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Genetic Engineering-Dream or Nightmare?

The Brave New World of Bad Science and Big Business in commercial floriculture crops.

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INTRODUCTION

Floriculture products mainly consist of cut flowers, pot plants, cut foilage, seeds bulbs, tubers, rooted cuttings and dried flowers or leaves. The important floricultural crops in the international cut flower trade are rose, carnation, chrysanthemum, gargera, gladiolus, gypsophila, liastris, nerine, orchids, archilea, anthuriu, tulip, and lilies. Floriculture crops like gerberas, carnation, etc. are grown in green houses. The open field crops are chrysanthemum, roses, gaillardia, lily marygold, aster, tuberose etc. In India about 255 thousand hectares area is under cultivation, and the production of flowers are estimated to be 17.54 million tonnes loose flowers and 543 million tonnes cut flowers. The country has exported 22,947.23 MT of floriculture products to the world for the worth of Rs. 460.75 crores in 2014-15.

Government of India has identified floriculture as a sunrise industry and accorded it 100% export oriented status. Owing to steady increase in demand of flower floriculture has become one of the important Commercial trades in Agriculture. Hence commercial floriculture has emerged as hi-tech activity-taking place under controlled climatic conditions inside greenhouse. Floriculture in India, is being viewed as a high growth Industry. Commercial floriculture is becoming important from the export angle. The liberalization of industrial and trade policies paved the way for development of export-oriented production of cut flowers. The new seed policy had already made it feasible to import planting material of international varieties. It has been found that commercial floriculture has higher potential per unit area than most of the field crops and is therefore a lucrative business. Indian floriculture industry has been shifting from traditional flowers to cut flowers for export purposes. The liberalized economy has given an impetus to the Indian entrepreneurs for establishing export oriented floriculture units under controlled climatic conditions. Agricultural and Processed Food Products Export Development Authority (APEDA), is responsible for export promotion and development of floriculture in India.

Flower colour

Flower color is one of the most attractive characteristics in ornamental plants, contributing to the major value in the floricultural market. In nature, various patterns regarding to the flower color can be easily observed. However, most of these phenotypic changes are not transmittable and thus novel varieties with commercial value cannot be obtained. Furthermore, alteration in flower pigmentation is a visible indicator to study expression and regulation of floral genes in plant molecular biology. Thus, examination and manipulation of flower color is not only important in basic research areas, it also has a great benefit in biotechnological applications.

Generally speaking, flower color is predominantly determined by two classes of pigments: flavonoids and carotenoids. Flavonoids (mainly anthocyanins) are the most common flower pigments contributing to a range of colors from yellow to orange to red to purple; and carotenoids are the red, orange and yellow lipid-soluble pigments found embedded in the membranes of chloroplasts and chromoplasts (Bartley and Scolnik 1995). In addition, a third class of pigments, betalains, can be found only in certain plants from 10 families of the order Caryophyllales.

Betalains are water soluble alkaloids localized in the cell vacuole; interestingly, betalains and anthocyanins have never been reported in the same plants (Stafford 1994). Betalains can be further divided into two major groups: the red to red-violet betacyanins and the yellow betaxanthins. The presence of these pigments in flowers is used as an attractant for some insects and animals. Betalains have been used as natural pigments for food coloration for many years (Cai *et al*. 2005); however, metabolic engineering of betalains has not been reported yet.

Carotenoids are C40-tetraterpenoid compounds that are synthesized from the basic C5-isoprene units (isopentenyl diphosphate and its isomer dimethylallyl diphosphate) in great varieties by bacteria, fungi, algae and higher plants. Animals appear to be incapable of biosynthesizing carotenoids, but all kinds of animals use carotenoids for a variety of purposes including coloration and as a precursor of vitamin A (Bartley and Scolnik 1995, Britton 1998). Carotenoids are lipid-soluble pigments and are located in the plastids, contributing to the majority of yellow hues in a number of flowers (Forkmann 1991). In some flowers such as roses and chrysanthemums, the orange/red, bronze and brown colors are contributed from carotenoids, or along with red or magenta anthocyanins (Tanaka *et al*. 2005).

