletion of the *BpGLK* gene on chromosome 2 caused the destruction of the chloroplast structure, blocked Chl synthesis, and resulted in leaf color mutation (Gang *et al.*, 2019). In addition, the ectopic expression of *GLKs* increased the number of chloroplasts in the roots of rice and *A. thaliana* (Kobayashi *et al.*, 2012, 2013).

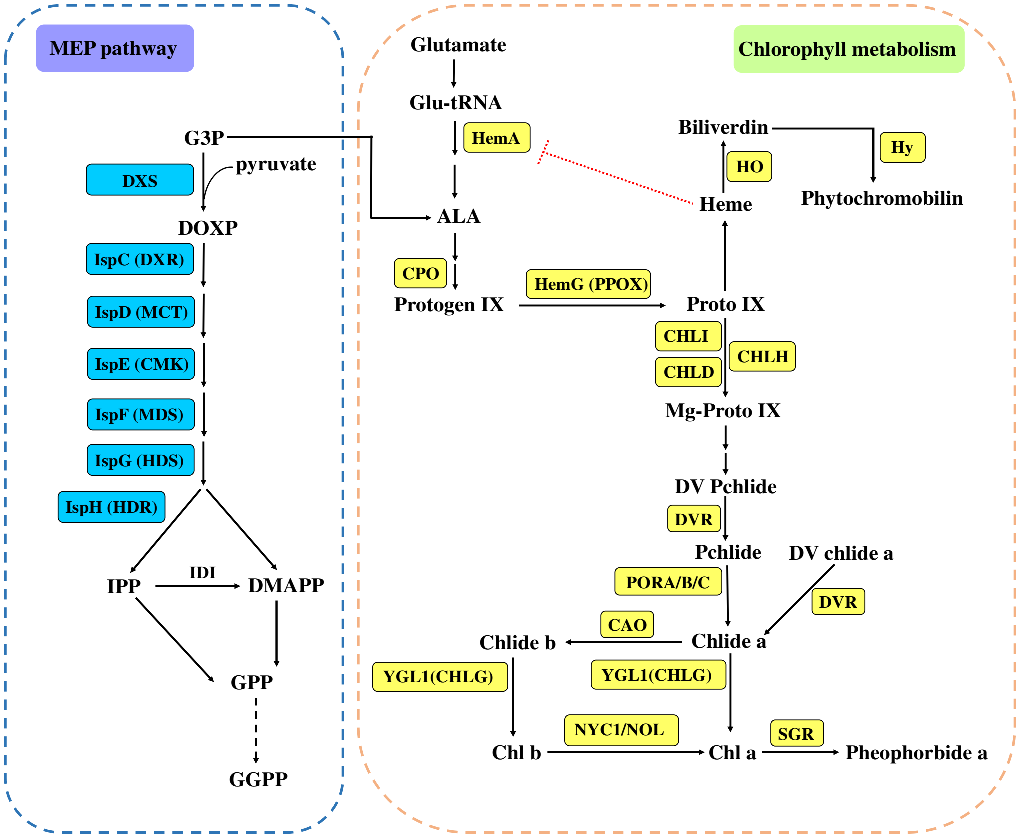

Figure 1. Regulation model of MEP pathway and chlorophyll metabolism pathway on leaf colour mutation
The blue box represents the key genes of MEP pathway related to leaf colour mutation, while the key genes of chlorophyll metabolism pathway involved in leaf colour mutation are marked with yellow box, and the red dotted "T" represents inhibition or hindrance. G3P, Glyceraldehyde 3-phosphate; DXS, 1-deoxy-D-xylulose 5-phosphate synthase; DXR, 1-deoxy-D-xylulose 5-phosphate reductoisomerase; IspD, 4-diphosphocytidyl-2-C-methyl-D-erythritol synthase; IspE, 4-diphosphocytidyl-2-C-methyl-D-erythritol kinase; IspF, 2-C-methyl-D-erythritol 2,4-cyclodiphosphate synthase; IspG, 1-hydroxy-2-methyl-2-(E)-butenyl 4-diphosphate synthase; IspH, 1-hydroxy-2-methyl-2-(E)-butenyl 4-diphosphate reductase; IPP, isopentenyl pyrophosphate; IDI, isopentenyl diphosphate isomerase; DMAPP, dimethylallyl pyrophosphate; GPP, geranyl diphosphate; GGPP, geranylgeranyl pyrophosphate; HemA, glutamyl-tRNA reductase; ALA, δ-aminolevulinic acid; CPO, coproporphyrinogen oxidative decarboxylase; Protogen IX, protoporphyrinogen IX; PPOX, protoporphyrinogen oxidase; Proto IX, protoporphyrin IX; CHLI, Mg chelatase I subunit; CHLD, Mg chelatase D subunit; CHLH, Mg chelatase H subunit; Mg-Proto IX, Mg-protoporphyrin IX; DV Pchlide, divinyl protochlorophyllide; DVR, divinyl reductase; PORA/B/C, NADPH: protochlorophyllide oxidoreductase; Chlide a, chlorophyllide a; Chlide b, chlorophyllide b; DV chlide a, divinyl chlorophyllide a; CAO, chlorophyllide a oxygenase; CHLG, chlorophyll synthase; NYC1, non-yellow colouring 1; NOL, NYC1-like; SGR, stay green gene; HO, heme oxygenase-1.

Plastid ribosomal proteins (PRPs) are involved in the assembly of chloroplast structure and have great significance in chloroplast division and formation (Zhang *et al.*, 2016). PRPs are highly conserved in chloroplasts and are indispensable for chloroplast development (Tiller and Bock, 2014). Lacking PRPs, the maize mutant *lem1* and *hcf60* both exhibited a lethal phenotype, whereas the tobacco mutant *prps18* showed chloroplast development defects (Schultes *et al.*, 2000; Ma and Dooner, 2004; Rogalski *et al.*, 2006). The PRPs in *A. thaliana* are involved in many biological processes, such as leaf development, photosynthesis, and low-temperature response (Zhang *et al.*, 2016). In rice, many PRPs mutants, such as *asl1*, *asl2*, and *al1*, cannot develop into fully functional chloroplasts, leading to the development of albino leaves (Gong *et al.*, 2013; Lin *et al.*, 2015; Zhao *et al.*, 2016). PRPs are necessary for chloroplast development under low temperatures (Song *et al.*, 2014; Wang *et al.*, 2017a). In the rice mutant *wgl2*, a single-base mutation (G to T) in the *PRP* gene results in defects in chloroplast development. Then, the leaves showed an albino phenotype and reduced contents of Chl and carotenoid (Qiu *et al.*, 2018). In addition, other genes related to chloroplast development have been identified in previous studies, such as *V1*, *V2*, *V3*, *St1*, *GRY79*, and *YCL1*. These genes have a function similar to that of *AtGLK* indirectly regulate the function of chloroplasts (Kusumi *et al.*, 2011; Sugimoto *et al.*, 2007; Yoo *et al.*, 2009; Wan *et al.*, 2015; Zhou *et al.*, 2013b). Furthermore, *YL1* and *WP1* in rice are indispensable for early chloroplast development (Chen *et al.*, 2016; Wang *et al.*, 2016a). Studies have shown that the members of *Accumulation and Replication of Chloroplast* (*ARC*) gene family cooperate with FtsZ protein to regulate the division of chloroplasts (Osteryoung and Nunnari, 2003; Maple and Moller, 2007). In this family, *ARC3*, *ARC5*, and *ARC6* are key regulators for chloroplast development (Gao *et al.*, 2003; Shimada *et al.*, 2004; Vitha *et al.*, 2003).

Key Transcription Factor and Non-coding RNAs Regulate Leaf Colour Mutation

In the process of plant pigment synthesis, many coding RNAs are involved. For example, structural genes encode various enzymes in the pigment synthesis pathway, which directly determine the accumulation or degradation of pigments. TFs regulate pigment synthesis by binding to cis-acting elements in their target gene promoters to induce or inhibit the expression of structural genes (Wang *et al.*, 2016b; Kim *et al.*, 2017). In the anthocyanin synthesis pathway, MYB TFs can combine with bHLH and WD40 proteins to form the MBW protein complex. The MBW protein complex is the core component of anthocyanin synthesis regulation that can directly control the key enzymes of anthocyanin synthesis pathway, such as *ANS*, *DFR*, and *F3′ H* (Tohge *et al.*, 2005; Gonzalez *et al.*, 2008) (Figure 2).

In addition to the role of coding RNAs, many non-coding RNAs (ncRNAs) participate in the regulation of pigment synthesis (Li *et al.*, 2019b). Moreover, several lncRNAs and miRNAs related to pigment synthesis have been identified along with genes mainly involved in the anthocyanin synthesis pathway (Zhao *et al.*, 2017; Wu *et al.*, 2019) (Figure 2). Through the study of non-coding RNAs in *C. sinensis* (Jeyaraj *et al.*, 2017), *csn-miRn27*, *csn-miRn49*, *csn-miRn56*, and *csn-miRn23* were found to be co-targeted to the *F3′ 5′ H* gene and participated in the synthesis of anthocyanin and in the accumulation of flavonoids. Furthermore, the study confirmed that csn-miRn70 and *csn-miRn30* target *F3H* and *UFGT* genes, respectively, to jointly regulate the accumulation of anthocyanin in new leaves (Jeyaraj *et al.*, 2017). Previous studies have shown that *miR156* interferes with the function of the MBW protein complex by targeting *SPL9* and inhibits the synthesis of anthocyanin (Gou *et al.*, 2011). This mechanism has been verified in a variety of plants (Liu *et al.*, 2017; He *et al.*, 2019). It is worth mentioning that *miR156-SPL* is also involved in plant stress response (Wang *et al.*, 2013b; Stief *et al.*, 2014), synthesis of secondary metabolites (Ye *et al.*, 2020), and floral organ development (Wang *et al.*, 2009b).

