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
Pal	Phage library screening	2 full-length, genomic DNA	X99705 (Li and Liao 2003)	3A, 3B, 3D, 6A, 6B, 6D (Li et al. 1999)
Chs	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)
Chi	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)
F3h	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)
F3'5'h	Cloning of the PCR-product	1 partial, cDNA	AY519468 (Yang et al. 2004)	–
Dfr	Cloning of the PCR-product + RACE	3 full-length, cDNA	AB162138, AB162139, AB162140 (Himi and Noda 2004)	3AL, 3BL, 3DL (Himi and Noda 2004)
Ans	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)
Ufgt	Cloning of the PCR-product	1 partial, genomic DNA	– (Ahmed et al. 2006)	–
3Rt	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

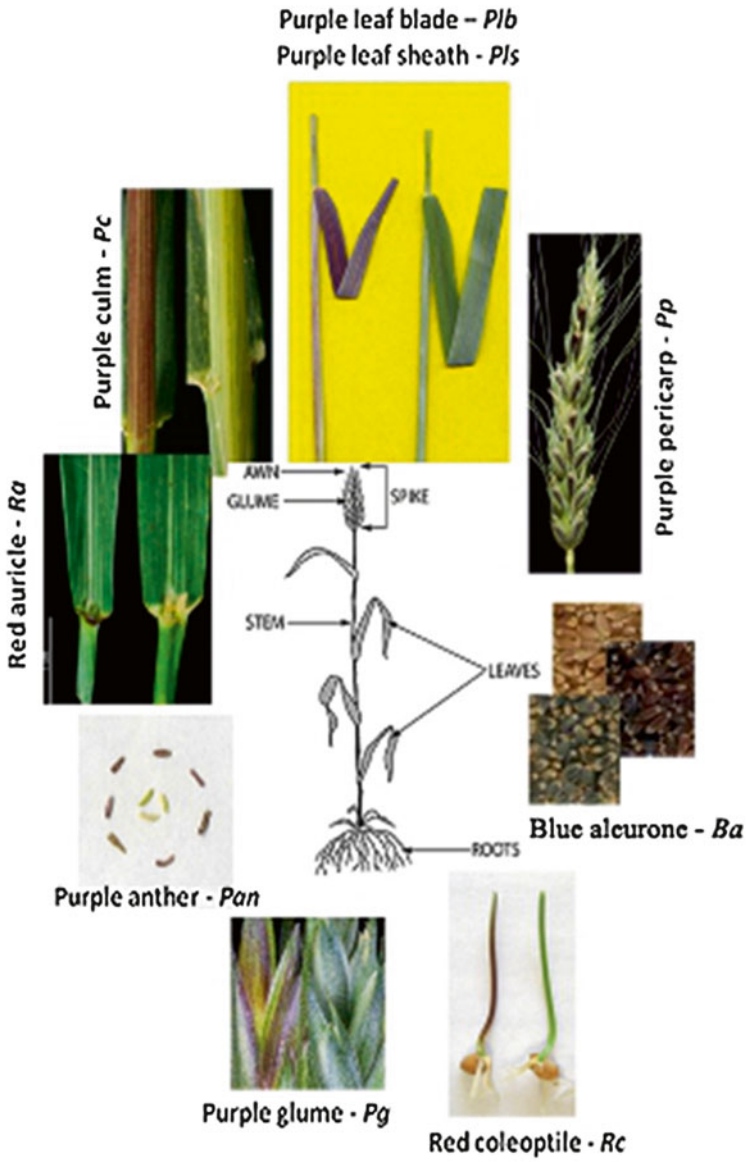

Fig. 16.1 Anthocyanin pigmentation of different parts of wheat plant. The picture was taken from (Khlestkina 2012) with modifications

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; Arbuzova 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 *C1* and rice gene *OsC1*, encoding Myb-like transcription activators of anthocyanin biosynthesis (Saitoh et al. 2004; Khlestkina 2013b). Furthermore, the maize *C1* 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 *Pb* /*Ra* (Hu et al. 1996; Wang and Shu 2007) and maize *Lc* /*R* (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.