As mentioned, flavonoids are the most common of the three types of pigment in flower tissue. Flavonoids are water-soluble compounds and are based on a C15 skeleton. Flavonoids,

starting from the general phenylpropanoid pathway, can be subdivided into 9 major groups according to their structures: chalcones, aurones, isoflavonoids, flavones, flavonols, flavandiols, anthocyanins, condensed tannins (proanthocyanins) and phlobaphenes. Among them, the major classes of flavonoids which contribute color to plants are the anthocyanins, flavonols, chalcones and aurones. Anthocyanins are the largest class of flavonoids that are responsible for the pink, red, violet, blue and purple colors of flowers and other tissues. Anthocyanins are water-soluble pigments that accumulate in vacuoles or anthocyanoplasts. The anthocyanin biosynthetic pathways from higher plants including *Petunia*, maize, snapdragon and *Arabidopsis* have been well established (Holton and Cornish 1995, Mol *et al*. 1998, Winkel-Shirley 2001). Three common anthocyanins are pelargonidin-, cyanidin-, and delphinidin-based pigments.

BIOSYNTHESIS AND FUNCTION OF FLAVONOIDS

During the past few decades, nearly all enzymes involved in the pathways to the different flavonoid classes have been determined. It should be kept in mind that some branch/modifying enzymes are limited in certain plant species. All flavonoids are derived from a general phenylpropanoid pathway which starts from an aromatic amino acid phenylalanine. The first committed step is catalyzed by chalcone synthase (CHS). CHS catalyzes condensation of one molecule of *p*-coumaroyl-CoA and three molecules of malonyl-CoA, resulting one molecule of 4′,2′,4′,6′- tetrahydroxychalcone (chalcone or naringenin chalcone), which is a key intermediate in the formation of flavonoids. Chalcone is rapidly converted into naringin by chalcone isomerase (CHI); however, in the absence of CHI, chalcone also spontaneously forms mixed enantiomers of naringenin. Subsequently, gene encoding flavanone 3-hydroxylase (F3H) of the unbranched flow in the flavonoid biosynthetic pathway catalyzes naringenin to dihydrokaempferol. Extensive modifications including hydrolation, glycosylation, methylation and acylation are carried out to form various compounds containing major classes of flavonoids. For simplification, the colored products of anthocyanins, anthocyanidin 3-glucosides, being the major components in flower color, are emphasized. These colored anthocyanins can be further modified by glycoslation, acylation or methylation in a species-specific manner.