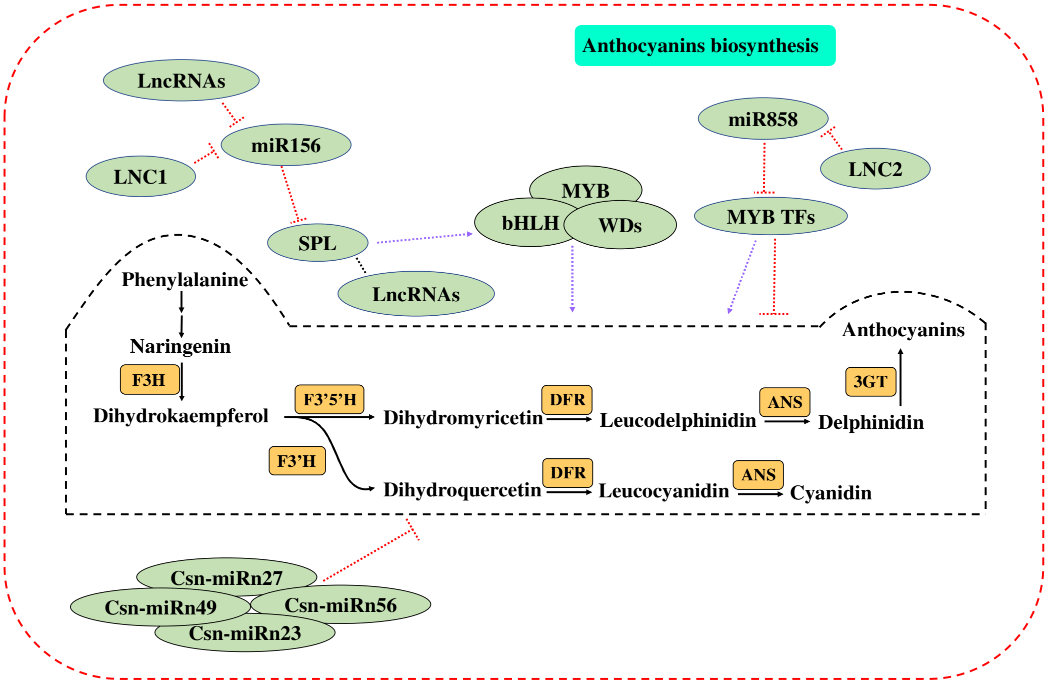

Figure 2. Regulation model of transcription factors and non-coding RNAs participate in leaf colour mutation

The orange box presents the key genes of anthocyanin synthesis pathway related to leaf colour mutation, while the transcription factors as well as non-coding RNAs are marked with green box. The red dotted "T" represents inhibition or hindrance, and purple dotted arrow represents promotion. F3H, flavanone 3-hydroxylase; F3′H, flavonoid 3'-hydroxylase; F3′5′H, flavonoid 3',5'-hydroxylase; DFR, dihydroflavonol reductase; ANS, anthocyanidin synthase; 3GT, anthocyanin 3'-O-beta-glucosyltransferase.

By comparing the gene expression profiles of different varieties of roses, five miRNAs (*miR171*, *miR166i*, *miR159e*, *miR845*, and *miR396e*) were found to be enriched only in white flowers of rose, suggesting that these miRNAs may negatively regulate the expressions of downstream genes. Thus, the accumulation of carotenoids or anthocyanins is hindered, resulting in the development of white flower in rose (Kim *et al.*, 2012). The analysis of miRNAs in *Malus pumila* showed that the R2R3-MYB TF gene involved in anthocyanin synthesis is the target gene of *miR858* (Xia *et al.*, 2012). Most MYBs are common target genes of *miR828* and *miR858*, indicating that *miR828* and *miR858* play a vital role in anthocyanin synthesis (Guan *et al.*, 2014). Interestingly, Wang *et al.* (2016b) found that *miR858a* positively regulates anthocyanin synthesis by inhibiting the expression of *MYBL2*. Mutant *dg* is a dark green mutant in *A. andraeanum*, whose leaves are thicker than the wild-type and whose petioles have turned red. The back of the leaf veins of the mutant changed from green to red, because of the enhanced pigment synthesis due to the expression of the mutant *dg* (Xu *et al.*, 2006; Yang *et al.*, 2015). Jiang *et al.* (2018) identified 10 differentially expressed miRNAs through a comparative analysis of the miRNA sequencing results of the *dg* mutant and the wild-type. *Aa-miR408* was significantly up-regulated in the *dg* mutant, suggesting that *Aa-miR408* may be closed to the colour mutation of the *dg* mutant. Recently, Wu *et al.* (2020) screened a total of eight up-regulated miRNAs from the yellow leaf mutant of *G. biloba*. Among them, the *novel 158_mature* is involved the synthesis of lutein through the regulation of the expression of the target *gma-miR2118a-3p* gene. Moreover, three miRNAs (*novel 151_mature*, *ptc-miR396e-3p*, and *aly-miR156a-5p*) were the key regulators of leaf colour mutation (Wu *et al.*, 2020).

LncRNAs are small RNA molecules with lengths greater than 200nt and no protein-coding ability (Laurent *et al.*, 2015). LncRNAs are widely distributed in plants, and many have been identified in *A. thaliana* (Liu *et al.*, 2012a), *Z. mays* (Lv *et al.*, 2016), *Salvia miltiorrhiza* (Li *et al.*, 2015), and *Populus euphratica* (Liu *et al.*, 2018). For the synthesis of pigments also involves the regulation of multiple lncRNAs (Wu *et al.*, 2019).

Previous studies showed that lncRNAs perform their functions by interacting with miRNAs (Wu *et al.*, 2013). Two differentially expressed lncRNAs (*LNC1* and LNC2) were screened through the transcriptome analysis of *Hippophae rhamnoides* fruits at different maturation stages. Transient expression experiments verified that *LNC1* positively regulates *SPL9* expression by interacting with *miR156* and promotes anthocyanin synthesis by facilitating the stability of the MBW protein complex. On the contrary, *LNC2* interacts with *miR828*, and affects the expression of *MYB114* to regulate anthocyanin synthesis (Zhang *et al.*, 2018). However, for tomato, the accumulation of lycopene was significantly reduced in the *lncRNA1459* mutant, leading to the delay in fruit ripening (Li *et al.*, 2018c).

Leaf Colour Mutation Caused by Environmental Factor

The mechanism of plant leaf colour mutation is extremely complex. It is regulated by internal genes and affected by the external environment, which includes temperature and light. Temperature is critical to the formation of leaf colour in plants. In *C. sinensis*, the appearance of albino buds is controlled by temperature, and the synthesis of Chl a and b is inhibited under low temperature (≤15 °C), leading to albino buds. However, when the albino buds were cultured at a high temperature (≥15 °C), the process of Chl synthesis was restored, and the leaves turned green (Du *et al.*, 2008). Mutants that exhibit different leaf colour changes at various temperatures are known as temperature-sensitive leaf colour mutants. Previous studies have identified temperature-sensitive leaf colour mutants in plants, such as *O. sativa* (Huang *et al.*, 2011), *B. oleracea* (Zhou *et al.*, 2013c), *Z. mays* (Pasini *et al.*, 2005), and *T. aestivum* (Liu *et al.*, 2012b). Studies on wheat mutant *fa85* showed that with the extension of low temperature treatment time, the aboveground leaves of *fa85* completely bleared and gradually turned green increasing temperature (Liu *et al.*, 2012b). Results of comparisons between mutant *fa85* and its wild-type *Aibian* showed that the ultrastructure and molecular genetic characteristics of *fa85* are affected by low temperature treatment. Meanwhile, proteomics analysis indicated the presence of significant differences in the expression patterns of chloroplast protein between *fa85* and its parent *Aibian* at low temperatures (Hou *et al.*, 2009).

Temperature regulates the synthesis and accumulation of pigments by affecting gene expression, thereby controlling the features of leaf colour. For example, the Chl-deficient leaf in rice at low temperatures is caused by a mutation of the *NUS1* gene (Kusumi *et al.*, 2011). In tomato, the *WV* gene, which controls the yellowing phenotype, is sensitive to low temperature. Therefore, the leaves expressed an albino phenotype at low temperature (Gao *et al.*, 2019). The type and content of pigments of the temperature sensitive mutant *mt* of *Commelina purpurea* changed under different temperature conditions. At low temperature, the anthocyanin content in the leaves reached its peak, the Chl and carotenoid contents were significantly reduced. Thus, the leaves expressed a pink phenotype. At room temperature (25 °C), no significant difference was found between the mutant *mt* and the wild-type. The anthocyanin content decreased, whereas Chl content increased. Further experiments suggested that the expressions of structural genes (such as *PAL*, *CHS*, *CHI*, *F3'H*, *F3'5'H*, *DFR*, *ANS*, *UFGT*, and *OMT*) related to anthocyanin synthesis were induced at low temperatures, leading to the excessive accumulation of cyanidin, pelargonidin, delphinidin, and petunidin. Thus, the leaves presented a pink phenotype. Meanwhile, the chloroplast in mutant *mt* was replaced by leucoplast at low temperature, and this mutant could not accumulate Chl (Liu *et al.*, 2016b). A few temperature-sensitive leaf colour mutants exhibited multiple leaf colour changes at different temperatures. For example, the leaves of mutant *tsc1* showed albino, virescent, and green phenotypes at 23.0 °C, 26.0 °C, and 30.0 °C, respectively (Dong *et al.*, 2001).