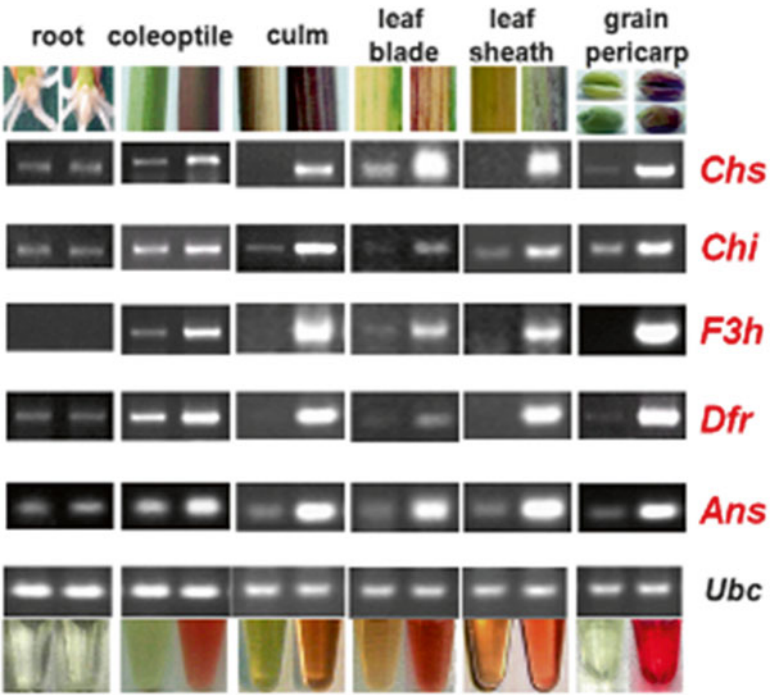

Fig. 16.2 RT-PCR analysis of the anthocyanin biosynthesis structural genes in different organs of wheat 'Saratovskaya 29' (*left* in each pair) and its near-isogenic line 'i:S29Pp1Pp3^{P}' (*right* in each pair). Anthocyanin extracts from the corresponding organs are shown below. *Ubc* (ubiquitin) –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

Ahmed N, Maekawa M, Utsugi S et al (2006) The wheat *Rc* gene for red coleoptile colour codes for a transcriptional activator of late anthocyanin biosynthesis genes. J Cereal Sci 44:54–58

Arbuzova VS, Maystrenko OI, Popova OM (1998) Development of near-isogenic lines of the common wheat cultivar 'Saratovskaya 29'. Cereal Res Commun 26:39–46

Arbuzova VS, Badaeva ED, Efremova TT et al (2012) A cytogenetic study of the blue-grain line of the common wheat cultivar Saratovskaya 29. Russ J Genet 48:785–791

Bell EA (1980) The possible significance of secondary compounds in plant. In: Bell EA, Charlwood BV (eds) Secondary plant products. Springer, New York

Blanco A, Bellomo MP, Cenci A et al (1998) A genetic linkage map of durum wheat. Theor Appl Genet 97:721–728

Bogdanova ED, Sarbaev AT, Makhmudova KK (2002) Resistance of common wheat to bunt. In: Proceedings of the research conference on genetics, Moscow

Boss PK, Davies C, Robinson SP (1996) Expression of anthocyanin biosynthesis genes in red and white grapes. Plant Mol Biol 32:565–569

Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. Photochem Photobiol 70:1–9

Dobrovolskaya OB, Arbuzova VS, Lohwasser U et al (2006) Microsatellite mapping of complementary genes for purple grain colour in bread wheat (*Triticum aestivum* L.). Euphytica 150:355–364

Dooner HK (1983) Coordinate genetic regulation of flavonoid biosynthetic enzymes in maize. Mol Gen Genet 189:136–141

