

Chapter 16

The Specific Features of Anthocyanin Biosynthesis Regulation in Wheat

Olesya Y. Shoeva and Elena K. Khlestkina

Abstract Anthocyanins are flavonoid pigments important for plant adaptation under biotic and abiotic stress conditions. In bread wheat (*Triticum aestivum* L.), purple pigmentation caused by anthocyanins can be present on leaves, culm, auricles, glumes, grains, coleoptile, and anthers. Since the first mentions on expression of purple color traits in wheat, the studies into inheritance of these characters have made big steps toward revealing molecular-genetic mechanisms of anthocyanin pigment biosynthesis and its regulation in wheat. Most of the structural genes, encoding enzymes of the biosynthesis, have been cloned and localized in wheat genome. The genetic mapping data suggest that different pigmentation patterns in wheat are determined by genetic loci, distinct from the enzyme encoding loci. The data on functional role of the genes underpinning phenotypic variation together with results of inter-genera comparative mapping suggest these genes to encode transcriptional activators of the anthocyanin biosynthesis structural genes. Here, a brief review is provided of recent findings in the genetic regulation of anthocyanin biosynthesis in wheat.

Keywords Purple pigmentation • Comparative mapping • Regulatory genes • Structural genes • Transcription analysis • *Triticum aestivum* L

Introduction

Anthocyanin pigmentation of different parts of plants is related with their adaptation to environment stress conditions (reviewed by Chalker-Scott 1999; Khlestkina 2013a). In addition, anthocyanins are important for human health maintenance, preventing cardiovascular diseases, carcinogenesis, inflammation and many others human pathological states (Lila 2004). All these findings stimulated intensive investigations of different aspects of anthocyanin biosynthesis in plants, and nowadays,

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it is considered to be one of the best characterized secondary metabolite pathways (Winkel-Shirley 2001). Identification of the anthocyanin biosynthesis regulatory and structural genes in the model plant species (maize, *Arabidopsis*, snapdragon, and petunia) (Mol et al. 1998) facilitates homology-based cloning of their orthologues in cultivated species with complex genomes, such as bread wheat (*Triticum aestivum* L., $2n=6x=42$).

In wheat, purple colour of coleoptile, culm and anthers is reportedly related with resistance to bunt (Bogdanova et al. 2002). Comparative analysis of wheat near-isogenic lines differing by anthocyanin content in the coleoptile and pericarp showed higher drought tolerance of intensely colored seedlings (Tereshchenko et al. 2012a). The relationship between accumulation of anthocyanins in wheat coleoptiles and cold treatment has been shown (Gordeeva et al. 2013). Furthermore, the purple-grained NILs had better viability after accelerated ageing compared to the recurrent parent lacking anthocyanins (Gordeeva and Khlestkina 2013). The knowledge about specific features of anthocyanin biosynthesis regulation in wheat can be useful for improvement of its adaptation to biotic and abiotic stress conditions.

Structural Genes of Anthocyanin Biosynthesis in Wheat

The anthocyanin biosynthesis pathway (ABP) is one of the branches of the whole flavonoid biosynthesis pathway (Winkel-Shirley 2001). The genes encoding enzymes are referred as structural genes. Most structural genes needed for anthocyanin biosynthesis have been studied in wheat (Table 16.1).

Two copies of phenylalanine ammonia-lyase gene (*Pal*) have been isolated from the same phage clone of the wheat genomic library (Li and Liao 2003). A total of six loci for the *Pal* gene have been mapped to chromosomes of homoeologous group 3 and 6 using Southern blot hybridization method with the nucleotide sequence of the maize *Pal* gene as a probe (Li et al. 1999; Table 16.1). Similarly, six loci for the chalcone synthase gene (*Chs*) have been identified in homoeologous group 1 and 2 chromosomes (Li et al. 1999). Only four full-length nucleotide sequences of this gene have been isolated thus far (Yang et al. 2004).

Three loci for chalcone-flavanone isomerase (*Chi*) have been assigned to homoeologous group 5 chromosomes using Southern blot hybridization method with nucleotide sequence of the maize *Chi* gene as a probe (Li et al. 1999). One partial sequence of the *Chi* gene was reported by Himi et al. (2005). Then, three homoeologous full-length *Chi* copies were isolated and precisely mapped to the long arms of 5 group chromosomes (Shoeva et al. 2014a).