Besides temperature, light also regulates the phenotype of leaves (Biswal *et al.*, 2012). Studies showed that the expression of golden leaf in plants is affected by environmental light intensity. Under high light conditions, the leaf colour turned golden, whereas in low light, the leaf colour was yellow-green due to the increase in Chl content (Hu *et al.*, 2007). Light can promote the differentiation of non-photosynthetic plastids into fully functional chloroplasts, thereby affecting the development of chloroplasts and the expression of genes related to Chl synthesis (Su *et al.*, 2012). Guo *et al.* (2013) found that the light regulates the expression of the *CPO* gene, which encodes an enzyme that catalyses the oxidative decarboxylation of Coprogen III to ProtoIX, resulting in light-dependent yellow leaves of tobacco and *A. thaliana*. In contrast, in *Hordeum vulgare*, high light leads to slow growth of mutant *nyb* and turns its leaves yellow (Yuan *et al.*, 2010). The leaf colour of mutant *gl1* in *L. indica* is regulated by light intensity (Wang *et al.*, 2017b). The leaf colour of *CPO* deletion mutant *line2* in *A. thaliana* is influenced by day-length. The leaves are yellow-green under long-day conditions, and leaves are yellow under short-day conditions (Ishikawa *et al.*, 2001).

Leaf Colour Mutation Regulated by the Mevalonate Pathway

Terpenoids are the most abundant secondary metabolites in organisms (Sacchettini and Poulter, 1997). Terpenoids, also known as isoprene compounds, participate in various plant life activities, such as photosynthesis (Chl and carotenoids), growth (phytosterols) and development (GA and ABA), and plant defence responses (Phillips *et al.*, 2008). As one of the pathways involved in the synthesis of terpenoids, the mevalonate pathway (MEP) pathway is catalyzed by multiple enzymes, and its final synthesis products are IPP and DMAPP (Samad *et al.*, 2019). IsPF (MDS), the fifth synthetase in the MEP pathway, catalyses the cyclization reaction of CDP-MEP to generate ME-cPP. The *IsPF* gene is also involved in the regulation of leaf colour in plants (You *et al.*, 2020). In the rice yellow-green leaf mutant *505ys*, the *IsPF* gene has a base substitution (C to T), thereby changing the encoded amino acid. Moreover, the overexpression of the wild-type *OsIsPF* gene in the mutant can restore the phenotype of mutant *505ys*, proving that the *IsPF* gene is the cause of leaf colour variations in mutant *505ys* (Huang *et al.*, 2018). qRT-PCR results of key genes in the Chl synthesis pathway of rice mutant indicated that *YGL* gene expression in the mutant *505ys* significantly declined, suggesting the existence of a positive regulation between the *OsIspF* and *YGL* gene (Huang *et al.*, 2018).

In *A. thaliana*, *IspF* T-DNA insertion mutant and *IspF* RNAi mutant showed albino phenotypes with extremely low Chl and carotenoid contents (1% and 2% of the contents in the wild-type, respectively). Further ultrastructure analysis results showed that chloroplast development was inhibited in the mutant, and thylakoids were replaced by numerous vesicles (Hsieh and Goodman, 2006). Therefore, the mutant *505ys* possibly did not appear with the albino phenotype, because single-base mutation could not completely replace the function of the *IspF* gene, thereby further verifying the key role of the *IspF* gene in the development of plant leaf color. Similarly, the *IspE* gene on chromosome 1 of the rice mutant *gry340* has base substitutions, resulting in the yellow-green leaf phenotype (Chen *et al.*, 2018). Through the studies on *A. thaliana* and tobacco, *IspD*, *IspH*, *IspG*, *DXS*, *DXR*, and *IspE* genes were verified to have functions similar to those of the *IspF* gene. These genes are at the key cores of plant leaf mutation, pigment reduction, and thylakoid structure destruction (Mandel *et al.*, 1996; Estevez *et al.*, 2000; Budziszewski *et al.*, 2001; Gutierrez *et al.*, 2004; Guevara *et al.*, 2005; Hsieh and Goodman, 2006; Xing *et al.*, 2010; Hsieh *et al.*, 2008; Ahn and Pai, 2008). During the ripening process of tomatoes, the transcription level of the *DXS* gene significantly increases, and a large amount of carotenoids accumulates, further promoting the colouring of tomato fruits at the ripening stage (Lois *et al.*, 2000). Zhang *et al.* (2019) found that the albino leaves of the maize mutant *scd* was caused by a mutation of the *IspH* (*HDS*) gene in the MEP pathway. Moreover, the decreased activity of the key enzymes of the MEP pathway indirectly affects the accumulation of downstream products, such as carotenoid and Chl.

Conclusions

As a visible mutant, leaf colour mutant is an ideal material that can be used for plasmid development and photosynthesis. Also, leaf colour mutant has an important research value. Leaf colour mutation in higher plants is mostly related to the content changes of Chl and anthocyanin. The regulation mechanism of leaf colour mutation is extremely complicated. It involves the enzymes of pigment synthesis and is affected by chloroplast structure, the regulation of TFs, small RNAs, the interaction between plants and external environment, and the regulation of the plant secondary metabolite synthesis pathway. Although many studies have been conducted on leaf colour mutants, most of them reported the role of key Chl synthesis genes and chloroplast structure. Moreover, most of the studies used big data joint analysis methods, such as transcriptome, proteome, and metabolome. Few studies have been conducted on the upstream regulatory mechanism of the vital genes related to leaf colour mutation, such as the functions of miRNA and lncRNA in leaf colour mutation, which needs to be further analysed. At present, most miRNA and lncRNA studies on plant colour regulation focus on fruit and flower colour. Few studies on small RNA include leaf colour formation. Furthermore, the development of leaf colour involves the interaction of nuclear coding and chloroplast genes. However, studies on the plastid-nuclear reverse signal pathway have been slow, and the regulation process, and regulation molecular mechanisms are still unclear. Therefore, follow-up research works should focus on these two centres and maximize the advanced means of molecular biology to further analyse the regulation mechanism of leaf colour mutation, which would serve as the theoretical foundation for the improvement of leaf colour varieties of more plants.

Authors' Contributions

M.Y.F. and F.X. designed and wrote the manuscript; S.Y.C., W.W.Z., J.R.Z., and L.W. collected and analysed the data; Z.X.C. and Z.B.L. revised the manuscript. All authors read and approved the final manuscript

Acknowledgements

This work was supported by the National Natural Science Foundation of China, grant number 31971693.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

Ahn CS, Pai HS (2008). Physiological function of IspE, a plastid MEP pathway gene for isoprenoid biosynthesis, in organelle biogenesis and cell morphogenesis in *Nicotiana benthamiana*. Plant Molecular Biology 66(5):503-517. *https://doi.org/10.1007/s11103-007-9286-0*

Akhter D, Qin R, Nath UK, Alamin M, Jin X, Shi C (2018). The brown midrib leaf (bml) mutation in rice (*Oryza sativa* L.) causes premature leaf senescence and the induction of defense responses. Genes 9(4):203. *https://doi.org/10.3390/genes9040203*

Albert NW, Davies KM, Schwinn KE (2014). Gene regulation networks generate diverse pigmentation patterns in plants. Plant Signaling & Behavior 9(9):962-80. *https://doi.org/10.4161/psb.29526*

Ansari MJ, Kumar R, Singh K, Dhaliwal HS (2012). Characterization and molecular mapping of EMS-induced brittle culm mutants of diploid wheat (*Triticum monococcum* L.). Euphytica 186(1):165-176.

Barry CS, McQuinn RP, Chung MY, Besuden A, Giovannoni JJ (2008). Amino acid substitutions in homologs of the STAY-GREEN protein are responsible for the green-flesh and chlorophyll retainer mutations of tomato and pepper. Plant Physiology 147(1):179-187. *https://doi.org/10.1104/pp.108.118430*

Beale SI (2005). Green genes gleaned. Trends in Plant Science 10(7):309-312. *https://doi.org/10.1016/j.tplants.2005.05.005*

Biswal AK, Pattanayak GK, Pandey SS, Leelavathi S, Reddy VS, Tripathy BC (2012). Light intensity-dependent modulation of chlorophyll b biosynthesis and photosynthesis by overexpression of chlorophyllide an oxygenase in tobacco. Plant Physiology 159(1):433-449. *https://doi.org/10.1104/pp.112.195859*

Borovsky Y, Paran I (2008). Chlorophyll breakdown during pepper fruit ripening in the chlorophyll retainer mutation is impaired at the homolog of the senescence-inducible stay-green gene. Theoretical and Applied Genetics 117(2):235-240. *https://doi.org/10.1007/s00122-008-0768-5*

Budziszewski GJ, Lewis SP, Glover LW, Reineke J, Jones G, Ziemnik LS, ... McElver J (2001). Arabidopsis genes essential for seedling viability: isolation of insertional mutants and molecular cloning. Genetics 159(4):1765-1778.

