Advance in mechanism of plant leaf colour mutation

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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
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.
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 (Figure 1). 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. HEMA4 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 (PY7 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 leaf2 (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 NYCI, 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 to 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-xullose 5-phosphate synthase; DXR, 1-deoxy-D-xullose 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)-buteinyl 4-diphosphate synthase; IspH, 1-hydroxy-2-methyl-2-(E)-buteinyl 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; Proto 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-Protop IX, Mg-protoporphyrin IX; DVR, divinyl chlade a reductase; PORAB/C, NDAPH, protoporphyrilide oxidoreductase; Chl a, chlorophylide a; Chl b, chlorophylide b; DV chlade a, divinyl chlorophylide a; CAO, chlorophylide 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 *lm1* and *hcI60* 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 *all*, 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 *YCLI*. 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, *YLI* and *WPJ* 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 IncRNAs 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-miRn*27, *csn-miRn*49, *csn-miRn*56, and *csn-miRn*23 were found to be co-targeted to the *F3′ H* gene and participated in the synthesis of anthocyanin and in the accumulation of flavonoids. Furthermore, the study confirmed that *csn-miRn*70 and *csn-miRn*30 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; Stieß et al., 2014), synthesis of secondary metabolites (Ye et al., 2020), and floral organ development (Wang et al., 2009b).
By comparing the gene expression profiles of different varieties of roses, five miRNAs (miR171, miR166i, miR159c, 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 target 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).
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 (*PAL, CHS, CHI, F3’H, F3’S’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.

Previous studies showed that IncRNAs perform their functions by interacting with miRNAs (Wu *et al.*, 2013). Two differentially expressed IncRNAs (*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 *IncRNA1459* mutant, leading to the delay in fruit ripening (Li *et al.*, 2018c).
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, IspFT-DNA insertion mutant and IspFRNAi 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 IncRNA in leaf colour mutation, which needs to be further analysed. At present, most miRNA and IncRNA 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.

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Conflict of Interests

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

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