Four copies of the flavanone 3-hydroxylase (*F3h*) gene are present in wheat genome (Khlestkina et al. 2008, 2013; Himi et al. 2011). These copies have been mapped to chromosomes 2AL, 2BL (two copies) and 2DL (Khlestkina et al. 2011).

The genes for flavonoid 3'5'-hydroxylase (*F3'5'h*) and flavonoid 3'-hydroxylase (*F3'h*) belong to the gene family of cytochrome P450 monooxygenases (Tanaka

Table 16.1 Known structural genes encoding enzymes needed for anthocyanin biosynthesis in wheat

Gene	Cloning method	Number of cloning copies	GeneBank accession number, references	Mapping/ chromosome location, references
<i>Pal</i>	Phage library screening	2 full-length, genomic DNA	X99705 (Li and Liao 2003)	3A, 3B, 3D, 6A, 6B, 6D (Li et al. 1999)
<i>Chs</i>	Cloning of the PCR-product+RACE	4 full-length, cDNA	AY286093, AY286095, AY286096, AY286097 (Yang et al. 2004)	1A, 1B, 1D, 2A, 2B, 2D (Li et al. 1999)
<i>Chi</i>	Cloning of the PCR-product	3 full-length, genomic DNA	AB187026 (Himi et al. 2005); JN039037, JN039038, JN039039 (Shoeva et al. 2014a)	5AL, 5BL, 5DL (Li et al. 1999; Shoeva et al. 2014a)
<i>F3h</i>	Cloning of the PCR-product	4 full-length, genomic DNA	EF463100, DQ233636, EU402957, EU402958 (Khlestkina et al. 2008); AB223024, AB223025, AB223026 (Himi et al. 2011); JN384122 (Khlestkina et al. 2013)	2AL, 2BL (2 genes), 2DL (Himi et al. 2011; Khlestkina et al. 2011)
<i>F3'5'h</i>	Cloning of the PCR-product	1 partial, cDNA	AY519468 (Yang et al. 2004)	–
<i>Dfr</i>	Cloning of the PCR-product+RACE	3 full-length, cDNA	AB162138, AB162139, AB162140 (Himi and Noda 2004)	3AL, 3BL, 3DL (Himi and Noda 2004)
<i>Ans</i>	Cloning of the PCR-product+RACE	5 full-length, cDNA	AB247917, AB247918, AB247919, AB247920, AB247921 (Himi et al. 2006)	6AS (2 genes), 6BS (2 genes), 6DS (Himi et al. 2006)
<i>Ufgt</i>	Cloning of the PCR-product	1 partial, genomic DNA	– (Ahmed et al. 2006)	–
<i>3Rt</i>	Cloning of the PCR-product	2 partial, genomic DNA	EU815627 (Khlestkina et al. 2009b)	5BL, 5DL (Khlestkina et al. 2009b and unpublished)

et al. 2009). There are no data on cloning and/or mapping of these genes in wheat with the exception of one partial nucleotide sequence of *F3'5'h* (Yang et al. 2004).

Three copies of the dihydroflavonol-4-reductase gene (*Dfr*) have been isolated from wheat genome and localized in homoeologous group 3 chromosomes (Himi and Noda 2004). Five copies of the anthocyanidin synthase gene (*Ans*) assigned to chromosomes 6A (two copies), 6B (two copies) and 6D (one copy) have been sequenced (Himi et al. 2006).

The genes participating at the latest stages of anthocyanin biosynthesis encode for different transferase enzymes. From these genes, only two have been partially isolated from wheat genome thus far: UDP-glucose: flavonoid 3-*O*-glucosyltransferase (*Ufgt*; Ahmed et al. 2006) and UDP-rhamnose:anthocyanidin-3-glucoside

rhamnosyltransferase gene (*3Rt*; Khlestkina et al. 2009b). Two *3Rt* gene copies have been mapped to chromosomes 5BL and 5DL (Khlestkina et al. 2009b; unpublished results).

The genetic mapping data suggest that the ABP structural genes locations (Table 16.1) are different from that of the genes underpinning phenotypic variation in coloration traits (see below).

Genes Determining Anthocyanin Pigmentation in Different Parts of Wheat Plant

In bread wheat, anthocyanin pigments determine purple (culm, leaf blades, leaf sheaths, glumes, anthers, and grain pericarp), red/purple (coleoptile and auricles) or blue (aleurone layer) coloration (Fig. 16.1). Most genes determining anthocyanin pigmentation of different parts of wheat plant have been already identified and mapped (Khlestkina 2013b; McIntosh et al. 2013).