Dubcovsky J, Luo MC, Zhong GY et al (1996) Genetic map of diploid wheat, *Triticum monococcum* L., and its comparison with maps of *Hordeum vulgare* L. Genetics 143:983–999

Gale MD, Flavell RB (1971) The genetic control of anthocyanin biosynthesis by homoeologous chromosomes in wheat. Genet Res Camb 18:237–244

Gordeeva EI, Khlestkina EK (2013) Relationship between accumulation of anthocyanins in wheat pericarp and response to artificial ageing of seeds. In: Abstracts of conference free radicals and antioxidants in chemistry, biology and medicine, Novosibirsk (in Russian)

Gordeeva EI, Shoeva OY, Khlestkina EK (2013) Cold stress response of wheat genotypes having different *Rc* alleles. Cereal Res Commun 41:519–526

Gulyaeva ZB (1984) Localization of the genes for pubescence of the glumes and coloration of the auricles in the leaf sheath in winter wheat variety Ul'yanovka. Bull Appl Bot Genet Plant Breed 85:95–96

Himi E, Noda K (2004) Isolation and location of three homoeologous dihydroflavonol-4-reductase (DFR) genes of wheat and their tissue-dependent expression. J Exp Bot 55:365–375

Himi E, Nisar A, Noda K (2005) Colour genes (*R* and *Rc*) for grain and coleoptile upregulate flavonoid biosynthesis genes in wheat. Genome 48:747–754

Himi E, Osaka T, Noda K (2006) Isolation and characterization of wheat ANS genes. GenBank. http://www.ncbi.nlm.nih.gov/sites/entrez?term=himi%20osaka%20noda&cmd=Search&db=nuccore&QueryKey=4

Himi E, Maekawa M, Noda K (2011) Differential expression of three flavanone 3-hydroxylase (F3H) genes in grains and coleoptiles of wheat. Int J Plant Genomics 369460. doi:10.1155/2011/369460

Honda C, Kotoda N, Wada M et al (2002) Anthocyanin biosynthetic genes are coordinately expressed during red coloration in apple skin. Plant Physiol Biochem 40:955–962

Hu J, Anderson B, Wessler R (1996) Isolation and characterization of rice *R* genes: evidence for distinct evolutionary paths in rice and maize. Genetics 142:1021–1031

Jha KK (1964) The association of a gene for purple coleoptile with chromosome 7D of common wheat. Can J Genet Cytol 6:370–372

Jha KK (1971) Summary of aneuploid studies. In: Law CN (ed) Proceedings of the 2nd EWAC conference, European wheat aneuploid co-operative newsletter, vol 3. Weihenstephan, pp 58–59

Keppenne VD, Baenziger S (1990) Inheritance of the blue aleurone trait in diverse wheat crosses. Genome 33:525–529

Khlestkina EK (2012) Genes determining coloration of different organs in wheat. Vavilovskii Zhurnal Genetiki i Selektsii – Vavilov Journal of Genetics and Breeding 16:202–216