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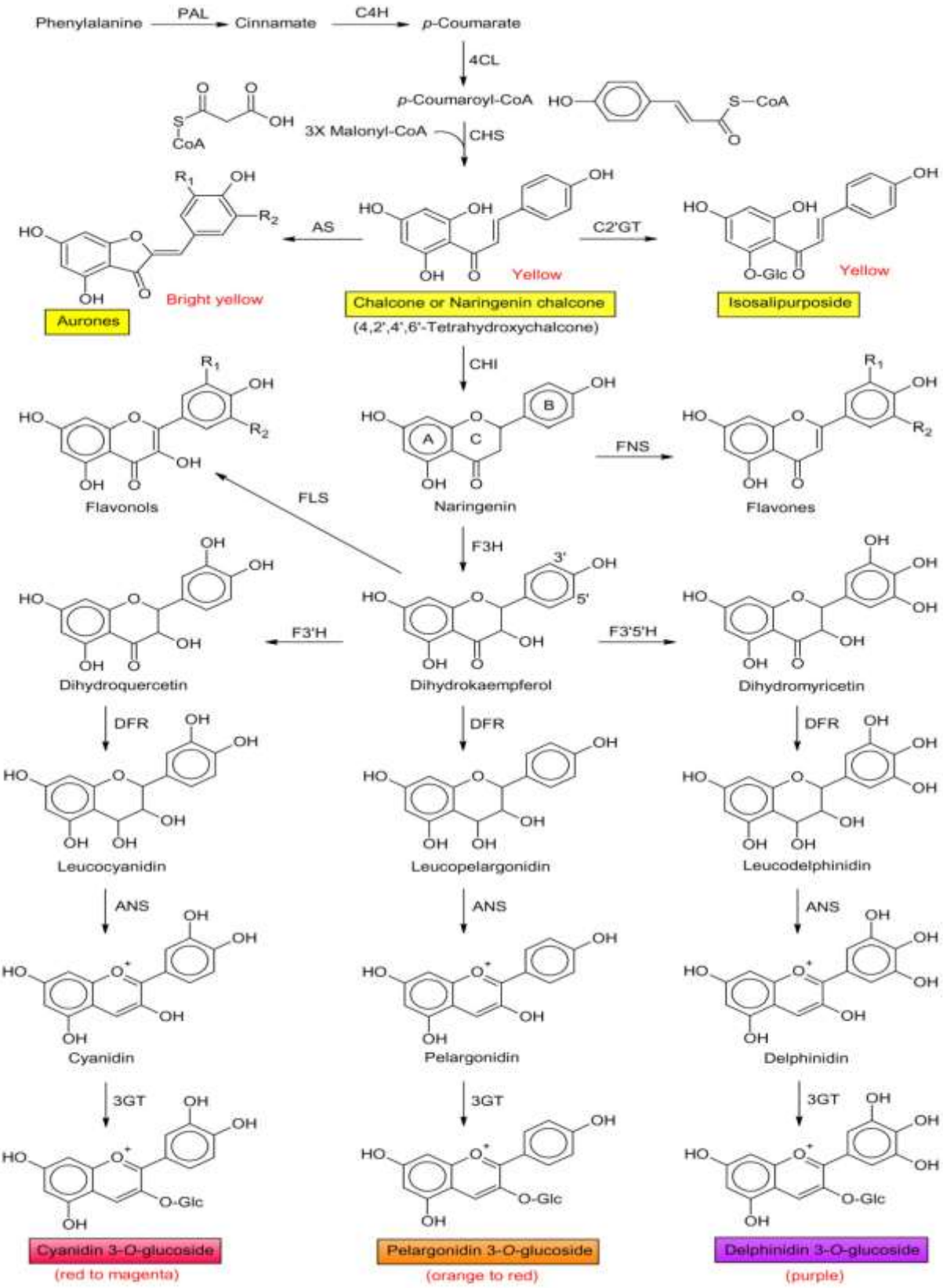
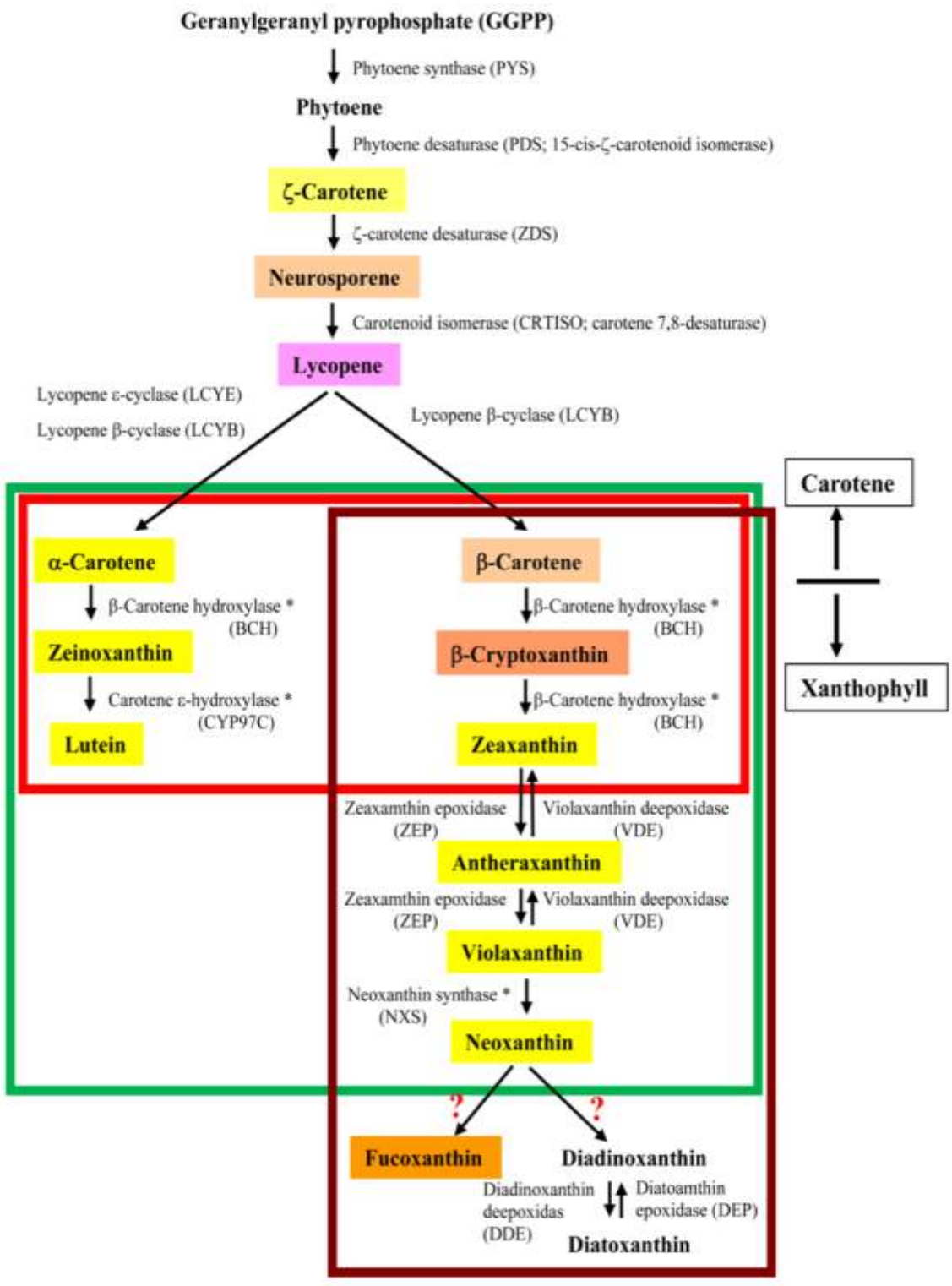