Chao Y, Kang J, Zhang T, Yang Q, Gruber MY, Sun Y (2014). Disruption of the homogentisate solanesyltransferase gene results in albino and dwarf phenotypes and root, trichome and stomata defects in *Arabidopsis thaliana*. PloS One 9(4):e94031. *https://doi.org/10.1371/journal.pone.0094031*

Chen F, Dong G, Wu L, Wang F, Yang X, Ma X, ... Qian Q (2016). A nucleus-encoded chloroplast protein YL1 is involved in chloroplast development and efficient biogenesis of chloroplast ATP synthase in rice. Scientific Reports 6(1):1-14. *https://doi.org/10.1038/srep32295*

Chen H, Cheng Z, Ma X, Wu H, Liu Y, Zhou K, ... Guo X (2013). A knockdown mutation of YELLOW-GREEN LEAF2 blocks chlorophyll biosynthesis in rice. Plant Cell Reports 32(12):1855-1867. *https://doi.org/10.1007/s00299-013-1498-y*

Chen N, Wang P, Li C, Wang Q, Pan J, Xiao F, ... Sun C (2018). A single nucleotide mutation of the IspE gene participating in the MEP pathway for isoprenoid biosynthesis causes a green-revertible yellow leaf phenotype in rice. Plant and Cell Physiology 59(9):1905-1917. *https://doi.org/10.1093/pcp/pcy108*

Chen Z, Lu X, Xuan Y, Tang F, Wang J, Shi D, ... Ren J (2019). Transcriptome analysis based on a combination of sequencing platforms provides insights into leaf pigmentation in *Acer rubrum*. BMC Plant Biology 19(1):240. *https://doi.org/10.1186/s12870-019-1850-7*

Clement JS, Mabry TJ (1996). Pigment evolution in the Caryophyllales: a systematic overview. Botanica Acta 109(5):360-367. *https://doi.org/10.1111/j.1438-8677.1996.tb00584.x*

Deng XJ, Zhang HQ, Wang Y, He F, Liu JL, Xiao X, ... Wang GL (2014). Mapped clone and functional analysis of leaf-color gene Ygl7 in a rice hybrid (*Oryza sativa* L. ssp. *indica*). PloS One 9(6):e99564. *https://doi.org/10.1371/journal.pone.0099564*

Ding Y, Yang W, Su C, Ma H, Pan Y, Zhang X, Li J (2019). Tandem 13-lipoxygenase genes in a cluster confers yellow-green leaf in cucumber. International Journal of Molecular Sciences 20(12):3102. *https://doi.org/10.3390/ijms20123102*

Dong Y, Dong W, Shi S, Jin Q (2001). Identification and genetic analysis of a thermo-sensitive seedling-colour mutant in rice (*Oryza sativa* L.). Breeding Science 51(1):1-4.

Du W, Hu F, Yuan S, Liu C (2020). The identification of key candidate genes mediating yellow seedling lethality in a *Lilium regale* mutant. Molecular Biology Reports 1-13. *https://doi.org/10.1007/s11033-020-05323-8*

Du YY, Chen H, Zhong WL, Wu LY, Ye JH, Lin C, ... Liang YR (2008). Effect of temperature on accumulation of chlorophylls and leaf ultrastructure of low temperature induced albino tea plant. African Journal of Biotechnology 7(12). *https://doi.org/10.5897/AJB2008.000-5036*

Estévez JM, Cantero A, Romero C, Kawaide H, Jiménez LF, Kuzuyama T, ... León P (2000). Analysis of the expression of CLA1, a gene that encodes the 1-deoxyxylulose 5-phosphate synthase of the 2-C-methyl-D-erythritol-4-phosphate pathway in *Arabidopsis*. Plant Physiology 124(1):95-104. *https://doi.org/10.1104/pp.124.1.95*

Fitter DW, Martin DJ, Copley MJ, Scotland RW, Langdale JA (2002). GLK gene pairs regulate chloroplast development in diverse plant species. The Plant Journal 31(6):713-727. *https://doi.org/10.1046/j.1365-313x.2002.01390.x*

Gang H, Li R, Zhao Y, Liu G, Chen S, Jiang J (2019). The birch GLK1 transcription factor mutant reveals new insights in chlorophyll biosynthesis and chloroplast development. Journal of Experimental Botany 70:3125-3138. *https://doi.org/10.1093/jxb/erz128*

Gao H, Kadirjan-Kalbach D, Froehlich JE, Osteryoung KW (2003). ARC5, a cytosolic dynamin-like protein from plants, is part of the chloroplast division machinery. Proceedings of the National Academy of Sciences 100(7):4328-4333. *https://doi.org/10.1073/pnas.0530206100*

Gao S, Gao W, Liao X, Xiong C, Yu G, Yang Q, … Ye Z (2019). The tomato WV gene encoding a thioredoxin protein is essential for chloroplast development at low temperature and high light intensity. BMC Plant Biology 19(1):1-14. *https://doi.org/10.1186/s12870-019-1829-4*

Gao TM, Wei SL, Chen J, Wu Y, Li F, Wei LB, … Zhang HY (2020). Cytological, genetic, and proteomic analysis of a sesame (*Sesamum indicum* L.) mutant Siyl-1 with yellow-green leaf color. Genes & Genomics 42(1):25-39. *https://doi.org/10.1007/s13258-019-00876-w*

Gong X, Jiang Q, Xu J, Zhang J, Teng S, Lin D, Dong Y (2013). Disruption of the rice plastid ribosomal protein S20 leads to chloroplast developmental defects and seedling lethality. G3: Genes, Genomes, Genetics 3(10):1769-1777. *https://doi.org/10.1534/g3.113.007856*

Gonzalez A, Zhao M, Leavitt JM, Lloyd AM (2008). Regulation of the anthocyanin biosynthetic pathway by the TTG1/bHLH/Myb transcriptional complex in *Arabidopsis* seedlings. The Plant Journal 53(5):814-827. *https://doi.org/10.1111/j.1365-313X.2007.03373.x*

Gou JY, Felippes FF, Liu CJ, Weigel D, Wang JW (2011). Negative regulation of anthocyanin biosynthesis in *Arabidopsis* by a miR156-targeted SPL transcription factor. The Plant Cell 23(4):1512-1522. *https://doi.org/10.1105/tpc.111.084525*

Gu C, Liao L, Zhou H, Wang L, Deng X, Han Y (2015). Constitutive activation of an anthocyanin regulatory gene PcMYB10. 6 is related to red coloration in purple-foliage plum. PloS One 10(8):e0135159. *https://doi.org/10.1371/journal.pone.0135159*

Guan X, Pang M, Nah G, Shi X, Ye W, Stelly DM, Chen ZJ (2014). miR828 and miR858 regulate homoeologous MYB2 gene functions in *Arabidopsis* trichome and cotton fibre development. Nature Communications 5(1):1-14. *https://doi.org/10.1038/ncomms4050*

Guevara-García A, San Román C, Arroyo A, Cortés ME, Gutiérrez-Nava MDL, León P (2005). Characterization of the Arabidopsis clb6 mutant illustrates the importance of posttranscriptional regulation of the methyl-D-erythritol 4-phosphate pathway. The Plant Cell 17(2):628-643.

Guo CY, Wu GH, Xing J, Li WQ, Tang DZ, Cui BM (2013). A mutation in a coproporphyrinogen III oxidase gene confers growth inhibition, enhanced powdery mildew resistance and powdery mildew-induced cell death in *Arabidopsis*. Plant Cell Reports 32(5):687-702. *https://doi.org/10.1007/s00299-013-1403-8*

Gutiérrez-Nava ML, Gillmor CS, Jiménez LF, Guevara-García A, León P (2004). CHLOROPLAST BIOGENESIS genes act cell and noncell autonomously in early chloroplast development. Plant Physiology 135:471-482. *https://doi.org/10.1104/pp.103.036996*

Hansson A, Willows RD, Roberts TH, Hansson M (2002). Three semidominant barley mutants with single amino acid substitutions in the smallest magnesium chelatase subunit form defective AAA+ hexamers. Proceedings of the National Academy of Sciences 99(21):13944-13949. *https://doi.org/10.1073/pnas.212504499*

Hayashi-Tsugane M, Takahara H, Ahmed N, Himi E, Takagi K, Iida S, … Maekawa M (2014). A mutable albino allele in rice reveals that formation of thylakoid membranes requires the SNOW-WHITE LEAF1 gene. Plant and Cell Physiology 55(1):3-15. *https://doi.org/10.1093/pcp/pct149*

He L, Tang R, Shi X, Wang W, Cao Q, Liu X, … Jia X (2019). Uncovering anthocyanin biosynthesis related microRNAs and their target genes by small RNA and degradome sequencing in tuberous roots of sweet potato. BMC Plant Biology 19(1):232. *https://doi.org/10.1186/s12870-019-1790-2*

He L, Zhang S, Qiu Z, Zhao J, Nie W, Lin H, … Zhu L (2018). FRUCTOKINASE-LIKE PROTEIN 1 interacts with TRXz to regulate chloroplast development in rice. Journal of Integrative Plant Biology 60(2):94-111. *https://doi.org/10.1111/jipb.12631*

Horie Y, Ito H, Kusaba M, Tanaka R, Tanaka A (2009). Participation of chlorophyll b reductase in the initial step of the degradation of light-harvesting chlorophyll a/b-protein complexes in *Arabidopsis*. Journal of Biological Chemistry 284(26):17449-17456. *https://doi.org/10.1074/jbc.M109.008912*

Hou DY, Xu H, Du GY, Lin JT, Duan M, Guo AG (2009). Proteome analysis of chloroplast proteins in stage albinism line of winter wheat (*Triticum aestivum*) FA85. BMB Reports 42(7):450-455. *https://doi.org/10.5483/bmbrep.2009.42.7.450*

Hsieh MH, Chang CY, Hsu SJ, Chen JJ (2008). Chloroplast localization of methylerythritol 4-phosphate pathway enzymes and regulation of mitochondrial genes in ispD and ispE albino mutants in *Arabidopsis*. Plant Molecular Biology 66(6):663-673. *https://doi.org/10.1007/s11103-008-9297-5*

Hsieh MH, Goodman HM (2006). Functional evidence for the involvement of *Arabidopsis* IspF homolog in the non mevalonate pathway of plastid isoprenoid biosynthesis. Planta 223(4):779-784. *https://doi.org/10.1007/s00425-005-0140-9*

Hu HZ, Zhang R, Shang AQ, Zhao LJ, Lu ZM (2007). Response of pigment content of golden-leaf plants to light intensity. Acta Horticulturae Sinica 34(3):717.