Mapping of the Genes Determining Anthocyanin Pigmentation Traits

Three genes for red coleoptile (*Rc*) localized on chromosomes 7A (Sears 1954), 7B (Gale and Flavell 1971), and 7D (Jha 1964) have been precisely mapped in homoeologous positions of the chromosome arms 7AS, 7BS, and 7DS and designated *Rc-A1*, *Rc-B1*, and *Rc-D1*, respectively (Khlestkina et al. 2002). Three homoeologous genes for purple culm (*Pc-A1*, *Pc-B1*, *Pc-D1*), three homoeologues for purple leaf sheaths (*Pls-A1*, *Pls-B1*, *Pls-D1*) and three homoeologues for purple leaf blades (*Plb-A1*, *Plb-B1*, *Plb-D1*) have been mapped in close linkage with red coleoptile genes *Rc-A1*, *Rc-B1*, and *Rc-D1* (Khlestkina et al. 2009a, 2010b). Two genes determining purple anther (*Pan-A1* and *Pan-D1*) have been mapped on chromosomes 7A (Blanco et al. 1998) and 7D (Khlestkina et al. 2009a) at a short distance from *Rc-A1* and *Rc-D1*, respectively.

Two complementary genes for purple pericarp, *Pp1* and *Pp3*, have been mapped in chromosomes 7B and 2A of bread (Arbuzova et al. 1998; Dobrovolskaya et al. 2006) and durum (Khlestkina et al. 2010a) wheat. For the durum gene *Pp1* (*Pp-B1*), the homoeologue has been identified on chromosome 7D (*Pp-D1*) of bread wheat (Tereshchenko et al. 2012b). They have been mapped on the short arms of chromosomes 7B and 7D close to the *Rc-B1* and *Rc-D1*, respectively. The *Pp3* gene of durum wheat is closely linked to the gene for purple glume (*Pg*), however, unlike purple pericarp, the purple glume color is a monogenically inherited trait (Khlestkina et al. 2010a).

Chromosome locations and a number of the genes for red auricles (*Ra*) still remain a matter of contention. The genes determining this trait have been assigned

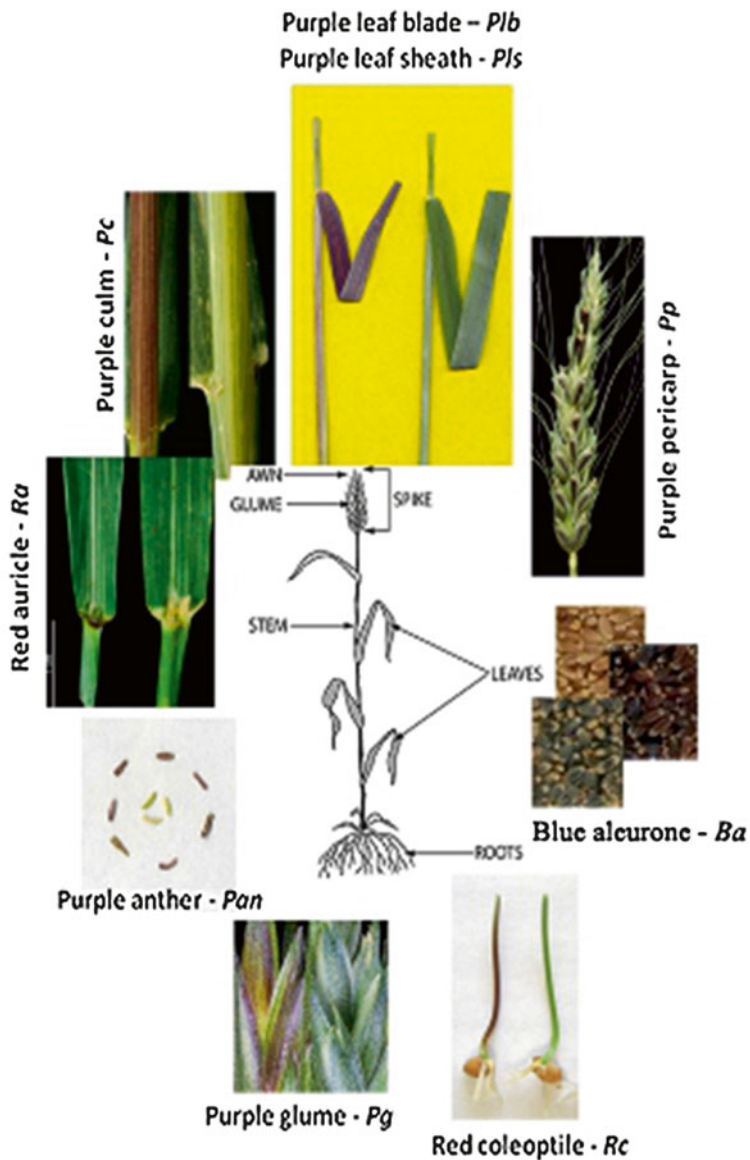


Fig. 16.1 Anthocyanin pigmentation of different parts of wheat plant. The picture was taken from (Khlestkina 2012) with modifications