via cryptoxanthin. The enzyme epsilon ring hydroxylase is responsible for this reaction.



Likewise beta carotene also undergoes hydroxylation to synthesise zeaxanthin via beta cryptoxanthin, which is catalysed by beta ring hydroxylase. Epoxidation of zeax- anthin by zeaxanthin epoxidase produces violaxanthin via antheraxanthin. This reaction is reversible as de-epoxidat- ion by violaxanthin deepoxidase can lead to the formation of zeaxanthin. Neoxanthin synthase is responsible for the conversion of violaxanthin to neoxanthin. Capsanthin synthase and capsorubin synthase produce the ketolated carotenoids such as capsanthin and capsorubin from anther- axanthin and violaxanthin respectively15. The schematic representation of carotenoid biosynthetic pathway is shown in fig.1. Carotenoid biosynthetic pathway is a highly branched pathway with a complex regulatory network. Experimental data indicate that both transcriptional and post transcriptional events account for the regulation of carotenoid biosynthesis.

APPROACHES TOWARDS FLOWER COLOR MODIFICATION

Flavonoids are major contributors to flower coloration. As a result, most studies on genetic engineering of flower color have been carried out via the flavonoid biosynthetic pathway. One major approach is alteration of anthocyanin contents/composition. Other factors including copigments, vacular pH value and cell shape will also be described briefly. Recently, genetic engineering of flavonoids has been reviewed extensively (Forkmann and Martens 2001, Winkel-Shirley 2001, Schijlen *et al*. 2004, Tanaka *et al.* 2005), and here we summarize what we know in this field, and describe the recent progress and future prospects based on this information.

OVEREXPRESSING OR SILENCING THE STRUCTURAL GENE EXPRESSION IN FLAVONOID BIOSYNTHETIC PATHWAY

Chalcone synthase

So far, most efforts to modify flower color have focused on the general phenylpropanoid pathway, which produces *p*-coumaroyl-CoA and subsequently leads to the synthesis of anthocyanin pigments. An effective approach of pigment engineering is overexpressing or silencing the structural gene in the flavonoid biosynthetic pathway by transgenic technology. Chalcone synthase is the first key enzyme catalyzing 3 molecules of malonyl-CoA and 1 molecule of *p*-coumaroyl-CoA into 1 molecule of chalcone, which can be converted into other classes of flavonoids including anthocyanins. The CHS enzyme, usually found in plant epidermal

cells, has a molecular weight of about 42,000, requires no co-factors, and has been purified from various plant species. In addition, three-dimensional structure and functional studies of alfafa CHS enzyme have shown that four residues (Cys164, Phe215, His303, Asn336) in the catalytic site are responsible for decarboxylation and condensation reactions for this enzyme, and are highly conserved among different species. Thus, the gene encoding CHS enzyme is the major target for controlling flower color.