Huang QN, Shi YF, Yang Y, Feng BH, Wei YL, Chen J, … Wu JL (2011). Characterization and genetic analysis of a light- and temperature-sensitive spotted-leaf mutant in rice. Journal of Integrative Plant Biology 53(8):671-681. *https://doi.org/10.1111/j.1744-7909.2011.01056.x*

Huang R, Wang Y, Wang P, Li C, Xiao F, Chen N, … Chen R (2018). A single nucleotide mutation of IspF gene involved in the MEP pathway for isoprenoid biosynthesis causes yellow-green leaf phenotype in rice. Plant Molecular Biology 96:5-16. *https://doi.org/10.1007/s11103-017-0668-7*

Ishikawa A, Okamoto H, Iwasaki Y, Asahi T (2001). A deficiency of coproporphyrinogen III oxidase causes lesion formation in *Arabidopsis*. The Plant Journal 27(2):89-99. *https://doi.org/10.1046/j.1365-313x.2001.01058.x*

Jeyaraj A, Zhang X, Hou Y, Shangguan M, Gajjeraman P, Li Y, Wei C (2017). Genome-wide identification of conserved and novel microRNAs in one bud and two tender leaves of tea plant (*Camellia sinensis*) by small RNA sequencing, microarray-based hybridization and genome survey scaffold sequences. BMC Plant Biology 17(1):1-16. *https://doi.org/10.1186/s12870-017-1169-1*

Jiang L, Tian X, Fu Y, Liao X, Wang G, Chen F (2018). Comparative profiling of microRNAs and their effects on abiotic stress in wild-type and dark green leaf color mutant plants of *Anthurium andraeanum* 'Sonate'. Plant Physiology and Biochemistry 132:258-270. *https://doi.org/10.1016/j.plaphy.2018.09.008*

Jiang L, Shen X, Shoji T, Kanda T, Zhou J, Zhao L (2013). Characterization and activity of anthocyanins in Zijuan tea (*Camellia sinensis* var. *kitamura*). Journal of Agricultural and Food Chemistry 61(13):3306-3310. *https://doi.org/10.1021/jf304860u*

Jiang Y, He Y, Fan SL, Yu JN, Song MZ (2011). The identification and analysis of RNA editing sites of 10 chloroplast protein-coding genes from virescent mutant of *Gossypium hirsutum*. Cotton Science 23(1):3-9.

Jin SW, Rahim MA, Afrin KS, Park JI, Kang JG, Nou IS (2018). Transcriptome profiling of two contrasting ornamental cabbage (*Brassica oleracea* var. *acephala*) lines provides insights into purple and white inner leaf pigmentation. BMC Genomics 19(1):797. *https://doi.org/10.1186/s12864-018-5199-3*

Jung KH, Hur J, Ryu CH, Choi Y, Chung YY, Miyao A, … An G (2003). Characterization of a rice chlorophyll-deficient mutant using the T-DNA gene-trap system. Plant and Cell Physiology 44(5):463-472. *https://doi.org/10.1093/pcp/pcg064*

Kim J, Park JH, Lim CJ, Lim JY, Ryu JY, Lee BW, … Kim D (2012). Small RNA and transcriptome deep sequencing proffers insight into floral gene regulation in *Rosa* cultivars. BMC Genomics 13(1):657. *https://doi.org/10.1186/1471-2164-13-657*

Kim J, Lee WJ, Vu TT, Jeong CY, Hong SW, Lee H (2017). High accumulation of anthocyanins via the ectopic expression of AtDFR confers significant salt stress tolerance in *Brassica napus* L. Plant Cell Reports 36(8):1215-1224. *https://doi.org/10.1007/s00299-017-2147-7*

Kobayashi K, Baba S, Obayashi T, Sato M, Toyooka K, Keränen M, … Masuda T (2012). Regulation of root greening by light and auxin/cytokinin signaling in *Arabidopsis*. The Plant Cell 24(3):1081-1095. *https://doi.org/10.1105/tpc.111.092254*

Kobayashi K, Sasaki D, Noguchi K, Fujinuma D, Komatsu H, Kobayashi M, … Wada H (2013). Photosynthesis of root chloroplasts developed in *Arabidopsis* lines overexpressing GOLDEN2-LIKE transcription factors. Plant and Cell Physiology 54(8):1365-1377. *https://doi.org/10.1093/pcp/pct086*

Kumar AM, Söll D (2000). Antisense HEMA1 RNA expression inhibits heme and chlorophyll biosynthesis in *Arabidopsis*. Plant Physiology 122(1):49-56. *https://doi.org/10.1104/pp.122.1.49*

Kusumi K, Sakata C, Nakamura T, Kawasaki S, Yoshimura A, Iba K (2011). A plastid protein NUS1 is essential for build-up of the genetic system for early chloroplast development under cold stress conditions. The Plant Journal 68(6):1039-1050. *https://doi.org/10.1111/j.1365-313X.2011.04755.x*

La RN, Rascio N, Oster U, Rüdiger W (2007). Inhibition of lycopene cyclase results in accumulation of chlorophyll precursors. Planta 225(4):1019-1029. *https://doi.org/10.1007/s00425-006-0409-7*

Lai YS, Li S, Tang Q, Li HX, Chen SX, Li PW, ... Guo X (2016). The dark-purple tea cultivar 'Ziyan' accumulates a large amount of delphinidin-related anthocyanins. Journal of Agricultural and Food Chemistry 64(13):2719-2726. *https://doi.org/10.1021/acs.jafc.5b04036*

Laurent GS, Wahlestedt C, Kapranov P (2015). The Landscape of long noncoding RNA classification. Trends in Genetics 31(5):239-251. *https://doi.org/10.1016/j.tig.2015.03.007*

Lee S, Kim JH, Yoo ES, Lee CH, Hirochika H, An G (2005). Differential regulation of chlorophyll a oxygenase genes in rice. Plant Molecular Biology 57(6):805-818. *https://doi.org/10.1007/s11103-005-2066-9*

Li CF, Ma JQ, Huang DJ, Ma CL, Jin JQ, Yao MZ, Chen L (2018b). Comprehensive dissection of metabolic changes in albino and green tea cultivars. Journal of Agricultural and Food Chemistry 66(8):2040-2048. *https://doi.org/10.1021/acs.jafc.7b05623*

Li D, Shao F, Lu S (2015). Identification and characterization of mRNA-like noncoding RNAs in *Salvia miltiorrhiza*. Planta 241(5):1131-1143. *https://doi.org/10.1007/s00425-015-2246-z*

Li NN, Lu JL, Li QS, Zheng XQ, Wang XC, Wang L, ... Yang YJ (2019a). Dissection of chemical composition and associated gene expression in the pigment-deficient tea cultivar 'Xiaoxueya' reveals an albino phenotype and metabolite formation. Frontiers in Plant Science 10:1543. *https://doi.org/10.3389/fpls.2019.01543*

Li Q, Zhu FY, Gao X, Sun Y, Li S, Tao Y, ... Liu H (2014). Young leaf chlorosis 2 encodes the stroma-localized heme oxygenase 2 which is required for normal tetrapyrrole biosynthesis in rice. Planta 240(4):701-712. *https://doi.org/10.1007/s00425-014-2116-0*

Li R, Fu D, Zhu B, Luo Y, Zhu H (2018c). CRISPR/Cas9-mediated mutagenesis of lncRNA1459 alters tomato fruit ripening. The Plant Journal 94(3):513-524. *https://doi.org/10.1111/tpj.13872*

Li WX, Yang SB, Lu Z, He ZC, Ye YL, Zhao BB, ... Jin B (2018a). Cytological, physiological, and transcriptomic analyses of golden leaf coloration in *Ginkgo biloba* L. Horticulture Research 5(1):1-14. *https://doi.org/10.1038/s41438-018-0015-4*

Li Y, Cui W, Wang R, Lin M, Zhong Y, Sun L, ... Fang J (2019b). MicroRNA858-mediated regulation of anthocyanin biosynthesis in kiwifruit (*Actinidia arguta*) based on small RNA sequencing. Plos One 14(5):e0217480. *https://doi.org/10.1371/journal.pone.0217480*

Li Y, Zhang Z, Wang P, Ma L, Li L, Yang R, ... Wang Q (2015). Comprehensive transcriptome analysis discovers novel candidate genes related to leaf color in a *Lagerstroemia indica* yellow leaf mutant. Genes & Genomics 37(10):851-863. https;//doi.org/10.1007/s13258-015-0317-y

Lin D, Jiang Q, Zheng K, Chen S, Zhou H, Gong X, ... Dong Y (2015). Mutation of the rice ASL2 gene encoding plastid ribosomal protein L21 causes chloroplast developmental defects and seedling death. Plant Biology 17(3):599-607. *https://doi.org/10.1111/plb.12271*

Linley PJ, Landsberger M, Kohchi T, Cooper JB, Terry MJ (2006). The molecular basis of heme oxygenase deficiency in the pcd1 mutant of pea. The FEBS Journal 273(12):2594-2606. *https://doi.org/10.1111/j.1742-4658.2006.05264.x*

Liu J, Jung C, Xu J, Wang H, Deng S, Bernad L, ... Chua NH (2012a). Genome-wide analysis uncovers regulation of long intergenic noncoding RNAs in *Arabidopsis*. The Plant Cell 24(11):4333-4345. *https://doi.org/10.1105/tpc.112.102855*

Liu M, Wang Y, Nie Z, Gai J, Bhat JA, Kong J, Zhao T (2020). Double mutation of two homologous genes YL1 and YL2 results in a leaf yellowing phenotype in soybean [*Glycine max* (L.) Merr]. Plant Molecular Biology 1-17.