to chromosomes 7A and 7D (Jha 1971), 1D (Gulyaeva 1984), 4B or 6B (Melz and Thiele 1990). None of these loci has been mapped. The reason for inconsistency in determining chromosome location and inability of mapping of the *Ra* genes is unstable expression of this trait. Near-isogenic lines and modern DNA-based genotyping approaches provide a powerful means of chromosome localization and fine mapping of genes with unstable expression. Using this approach we localized recently the gene *Ra-D1* in a vicinity of *Rc-D1* on chromosome 7DS (Khlestkina et al. 2014). There is a good agreement between our data and that reported by Jha (1971).

The blue aleurone (*Ba*) color had been inherited by wheat from its related species (Zeven 1991). For instance, the *Ba* genes have been identified in *Thynopirum ponticum* (*Ba1*; Keppenne and Baenziger 1990), *Th. bessarabicum* (*BaThb*; Shen et al. 2013), *T. monococcum* (*Ba2*; Dubcovsky et al. 1996), *T. boeoticum* (*Ba2*; Singh et al. 2007). In blue-grained wheat lines, alien substitutions or introgressions into homoeologous group 4 chromosomes are usually observed (Zeven 1991; Arbutova et al. 2012; Shen et al. 2013).

Comparative mapping data in wheat, rice, and maize indicate that loci for anthocyanin pigmentation, mapped to homoeologous group 7 chromosomes, are orthologous to the maize gene *Cl* and rice gene *OsCl*, encoding Myb-like transcription activators of anthocyanin biosynthesis (Saitoh et al. 2004; Khlestkina 2013b). Furthermore, the maize *Cl* gene was used as a probe in Southern hybridization-based mapping in wheat, and its homologue has been mapped to chromosome 7D (Li et al. 1999) in position highly comparable with that of the wheat *Rc/Pc/Pls/Plb/Pan/Pp1* genic cluster.

Similarly, comparative mapping data demonstrate that the wheat *Pp3* gene is orthologous to rice *Pb1Ra* (Hu et al. 1996; Wang and Shu 2007) and maize *Lc1R* (Ludwig et al. 1989), encoding Myc-like protein needed for anthocyanin biosynthesis regulation. Recently nucleotide sequence of the candidate gene for *Pp3* was isolated from wheat genome (Shoeva et al. 2014b).

Thus, the inter-genera comparative mapping suggests the anthocyanin biosynthesis genes on homoeologous group 7 chromosomes to encode Myb-like (C1-like) regulatory factors and that on chromosome 2A to encode Myc-like regulatory factors. Following this suggestion, the effect of different alleles of the *Rc*, *Pc*, *Pls*, *Plb*, and *Pp* genes on transcriptional activity of the ABP structural genes was investigated using wheat precise genetic stocks (see below).

Transcriptional Analysis of Anthocyanin Biosynthesis Structural Genes in Different Wheat Organs

Using comparative transcriptional approach, regulatory role of the genes, determining anthocyanin pigmentation of wheat organs, has been investigated. Ahmed et al. (2006) compared expression of the ABP structural genes in the red and green coleoptiles of the chromosome substitution line 'Chinese Spring' ('Hope' 7A) and cv.