Chalcone isomerase

Chalcone isomerase (CHI) catalyzes yellow-colored chalcone to colorless pigment naringenin (or flavanone naringenin). This conversion can also occur spontaneously. Thus, most plants do not accumulate chalcones. However, some mutant plants accumulate chalcones due to mutation in the *chi* locus. Yellow flowers have been reported in *chi* mutants of aster and carnation (Schijlen *et al*. 2004). However, in comparison with the effectiveness of color modification by the *chs* transgene, production of yellow flowers by transforming with the *chi* construct and suppressing the endogenous *chi* expression has not been reported yet.

Flavanone hydroxylase/Flavonoid-3′-hydroxylase/Flavonoid-3′,5′-hydroxylase

The hydroxylation in position 3 of the C ring in flavanones, resulting in dihydroflavonols, has been demonstrated in various plant species. The reaction is carried out by flavanone-3-hydroxylase (F3H), a member of the 2-oxoglutarate-dependent dioxygenase family. In *Petunia* and Antirrhinum, mutation in *f3h* locus caused a loss of F3H activity and, as a result, white flowers are produced (Schijlen *et al*. 2004). The transgenic carnation plants carrying *f3h* antisense exhibited various degrees of flower color modifications, ranging from partial to complete loss of their original orange/reddish color (Zuker *et al*. 2002).

Dihydrokaempferol (DHK), the product catalyzed by F3H, can be further hydroxylated by the cytochrome P450 enzyme hydroxylase flavonoid-3′-hydroxylase (F3′H) at the 3′ position of the B-ring, leading to the formation of dihydroquercetin (DHQ) and subsequently to the production of cyanidin-based pigments (red to magenta). On the other hand, DHK can also be further hydroxylated by the cytochrome P450 enzyme flavonoid-3′,5′-hydroxylase (F3′5′H) at both 3′ and 5′ positions of the B-ring, leading to the formation of dihydromyricetin (DHM) and

subsequently to the production of delphinidin-based pigments (purple). Since F3′H and F3′5′H are the direct enzymes for synthesizing colored anthocyanins, various plant species including *Petunia*, tobacco, lisianthus, torenia and carnation with novel flower colors have been reported by transgenic approach (Forkmann and Martens 2001, Tanaka *et al*. 2005).

Dihydroflavonol-4-reductase

The enzyme dihydroflavonol-4-reductase (DFR) catalyzes the stereo specific reduction of dihydroflavonols to leucoanthocyanidins (flavan-3,4-diol). These leucoanthocyanidins are the immediate precursors for the synthesis of anthocyanins. Breeding of transgenic orange *Petunia* cultivars by expression of the maize *dfr* gene and further by traditional crossing-over hybridization has been reported (Oud *et al*. 1995). Transgenic tobacco plants carrying cranberry *dfr* gene produced much darker pink flowers than the controls (Polashock *et al*. 2002), and transgenic Petunia plants overexpressing sense *dfr* construct from *Petunia* caused production of anthocyanins, resulting in a pink flowers as compared to wild-type white flowers (Davies *et al*. 2003). Transgenic carnation plants carrying sense *dfr* and sense *f3′5′h* from *Petunia* produced violet flowers as compared to the wild-type white flowers (Forkmann and Martens 2001), and transgenic forsythia plants carrying sense *dfr* and sense *ans* produced brownish flowers as compared to wild-type yellow flowers (Forkmann and Martens 2001). In addition, transgenic torenia plants carrying sense or antisense *dfr* constructs suppressed the endogenous *dfr* expression and led to the production of flowers with pale blue or white color (Aida *et al*. 2000).

Anthocyanidin synthase

Anthocyanidin synthase (ANS) catalyzes leucoanthocyanidins into anthocyanidin. It is well demonstrated that ANS, FLS (flavonol synthase) and F3H are involved in the flavonoid biosynthesis in plants and are all members of the family of 2-oxoglutarate- and ferrous iron-dependent oxygenases; furthermore, ANS, FLS and F3H are closely related by sequence and catalyze oxidation of the C-ring in the flavonoid. They have been shown to have overlapping substrate and product selectivities (Turnbull *et al*. 2004). Nucleotide sequences encoding *ans* have been isolated in various plant species (Schijlen *et al*. 2004). More recently, Kim *et al*. (2005) reported that the *ans* gene in yellow onions showed a point mutation in comparison with red onions. However, application of transgenic *ans* to pigment modification is less reported.