Liu R, Dong X, Gu W, Yu L, Jin W, Qu Y, ... Li W (2016b). Variation in the phenotypic features and transcripts of thermo-sensitive leaf-color mutant induced by carbon ion beam in Green wandering jew (*Tradescantia fluminensis*). Scientia Horticulturae 213:303-313. *https://doi.org/10.7717/peerj.7261*

Liu R, Lai B, Hu B, Qin Y, Hu G, Zhao J (2017). Identification of microRNAs and their target genes related to the accumulation of anthocyanins in *Litchi chinensis* by high-throughput sequencing and degradome analysis. Frontiers in Plant Science 7:2059. *https://doi.org/10.3389/fpls.2016.02059*

Liu S, Sun Z, Xu M (2018). Identification and characterization of long non-coding RNAs involved in the formation and development of poplar adventitious roots. Industrial Crops and Products 118:334-346. *https://doi.org/10.1016/j.indcrop.2018.03.071*

Liu X, Yu W, Wang G, Cao F, Cai J, Wang H (2016a). Comparative proteomic and physiological analysis reveals the variation mechanisms of leaf coloration and carbon fixation in a Xantha mutant of *Ginkgo biloba* L. International Journal of Molecular Sciences 17(11):1794. *https://doi.org/10.3390/ijms17111794*

Liu XG, Xu H, Zhang JY, Liang GW, Liu YT, Guo AG (2012b). Effect of low temperature on chlorophyll biosynthesis in albinism line of wheat (*Triticum aestivum*) FA85. Physiologia Plantarum 145(3):384-394. *https://doi.org/10.1111/j.1399-3054.2012.01604.x*

Lois LM, Rodríguez-Concepción M, Gallego F, Campos N, Boronat A (2000). Carotenoid biosynthesis during tomato fruit development: regulatory role of 1-deoxy-D-xylulose 5-phosphate synthase. The Plant Journal 22(6):503-513. *https://doi.org/10.1046/j.1365-313x.2000.00764.x*

Lv Y, Liang Z, Ge M, Qi W, Zhang T, Lin F, … Zhao H (2016). Genome-wide identification and functional prediction of nitrogen-responsive intergenic and intronic long non-coding RNAs in maize (*Zea mays* L.). BMC Genomics 17(1):1-15. *https://doi.org/10.1186/s12864-016-2650-1*

Ma X, Sun X, Li C, Huan R, Sun C, Wang Y, … Zhang K (2017). Map-based cloning and characterization of the novel yellow-green leaf gene ys83 in rice (*Oryza sativa*). Plant Physiology and Biochemistry 111:1-9. *https://doi.org/10.1016/j.plaphy.2016.11.007*

Ma Z, Dooner HK (2004). A mutation in the nuclear-encoded plastid ribosomal protein S9 leads to early embryo lethality in maize. The Plant Journal 37(1):92-103. *https://doi.org/10.1046/j.1365-313x.2003.01942.x*

Mandel MA, Feldmann KA, Herrera-Estrella L, Rocha-Sosa M, León P (1996). CLA1, a novel gene required for chloroplast development, is highly conserved in evolution. The Plant Journal 9(5):649-658. *https://doi.org/10.1046/j.1365-313x.1996.9050649.x*

Maple J, Møller SG (2007). Plastid division: evolution, mechanism and complexity. Annals of Botany 99(4):565-579. *https://doi.org/10.1093/aob/mcl249*

Martens S, Preuß A, Matern U (2010). Multifunctional flavonoid dioxygenases: flavonol and anthocyanin biosynthesis in *Arabidopsis thaliana* L. Phytochemistry 71(10):1040-1049. *https://doi.org/10.1016/j.phytochem.2010.04.016*

Meier S, Tzfadia O, Vallabhaneni R, Gehring C, Wurtzel ET (2011). A transcriptional analysis of carotenoid, chlorophyll and plastidial isoprenoid biosynthesis genes during development and osmotic stress responses in *Arabidopsis thaliana*. BMC Systems Biology 5(1):77. *https://doi.org/10.1186/1752-0509-5-77*

Meng X, Zhang P, Chen Q, Wang J, Chen M (2018). Identification and characterization of ncRNA-associated ceRNA networks in *Arabidopsis* leaf development. BMC Genomics 19(1):607. *https://doi.org/10.1186/s12864-018-4993-2*

Mol J, Grotewold E, Koes R (1998). How genes paint flowers and seeds. Trends in Plant Science 3(6):212-217. *https://doi.org/10.1016/S1360-1385(98)01242-4*

Murakami PF, Schaberg PG, Shane JB (2008). Stem girdling manipulates leaf sugar concentrations and anthocyanin expression in sugar maple trees during autumn. Tree Physiology 28(10):1467-1473. *https://doi.org/10.1093/treephys/28.10.1467*

Nguyen CV, Vrebalov JT, Gapper NE, Zheng Y, Zhong S, Fei Z, Giovannoni JJ (2014). Tomato GOLDEN2-LIKE transcription factors reveal molecular gradients that function during fruit development and ripening. The Plant Cell 26(2):585-601. *https://doi.org/10.1105/tpc.113.118794*

Osteryoung KW, Nunnari J (2003). The division of endosymbiotic organelles. Science 302(5651):1698-1704. *https://doi.org/10.1126/science.1082192*

Park SY, Yu JW, Park JS, Li J, Yoo SC, Lee NY, … Jeon JS (2007). The senescence-induced staygreen protein regulates chlorophyll degradation. The Plant Cell 19(5):1649-1664. *https://doi.org/10.1105/tpc.106.044891*

Pasini L, Bruschini S, Bertoli A, Mazza R, Fracheboud Y, Marocco A (2005). Photosynthetic performance of cold-sensitive mutants of maize at low temperature. Physiologia Plantarum 124(3):362-370. *https://doi.org/10.3929/ethz-a-005794605*

Phillips MA, León P, Boronat A, Rodríguez-Concepción M (2008). The plastidial MEP pathway: unified nomenclature and resources. Trends in Plant Science 13(12):619-623. *https://doi.org/10.1016/j.tplants.2008.09.003*

Powell AL, Nguyen CV, Hill T, Cheng KL, Figueroa-Balderas R, Aktas H, … Lopez-Baltazar J (2012). Uniform ripening encodes a Golden 2-like transcription factor regulating tomato fruit chloroplast development. Science 336(6089):1711-1715. *https://doi.org/10.1126/science.1222218*

Qin D, Dong J, Xu F, Guo G, Ge S, Xu Q, … Li M (2015). Characterization and fine mapping of a novel barley stage green-revertible albino gene (HvSGRA) by bulked segregant analysis based on SSR assay and specific length amplified fragment sequencing. BMC Genomics 16(1):1-14. *https://doi.org/10.1186/s12864-015-2015-1*

Qiu Z, Chen D, He L, Zhang S, Yang Z, Zhang Y, … Zhu L (2018). The rice white green leaf 2 gene causes defects in chloroplast development and affects the plastid ribosomal protein S9. Rice 11(1):1-12. *https://doi.org/10.1186/s12284-018-0233-2*

Ren G, An K, Liao Y, Zhou X, Cao Y, Zhao H, … Kuai B (2007). Identification of a novel chloroplast protein AtNYE1 regulating chlorophyll degradation during leaf senescence in *Arabidopsis*. Plant Physiology 144(3):1429-1441. *https://doi.org/10.1104/pp.107.100172*

Ren G, Zhou Q, Wu S, Zhang Y, Zhang L, Huang J, … Kuai B (2010). Reverse genetic identification of CRN1 and its distinctive role in chlorophyll degradation in *Arabidopsis*. Journal of Integrative Plant Biology 52(5):496-504. *https://doi.org/10.1111/j.1744-7909.2010.00945.x*

Roberts DJ, Werner DJ, Wadl PA, Trigiano RN (2015). Inheritance and allelism of morphological traits in eastern redbud (*Cercis canadensis* L.). Horticulture Research 2(1):1-11. *https://doi.org/10.1038/hortres.2015.49*

Rogalski M, Ruf S, Bock R (2006). Tobacco plastid ribosomal protein S18 is essential for cell survival. Nucleic Acids Research 34(16):4537-4545. *https://doi.org/10.1093/nar/gkl634*

Rong W, Wang X, Wang X, Massart S, Zhang Z (2018). Molecular and ultrastructural mechanisms underlying yellow dwarf symptom formation in wheat after infection of Barley Yellow Dwarf Virus. International Journal of Molecular Sciences 19(4):1187. *https://doi.org/10.3390/ijms19041187*

Rossini L, Cribb L, Martin DJ, Langdale JA (2001). The maize golden2 gene defines a novel class of transcriptional regulators in plants. The Plant Cell 13(5):1231-1244. *https://doi.org/10.1105/tpc.13.5.1231*

Sacchettini JC, Poulter CD (1997). Creating isoprenoid diversity. Science 277(5333):1788-1789. *https://doi.org/10.1126/science.277.5333.1788*

Samad AFA, Rahnamaie-Tajadod R, Sajad M, Jani J, Murad AMA, Noor NM, Ismail I (2019). Regulation of terpenoid biosynthesis by miRNA in *Persicaria minor* induced by *Fusarium oxysporum*. BMC Genomics 20(1):586. *https://doi.org/10.1186/s12864-019-5954-0*

Schaberg PG, Van-den-Berg AK, Murakami PF, Shane JB, Donnelly JR (2003). Factors influencing red expression in autumn foliage of sugar maple trees. Tree Physiology 23(5):325-333. *https://doi.org/10.1093/treephys/23.5.325*

Schultes NP, Sawers RJ, Brutnell TP, Krueger RW (2000). Maize high chlorophyll fluorescent 60 mutation is caused by an Ac disruption of the gene encoding the chloroplast ribosomal small subunit protein 17. The Plant Journal 21(4):317-327.