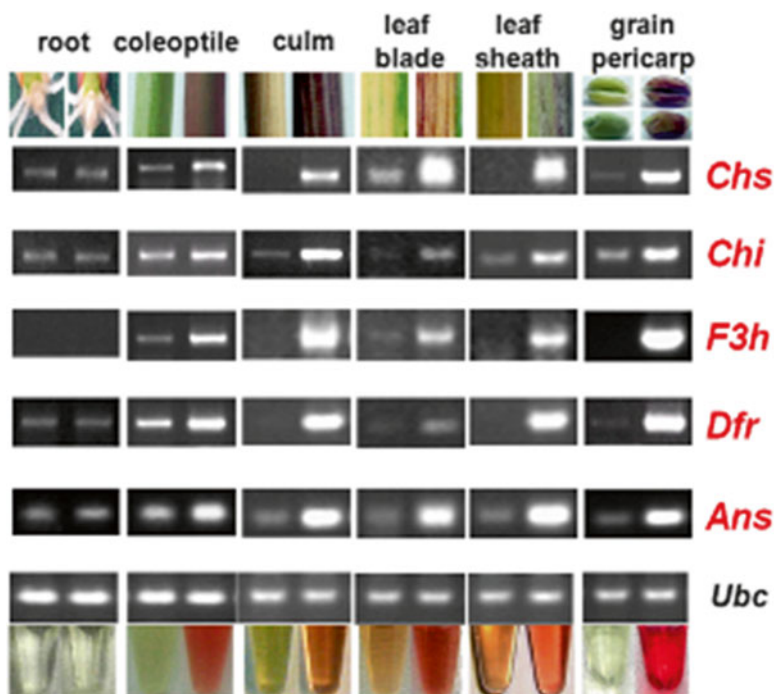


Fig. 16.2 RT-PCR analysis of the anthocyanin biosynthesis structural genes in different organs of wheat ‘Saratovskaya 29’ (left in each pair) and its near-isogenic line ‘i:S29Pp1Pp3^P’ (right in each pair). Anthocyanin extracts from the corresponding organs are shown below. *Ubc* (ubiquitin) – endogenous control

‘Chinese Spring’, respectively, and concluded that the *Rc-A1* gene activates expression of the structural genes *Dfr*, *Ans*, and *Ufgt*. Later the regulatory role of the *Rc-A1*, *Rc-B1*, and *Rc-D1* genes has been demonstrated using a wide range of wheat precise genetic stocks: near-isogenic and introgression lines, chromosome substitution and recombinant lines (Khlestkina et al. 2008, 2010b; Tereshchenko et al. 2013). In addition, it has been found that multiple dominant alleles of the same regulatory gene (*Rc-A1*) have different effects on dynamics and intensity of the structural gene expression (Khlestkina et al. 2010b).

Regulatory role of the *Pc*, *Pls*, *Plb*, and *Pp* genes has been demonstrated using near-isogenic lines (Fig. 16.2; Tereshchenko et al. 2013). It has been noted that the *F3h* gene is expressed only in colored tissues and is not expressed in non-colored ones such as roots of both lines or pericarp of ‘Saratovskaya 29’ (Fig. 16.2). The other structural genes are still transcribed in the absence of anthocyanin pigments, but at the lower level in comparison with the intensively colored tissues (Fig. 16.2; Tereshchenko et al. 2013). This specific regulation of *F3h* was also observed earlier by Khlestkina et al. (2009b) in coleoptiles of wheat-rye addition lines.

In some plant species, the whole set of anthocyanin biosynthesis genes is regulated as a single unit (Dooner 1983; Meldgaard 1992; Mato et al. 2000; Honda et al. 2002; Mano et al. 2007). In other plant species, anthocyanin biosynthesis can be regulated at different stages of the pathway (Boss et al. 1996; Ramazzotti et al. 2008; Zhao et al. 2012). However, the regulation of the anthocyanin biosynthesis at the stage of the *F3h* gene expression has been observed in wheat only and this may be a species-specific peculiarity of the anthocyanin biosynthesis regulation in *Triticum*. Such peculiarities of flavonoid biosynthesis regulation provide a basis for taxonomic distinguishing among plants (Bell 1980). However, biological meaning of the flavonoid biosynthesis interruption in non-colored tissues of wheat at the stage of F3H enzyme action, when flavanones are converted to dihydroflavonols, is not clear yet.

Conclusion

Anthocyanin pigments are reportedly the universal defense compounds produced in response to a wide range of biotic and abiotic stress factors. Most of the regulatory and structural anthocyanin biosynthesis genes have been mapped in wheat. The majority of the structural ABP genes and one of the two complementary genes determining purple grain trait have been sequenced. The other regulatory genes can be isolated and sequenced in the near future based on the data provided from investigations of their functions and from inter-genera comparative mapping. The knowledge of genetic basis of anthocyanins biosynthesis in wheat and the availability of wheat precise genetic stocks provide a highly appropriate basis for exploring the changes in expression of the ABP genes under stress conditions. These data will be useful in future for improvement wheat adaptation properties.

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