Anthocyanidin 3-*O*-glucosyltransferase (Flavonoid 3-*O*-glucosyltransferase)

The enzyme UDP-glucose:anthocyanidin 3-*O*-glucosyltransferase [3GT; this enzyme is also known as UDP-glucose:flavonoid 3-*O*- glucosyltransferase (UFGT)] transfers the glucose moiety from UDP-glucose to C-3 hydroxyl group of the anthocyanidin, resulting the colored pigments of anthocyanidin 3-*O*-glucosides (**Fig. 3**). This enzyme is not only important for generation of colored pigments, it is also essential for stabilizing anthocyanidins so that they can accumulate as water soluble pigments in the vacuoles (Schijlen *et al*. 2004). Anthocyanidin 3-*O*-glucosides can be further modified with sugars, methyl groups, aliphatic acids and aromatic acids. In addition, there are both species- and variety-specific differences in the extent of modification and the types of glycosyl and acyl groups attached to the anthocyanidin cores (Tanaka *et al*. 2005). It is interesting to find that *dfr, ans* and *3gt*, the late genes in anthocyanin biosynthesis pathway, are co-regulated or may exist as a functional complex, since mutants with decreased DFR and ANS activities also show decreased 3GT activity (Hrazdina and Jensen 1992). Overexpression of snapdragon *3GT* cDNA in lisianthus plants producing novel anthocyanins and modifying flavonoid glycosylation and acylation have been reported (Markham 1995, Schwinn *et al*. 1997).

Other enzymes

In some species such as snapdragon, cosmos, coreopsis and dahlia, the first key product chalcone can be converted into aureusidin (yellow color) by aureusidin synthase (AS). DNA sequence analysis revealed that AS belongs to the plant polyphenol oxidase family and is responsible for flower coloration (Nakayama *et al*. 2000 2001). By contrast, yellow flowers in carnation are due to the presence of isosalipurposide, an end product catalyzed by UDP-glucose:tetrahydroxychalcone 2′-*O*-glucosyltransferase (C2′GT) from chalcone. Other classes of flavonoids, such as flavones can be converted from naringenin by flavone synthase (FNS) or flavonols can be converted from dihydroflavonols (i.e., dihydrokaempferol) by flavonol synthase, will be discussed later in the "copigments" sub-section of this chapter.

In addition, some species-specific enzymes involved in flavonoid biosynthetic pathway have been proven successful in pigment modification. One example is chalcone reductase (CHR), CHR is an enzyme that co-acts with chalcone synthase (CHS), catalyzing 1 molecule of

p-coumaroyl-CoA and 3 molecules of malonyl-CoA to produce 1 molecule of 4,2′,4′-trihydroxychalcone (isoliquiritigenin; yellow in color), which is a precursor of 5-deoxy-isoflavonoids. Introducing a *chr* cDNA from *Medicago* into two different lines of *Petunia*, flower color was changed from either white to pale yellow or deep purple to pale purple (Davies *et al*. 1998), and introducing a *chr* gene from *Pueraria montana* into tobacco plants, flower color was changed from pink to white-to-pink (Joung *et al*. 2003).

Transformation with multiple genes

Since the complexity of the flavonoid biosynthetic pathway, introduction of a single gene into plants may not affect the metabolic flow as well as flower color. Metabolic engineering of flower color by transforming multiple genes has been attempted and few examples are given as follows (Forkmann and Martens 2001): transgenic Petunia plants carrying sense *dfr* and sense *f3′5′h* altered flower color from white to violet, transgenic Forsythia plants carrying sense *dfr* from snapdragon and sense *ans* from *Mattiola* altered flower color from yellow to brownish, and transgenic *Dianthus* plants carrying sense *difF* and sense *f3′5′h* from *Petunia* altered flower color from deep red with pale pink rim to deep purple with pale purple rim. To generate potato tubers with increased levels of flavonoids and thus modified antioxidant capacity, transgenic potato plants carrying single (*chs, chi,* or *dfr*), double (*chi* and *dfr*) and triple (*chs, chi* and *dfr*) gene constructs and in either of two orientations, sense or antisense; it was found that the most effective in anthocyanin production in potato is the single construct containing sense *dfr* cDNA (Lukaszewicz *et al*. 2004).