Shi D, Zheng X, Li L, Lin W, Xie W, Yang J, … Jin W (2013). Chlorophyll deficiency in the maize elongated mesocotyl2 mutant is caused by a defective heme oxygenase and delaying grana stacking. PLoS One 8(11):e80107. *https://doi.org/10.1371/journal.pone.0080107*

Shi JY, Zou XB, Zhao JW, Mel H, Wang KL, Wang X, Chen H (2012). Determination of total flavonoids content in fresh *Ginkgo biloba* leaf with different colors using near infrared spectroscopy. Spectrochimica Acta Part A: Molecular and Biomolecular Spectroscopy 94:271-276. *https://doi.org/10.1016/j.saa.2012.03.078*

Shimada H, Koizumi M, Kuroki K, Mochizuki M, Fujimoto H, Ohta H, … Takamiya KI (2004). ARC3, a chloroplast division factor, is a chimera of prokaryotic FtsZ and part of eukaryotic phosphatidylinositol-4-phosphate 5-kinase. Plant and Cell Physiology 45(8):960-967. *https://doi.org/10.1093/pcp/pch130*

Shin D, Lee S, Kim TH, Lee JH, Park J, Lee J, … Park JH (2020). Natural variations at the Stay-Green gene promoter control lifespan and yield in rice cultivars. Nature Communications 11(1):1-11. *https://doi.org/10.1038/s41467-020-16573-2*

Song J, Wei X, Shao G, Sheng Z, Chen D, Liu C, … Hu P (2014). The rice nuclear gene WLP1 encoding a chloroplast ribosome L13 protein is needed for chloroplast development in rice grown under low temperature conditions. Plant Molecular Biology 84(3):301-314. *https://doi.org/10.1007/s11103-013-0134-0*

Su N, Hu ML, Wu DX, Wu FQ, Fei GL, Lan Y, … Cheng ZJ (2012). Disruption of a rice pentatricopeptide repeat protein causes a seedling-specific albino phenotype and its utilization to enhance seed purity in hybrid rice production. Plant Physiology 159(1):227-238. *https://doi.org/10.1104/pp.112.195081*

Sugimoto H, Kusumi K, Noguchi K, Yano M, Yoshimura A, Iba K (2007). The rice nuclear gene, VIRESCENT 2, is essential for chloroplast development and encodes a novel type of guanylate kinase targeted to plastids and mitochondria. The Plant Journal 52(3):512-527. *https://doi.org/10.1111/j.1365-313x.2007.03251.x*

Sun XQ, Wang B, Xiao YH, Wan CM, Deng XJ, Wang PD (2011). Genetic analysis and fine mapping of gene ygl98 for yellow-green leaf of rice. Acta Agronomica Sinica 37(6):991-997.

Stern DB, Hanson MR, Barkan A (2004). Genetics and genomics of chloroplast biogenesis: maize as a model system. Trends in Plant Science 9(6):293-301. *https://doi.org/10.1016/j.tplants.2004.04.001*

Stief A, Altmann S, Hoffmann K, Pant BD, Scheible WR, Bäurle I (2014). Arabidopsis miR156 regulates tolerance to recurring environmental stress through SPL transcription factors. The Plant Cell 26(4):1792-1807. *https://doi.org/10.1105/tpc.114.123851*

Tanaka Y, Sasaki N, Ohmiya A (2008). Biosynthesis of plant pigments: anthocyanins, betalains and carotenoids. The Plant Journal 54(4):733-749. *https://doi.org/10.1111/j.1365-313X.2008.03447.x*

Terry MJ, Kendrick RE (1999). Feedback inhibition of chlorophyll synthesis in the phytochrome chromophore-deficient aurea andyellow-green-2 mutants of tomato. Plant Physiology 119(1):143-152. *https://doi.org/10.1104/pp.119.1.143*

Tian X, Ling Y, Fang L, Du P, Sang X, Zhao F, … He G (2013). Gene cloning and functional analysis of yellow green leaf3 (ygl3) gene during the whole-plant growth stage in rice. Genes & Genomics 35(1):87-93. *https://doi.org/10.1007/s13258-013-0069-5*

Tiller N, Bock R (2014). The translational apparatus of plastids and its role in plant development. Molecular Plant 7(7):1105-1120. *https://doi.org/10.1093/mp/ssu022*

Tohge T, Nishiyama Y, Hirai MY, Yano M, Nakajima JI, Awazuhara M, … Noji M (2005). Functional genomics by integrated analysis of metabolome and transcriptome of *Arabidopsis* plants over-expressing an MYB transcription factor. The Plant Journal 42(2):218-235. *https://doi.org/10.1111/j.1365-313X.2005.02371.x*

Vitha S, Froehlich JE, Koksharova O, Pyke KA, Van EH, Osteryoung KW (2003). ARC6 is a J-domain plastid division protein and an evolutionary descendant of the cyanobacterial cell division protein Ftn2. The Plant Cell 15(8):1918-1933.

Wan C, Li C, Ma X, Wang Y, Sun C, Huang R, … Zhu J (2015). GRY79 encoding a putative metallo-β-lactamase-trihelix chimera is involved in chloroplast development at early seedling stage of rice. Plant Cell Reports 34(8):1353-1363. *https://doi.org/10.1007/s00299-015-1792-y*

Wang F, Kong W, Wong G, Fu L, Peng R, Li Z, Yao Q (2016a). AtMYB12 regulates flavonoids accumulation and abiotic stress tolerance in transgenic *Arabidopsis thaliana*. Molecular Genetics and Genomics 291(4):1545-1559. *https://doi.org/10.1007/s00438-016-1203-2*

Wang JW, Czech B, Weigel D (2009b). miR156-regulated SPL transcription factors define an endogenous flowering pathway in *Arabidopsis thaliana*. Cell 138(4):738-749. https;//doi.org/10.1016/j.cell.2009.06.014

Wang L, Yue C, Cao H, Zhou Y, Zeng J, Yang Y, Wang X (2014). Biochemical and transcriptome analyses of a novel chlorophyll-deficient chlorina tea plant cultivar. BMC Plant Biology 14(1):1-13. *https://doi.org/10.1186/s12870-014-0352-x*

Wang Y, Wang C, Zheng M, Lyu J, Xu Y, Li X, … Terzaghi W (2016a). WHITE PANICLE1, a Val-tRNA synthetase regulating chloroplast ribosome biogenesis in rice, is essential for early chloroplast development. Plant Physiology 170(4):2110-2123. *https://doi.org/10.1104/pp.15.01949*

Wang M, Wang Q, Zhang B (2013b). Response of miRNAs and their targets to salt and drought stresses in cotton (*Gossypium hirsutum* L.). Gene 530(1):26-32. *https://doi.org/10.1016/j.gene.2013.08.009*

Wang N, Liu Z, Zhang Y, Li C, Feng H (2018b). Identification and fine mapping of a stay-green gene (Brnye1) in pakchoi (*Brassica campestris* L. ssp. *chinensis*). Theoretical and Applied Genetics 131(3):673-684. *https://doi.org/10.1007/s00122-017-3028-8*

Wang P, Gao J, Wan C, Zhang F, Xu Z, Huang X, … Deng X (2010). Divinyl chlorophyll (ide) a can be converted to monovinyl chlorophyll (ide) a by a divinyl reductase in rice. Plant Physiology 153(3):994-1003. *https://doi.org/10.1104/pp.110.158477*

Wang P, Fouracre J, Kelly S, Karki S, Gowik U, Aubry S, … Hibberd JM (2013a). Evolution of GOLDEN2-LIKE gene function in C3 and C4 plants. Planta 237(2):481-495. *https://doi.org/10.1007/s00425-012-1754-3*

Wang Q, Sang X, Ling Y, Zhao F, Yang Z, Li Y, He G (2009a). Genetic analysis and molecular mapping of a novel gene for zebra mutation in rice (*Oryza sativa* L.). Journal of Genetics and Genomics 36(11):679-684. *https://doi.org/10.1016/S1673-8527(08)60160-5*

Wang SA, Wang P, Gao L, Yang R, Li L, Zhang E, … Yin Z (2017b). Characterization and complementation of a chlorophyll-less dominant mutant GL1 in *Lagerstroemia indica*. DNA and Cell Biology 36(5):354-366. *https://doi.org/10.1089/dna.2016.3573*

Wang WJ, Zheng KL, Gong XD, Xu JL, Huang JR, Lin DZ, Dong YJ (2017a). The rice TCD11 encoding plastid ribosomal protein S6 is essential for chloroplast development at low temperature. Plant Science 259:1-11. https://doi.org/10.1016/j.plantsci.2017.02.007

Wang Y, Liu S, Tian X, Fu Y, Jiang X, Li Y, Wang G (2018a). Influence of light intensity on chloroplast development and pigment accumulation in the wild-type and etiolated mutant plants of *Anthurium andraeanum* 'Sonate'. Plant Signaling & Behavior 13(8):e1482174. *https://doi.org/10.1080/15592324.2018.1482174*

Wang Y, Wang Y, Song Z, Zhang H (2016b). Repression of MYBL2 by both microRNA858a and HY5 leads to the activation of anthocyanin biosynthetic pathway in *Arabidopsis*. Molecular Plant 9(10):1395-1405. *https://doi.org/10.1016/j.molp.2016.07.003*

Waters MT, Langdale JA (2009). The making of a chloroplast. The EMBO Journal 28(19):2861-2873. *https://doi.org/10.1038/emboj.2009.264*

Waters MT, Wang P, Korkaric M, Capper RG, Saunders NJ, Langdale JA (2009). GLK transcription factors coordinate expression of the photosynthetic apparatus in *Arabidopsis*. The Plant Cell 21(4):1109-1128. *https://doi.org/10.1105/tpc.108.065250*

Wei K, Wang L, Zhang Y, Ruan L, Li H, Wu L, ... Edwards R (2019). A coupled role for CsMYB75 and CsGSTF1 in anthocyanin hyperaccumulation in purple tea. The Plant Journal 97(5):825-840. *https://doi.org/10.1111/tpj.14161*

Wei K, Zhang Y, Wu L, Li H, Ruan L, Bai P, ... Cheng H (2016). Gene expression analysis of bud and leaf color in tea. Plant Physiology and Biochemistry 107:310-318. *https://doi.org/10.1016/j.plaphy.2016.06.022*