GENERATION OF VARIEGATED FLOWERS BY USING TRANSPOSONS

The method of molecular breeding new varieties is mediated by transposable elements. Variegation in either flowers or leaves often attracts attention from consumers and thus variegated plants can create high value in the ornamental market. Variegated flowers have been observed in natural populations including *Petunia*, snapdragon, morning glory, azalea and others, and some of this variegation is caused by transposable elements. Insertion or excision of transposons in flavonoid biosynthetic genes or regulatory genes produces a mosaic or variegated phenotype whose pattern is dependent on the frequency and timing. In general, insertion of a flavonoid biosynthetic gene or regulatory gene results in white sectors of a colored background, and excision of such a transposon from a particular gene often leads to produce colored sectors

on a white background; the sizes of sectors are dependent on the timing of excision: early excision produces large sectors, and late excision produces tiny sectors (Iida *et al*. 2004, Tanaka *et al.* 2005). Variegated flowers have been studied in various plant species, including *Petunia* and morning glory (van Houwelingen *et al*. 1998, Iida *et al*. 1999 2004).

In higher plants, transposons can be classified into 3 groups: the *Ac/Ds* superfamily, the *En/Spm* superfamily, and the *Mu* family (Iida *et al*. 2004). In Japanese morning glory, two mutants carrying variegated flowers were caused by integration of *En/Spm* transposable elements into the *dfr* or *chi* gene; another mutant in the common morning glory bearing variegated flowers was caused by insertion of *Tip100*, belonging to the *Ac/Ds* family, into the *chi* gene (Iida *et al*. 1999). Insertions of a transposable element *dTdic1*, belonging to the *Ac/Ds* superfamily, in both *chi* and *dfr* genes were found in carnation cultivars bearing variegated flowers (Itoh *et al*. 2002). To evaluate the potential of using transposons as molecular tools in producing variegated flowers and to ensure the effectiveness of changing color patterns, a new strategy of employing transposons and regulatory genes was developed (Liu *et al*. 2001). In brief, the *Arabidopsis* transposon *Tag1* (3.3 kb) was inserted between the CaMV 35S promoter and the maize *R* gene of the plant expression vector pAL69, and the resulting expression vector was transformed into tobacco via *Agrobacterium*-mediated method. The transposon *Tag1* belongs to the *Ac* family and is an autonomous element active in *Arabidopsis*, tobacco and rice. Once the expression cassette is integrated into host plant genome, the regulatory *R* gene can be actively transcribed only when *Tag1* is excised, as a result, up-regulating the anthocyanin biosynthetic genes and accumulating pigments can be observed. Half of the transgenic tobacco plants had observable variegated flower patterns; moreover, each line had a different pattern (Liu *et al*. 2001). It will be interesting to see whether this system can also be applied to other ornamental plants to produce flowers with commercial value.

COLOUR MODIFICATION THROUGH ANTISENSE RNA AND RNAi TECHNOLOG

Antisense RNA technology: Antisense RNA is a single stranded RNA that is complementary to mRNA strand transcribed within a cell. They are introduced in a cell to inhibit the translation machinery by base pairing with the sense RNA activating RnaseH, to develop perticular novel transgenic**.**