Weller JL, Terry MJ, Rameau C, Reid JB, Kendrick RE (1996). The phytochrome-deficient pcd1 mutant of pea is unable to convert Heme to Biliverdin IX [alpha]. The Plant Cell 8(1):55-67. *https://doi.org/10.1105/tpc.8.1.55*

Wu HJ, Wang ZM, Wang M, Wang XJ (2013). Widespread long noncoding RNAs as endogenous target mimics for microRNAs in plants. Plant Physiology 161(4):1875-1884. *https://doi.org/10.1104/pp.113.215962*

Wu Y, Guo J, Wang T, Cao F, Wang G (2019). Transcriptional profiling of long noncoding RNAs associated with leaf-color mutation in *Ginkgo biloba* L. BMC Plant Biology 19(1):1-13. *https://doi.org/10.1186/s12870-019-2141-z*

Wu Y, Li X, Wang T, Guo J, Cao F, Wang G (2020). *Ginkgo biloba* microRNA profiling reveals new insight into leaf color mutation. Scientia Horticulturae 265:109189. *https://doi.org/10.1016/j.scienta.2020.109189*

Wu Z, Zhang X, He B, Diao L, Sheng S, Wang J, ... Wang C (2007). A chlorophyll-deficient rice mutant with impaired chlorophyllide esterification in chlorophyll biosynthesis. Plant Physiology 145(1):29-40. *https://doi.org/10.1104/pp.107.100321*

Xia R, Zhu H, An YQ, Beers EP, Liu Z (2012). Apple miRNAs and tasiRNAs with novel regulatory networks. Genome Biology 13(6):R47. *https://doi.org/10.1186/gb-2012-13-6-r47*

Xie F, Yuan JL, Li YX, Wang CJ, Tang HY, Xia JH, ... Wan ZJ (2018). Transcriptome analysis reveals candidate genes associated with leaf etiolation of a cytoplasmic male sterility line in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*). International Journal of Molecular Sciences 19(4):922. *https://doi.org/10.3390/ijms19040922*

Xie Y, Xu D, Cui W, Shen W (2012). Mutation of Arabidopsis HY1 causes UV-C hypersensitivity by impairing carotenoid and flavonoid biosynthesis and the down-regulation of antioxidant defence. Journal of Experimental Botany 63(10):3869-3883. *https://doi.org/10.1093/jxb/ers078*

Xing S, Miao J, Li S, Qin G, Tang S, Li H, ... Qu LJ (2010). Disruption of the 1-deoxy-D-xylulose-5-phosphate reductoisomerase (DXR) gene results in albino, dwarf and defects in trichome initiation and stomata closure in *Arabidopsis*. Cell Research 20(6):688-700. *https://doi.org/10.1038/cr.2010.54*

Xu B, Xin W, Wang G, Guo W, Wen F, Jin J (2006). Characteristics of chimeras of *Anthurium andraeanum* from *in vitro* mutation. Chinese Bulletin of Botany 23(6):698-702.

Xu S, Wang L, Zhang B, Han B, Xie Y, Yang J, ... Cui W (2012). RNAi knockdown of rice SE5 gene is sensitive to the herbicide methyl viologen by the down-regulation of antioxidant defense. Plant Molecular Biology 80(2):219-235.

Yan J, Qian L, Zhu W, Qiu J, Lu Q, Wang X, ... Huang Y (2020). Integrated analysis of the transcriptome and metabolome of purple and green leaves of *Tetrastigma hemsleyanum* reveals gene expression patterns involved in anthocyanin biosynthesis. PloS One 15(3):e0230154. *https://doi.org/10.1371/journal.pone.0230154*

Yang Y, Chen X, Xu B, Li Y, Ma Y, Wang G (2015). Phenotype and transcriptome analysis reveal chloroplast development and pigment biosynthesis together influenced the leaf color formation in mutants of *Anthurium andraeanum* 'Sonate'. Frontiers in Plant Science 6:139. *https://doi.org/10.3389/fpls.2015.00139*

Ye J, Zhang X, Tan J, Xu F, Cheng S, Chen Z, ... Liao Y (2020). Global identification of *Ginkgo biloba* microRNAs and insight into their role in metabolism regulatory network of terpene trilactones by high-throughput sequencing and degradome analysis. Industrial Crops and Products 148:112289.

Yoo SC, Cho SH, Sugimoto H, Li J, Kusumi K, Koh HJ, … Paek NC (2009). Rice virescent3 and stripe1 encoding the large and small subunits of ribonucleotide reductase are required for chloroplast biogenesis during early leaf development. Plant Physiology 150(1):388-401. *https://doi.org/10.1104/pp.109.136648*

You MK, Lee YJ, Kim JK, Baek SA, Jeon YA, Lim SH, Ha SH (2020). The organ-specific differential roles of rice DXS and DXR, the first two enzymes of the MEP pathway, in carotenoid metabolism in *Oryza sativa* leaves and seeds. BMC Plant Biology 20:1-16. *https://doi.org/10.1186/s12870-020-02357-9*

Yuan M, Yuan S, Zhang ZW, Xu F, Chen YE, Du JB, Lin HH (2010). Putative mutation mechanism and light responses of a protochlorophyllide oxidoreductase-less barley mutant NYB. Plant and Cell Physiology 51(8):1361-1371. *https://doi.org/10.1093/pcp/pcq097*

Zhang G, Chen D, Zhang T, Duan A, Zhang J, He C (2018). Transcriptomic and functional analyses unveil the role of long non-coding RNAs in anthocyanin biosynthesis during sea buckthorn fruit ripening. DNA Research 25(5):465-476. *https://doi.org/10.1093/dnares/dsy017*

Zhang H, Liu L, Cai M, Zhu S, Zhao J, Zheng T, … Chen S (2015). A point mutation of magnesium chelatase OsCHLI gene dampens the interaction between CHLI and CHLD subunits in rice. Plant Molecular Biology Reporter 33(6):1975-1987. *https://doi.org/10.1007/s11105-015-0889-3*

Zhang H, Li J, Yoo JH, Yoo SC, Cho SH, Koh HJ, … Paek NC (2006). Rice Chlorina-1 and Chlorina-9 encode ChlD and ChlI subunits of Mg-chelatase, a key enzyme for chlorophyll synthesis and chloroplast development. Plant Molecular Biology 62(3):325-337. *https://doi.org/10.1007/s11103-006-9024-z*

Zhang J, Yuan H, Yang Y, Fish T, Lyi SM, Thannhauser TW, … Li L (2016). Plastid ribosomal protein S5 is involved in photosynthesis, plant development, and cold stress tolerance in *Arabidopsis*. Journal of Experimental Botany 67(9):2731-2744. *https://doi.org/10.1093/jxb/erw106*

Zhang K, Liu Z, Shan X, Li C, Tang X, Chi M, Feng H (2017a). Physiological properties and chlorophyll biosynthesis in a Pak-choi (*Brassica rapa* L. ssp. *chinensis*) yellow leaf mutant, pylm. Acta Physiologiae Plantarum 39(1):22.

Zhang K, Mu Y, Li W, Shan X, Wang N, Feng H (2020). Identification of two recessive etiolation genes (py1, py2) in pakchoi (*Brassica rapa* L. ssp. *chinensis*). BMC Plant Biology 20(1):1-14. *https://doi.org/10.1186/s12870-020-2271-3*

Zhang L, Zhang X, Wang X, Xu J, Wang M, Li L, … Yan J (2019). Seed carotenoid deficient functions in isoprenoid biosynthesis via the plastid MEP pathway. Plant Physiology 179(4):1723-1738. *https://doi.org/10.1104/pp.18.01148*

Zhang S, Zuo L, Zhang J, Chen P, Wang J, Yang M (2017b). Transcriptome analysis of *Ulmus pumila* 'Jinye' responses to different shading involved in chlorophyll metabolism. Tree Genetics & Genomes 13(3):64.

Zhao D, Wei M, Shi M, Hao Z, Tao J (2017). Identification and comparative profiling of miRNAs in herbaceous peony (*Paeonia lactiflora* Pall.) with red/yellow bicoloured flowers. Scientific Reports 7:44926. *https://doi.org/10.1038/srep44926*

Zhao DS, Zhang CQ, Li QF, Yang QQ, Gu MH, Liu QQ (2016). A residue substitution in the plastid ribosomal protein L12/AL1 produces defective plastid ribosome and causes early seedling lethality in rice. Plant Molecular Biology 91(1-2):161-17. *https://doi.org/10.1007/s11103-016-0453-z*

Zhou S, Hu Z, Zhu M, Zhang B, Deng L, Pan Y, Chen G (2013c). Biochemical and molecular analysis of a temperature-sensitive albino mutant in kale named 'White Dove'. Plant Growth Regulation 71(3):281-294. *https://doi.org/10.1007/s10725-013-9829-0*

Zhu X, Guo S, Wang Z, Du Q, Xing Y, Zhang T, … He G (2016). Map-based cloning and functional analysis of YGL8, which controls leaf colour in rice (*Oryza sativa*). BMC Plant Biology 16(1):134. *https://doi.org/10.1186/s12870-016-0821-5*

Zhou XW, Fan ZQ, Chen Y, Zhu YL, Li JY, Yin H F (2013a). Functional analyses of a flavonol synthase–like gene from *Camellia nitidissima* reveal its roles in flavonoid metabolism during floral pigmentation. Journal of Biosciences 38(3):593-604.

Zhou Y, Gong Z, Yang Z, Yuan Y, Zhu J, Wang M, … Xu T (2013b). Mutation of the light-induced yellow leaf 1 gene, which encodes a geranylgeranyl reductase, affects chlorophyll biosynthesis and light sensitivity in rice. PLoS One 8(9):e75299. *https://doi.org/10.1371/journal.pone.0075299*