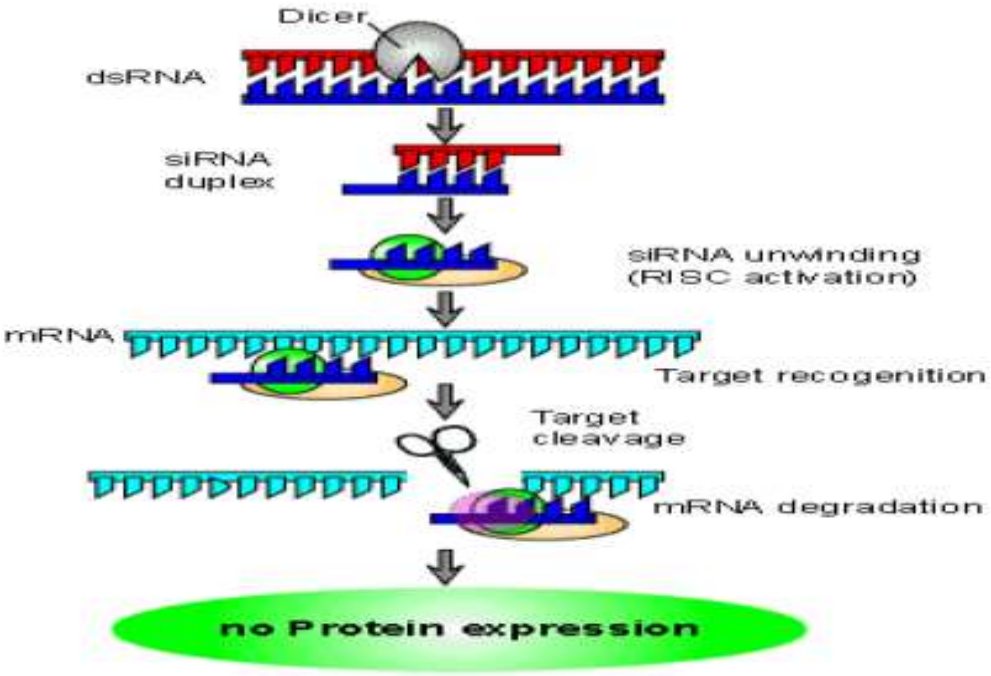
if mRNA sequence is **AUGAAACCCGUG**

then Antisence RNA **UACUUUGGGCAC**

RNAi technology : "The proces by which the dsRNA silence gene expression." RNAi is powerful biological process through which the small, double stranded RNAs specifically silence the expression of homologous genes, largely through degradation of congnate mRNA.

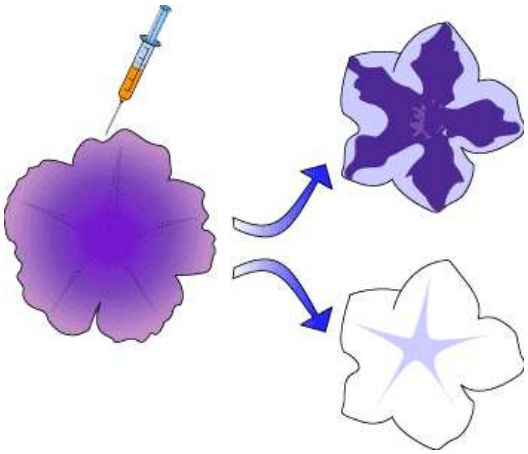
Mechanism

- Ds RNA are chopped in to short interfering RNA s (siRNA) by Dicer.
- The siRNA –Dicer complex is recruits to form an RNA Induced Silencing Complex (RISC).
- The siRNA unwinds .
- The unwond siRNA base pairs with complementory mRNA, thus guiding the RNAi machinery to the target mRNA.
- The target mRNA is effectively cleaved and subsequently degraded. Resulting in gene silencing.



RNAi was firstly discovered and observe in transcriptional inhibition by antisense RNA expressed in transgenic plants and more directly by reports of unexpected outcomes in

experiments performed in 1990s (Jorgensen *et al*.,). In an attempt to produce more intense purple coloured *Petunias*, researchers introduced additional copies of a transgene encoding chalcone synthase . But were surprised at the result that instead of a darker flower, the Petunias were variegated. This phenomenon was called co-suppression of gene expression , since both the expression of the existing gene (the initial purple colour) and the introduced gene/transgene (to deepen the purple) were suppressed. It was subsequently shown that suppression of gene activity could take place at the transcriptional level (transcriptional gene silencing, TGS) or at the post-transcriptional level (post-transcriptional gene silencing, PTGS.



Difference between antisense technology and RNAi

The intended effect in both will same i.e., gene silencing but the processing is little but different. Antisense technology degrades RNA by enzymes RNaseH while RNAi employed the enzyme DICER to degrade the mRNA. RNAi are twice larger than the antisense oligonucleotides.

CONCLUSION

Flower colour modification using molecular methods has now become reality .Flower colour is mainly determined by the ratio of different pigments and other factors such as vascular pH, co-pigments and metal ions.Knowledge at the biochemical and molecular level has made it

possible to develop novel colour which are otherwise absent in nature.Transgenic floricultural crops, only carnation and rose -commercialized, indicating development of commercial crops by GE is still very challenging.

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