Khlestkina EK (2013a) The adaptive role of flavonoids: emphasis on cereals. Cereal Res Commun 41:185–198
Khlestkina EK (2013b) Genes determining coloration of different organs in wheat. Russ J Genet Appl Res 3:54–65
Khlestkina EK, Pestsova EG, Röder MS et al (2002) Molecular mapping, phenotypic expression and geographical distribution of genes determining anthocyanin pigmentation of coleoptiles in wheat (*Triticum aestivum* L.). Theor Appl Genet 104:632–637
Khlestkina EK, Röder MS, Salina EA (2008) Relationship between homoeologous regulatory and structural genes in allopolyploid genome – a case study in bread wheat. BMC Plant Biol 8:88
Khlestkina EK, Pshenichnikova TA, Röder MS et al (2009a) Clustering anthocyanin pigmentation genes in wheat group 7 chromosomes. Cereal Res Commun 37:391–398
Khlestkina EK, Tereshchenko OY, Salina EA (2009b) Anthocyanin biosynthesis genes location and expression in wheat-rye hybrids. Mol Genet Genomics 282:475–485
Khlestkina EK, Röder MS, Börner A (2010a) Mapping genes controlling anthocyanin pigmentation on the glume and pericarp in tetraploid wheat (*Triticum durum* L.). Euphytica 171:65–69
Khlestkina EK, Röder MS, Pshenichnikova TA et al (2010b) Functional diversity at the *Rc* (red coleoptile) gene in bread wheat. Mol Breed 25:125–132
Khlestkina E, Salina E, Matthies I et al (2011) Comparative molecular marker-based genetic mapping of flavanone 3-hydroxylase genes in wheat, rye and barley. Euphytica 179:333–341
Khlestkina EK, Dobrovolskaya OB, Leonova IN et al (2013) Diversification of the duplicated *F3h* genes in Triticeae. J Mol Evol 76:261–266
Khlestkina EK, Gordeeva EI, Arbuzova VS (2014) Molecular and functional characterization of wheat near-isogenic line 'i:S29Ra' having intensive anthocyanin pigmentation of the coleoptile, culm, leaves and auricles. Plant Breed 133:454–458
Li HP, Liao YC (2003) Isolation and characterization of two closely linked phenylalanine ammonia-lyase genes from wheat. Yi Chuan Xue Bao 30:907–912
Li WL, Faris JD, Chittoor JM et al (1999) Genomic mapping of defense response genes in wheat. Theor Appl Genet 98:226–233
Lila AM (2004) Anthocyanins and human health: an in vitro investigative approach. J Biomed Biotechnol 5:306–313
Ludwig SR, Habera LF, Dellaporta SL et al (1989) *Lc*, a member of the maize *R* gene family responsible for tissue-specific anthocyanin production, encodes a protein similar to transcription activators and contains the myc-homology region. Proc Natl Acad Sci U S A 86:7092–7096
Mano H, Ogasawara F, Sato K et al (2007) Isolation of a regulatory gene of anthocyanin biosynthesis in tuberous roots of purple-fleshed sweet potato. Plant Physiol 143:1252–1268
Mato M, Onozaki T, Ozeki Y et al (2000) Flavonoid biosynthesis in white-flowered Sim carnations (*Dianthus caryophyllus*). Sci Hortic 84:333–347
McIntosh RA, Yamazaki Y, Dubcovsky J et al (2013) Catalogue of gene symbols for wheat. http://www.shigen.nig.ac.jp/wheat/komugi/genes/download.jsp
Meldgaard M (1992) Expression of chalcone synthase, dihydroflavonol reductase, and flavanone-3-hydroxylase in mutants of barley deficient in anthocyanin and proanthocyanidin biosynthesis. Theor Appl Genet 83:695–706
Melz G, Thiele V (1990) Chromosome locations of genes controlling 'purple leaf base' in rye and wheat. Euphytica 49:155–159
Mol J, Grotewold E, Koes R (1998) How genes paint flowers and seeds. Trends Plant Sci 3:212–217
Ramazzotti S, Filippetti I, Intrieri C (2008) Expression of genes associated with anthocyanin synthesis in red-purplish, pink, pinkish-green and green grape berries from mutated 'Sangiovese' biotypes: a case study. Vitis 47:147–151
Saitoh K, Onishi K, Mikami I et al (2004) Allelic diversification at the *C1* (*OsC1*) locus of wild and cultivated rice: nucleotide changes associated with phenotypes. Genetics 168:997–1007
Sears ER (1954) The aneuploids of common wheat. Univ Mo Agr Exp Sta Res Bul 572:1–59

Shen Y, Shen J, Dawadondup et al (2013) Physical localization of a novel blue-grained gene derived from *Thinopyrum bessarabicum*. Mol Breed 31:195–204

Shoeva OY, Khlestkina EK, Berges H et al (2014a) The homoeologous genes encoding chalcone-flavanone isomerase in *Triticum aestivum* L.: structural characterization and expression in different parts of wheat plant. Gene 538:334–341

Shoeva OY, Gordeeva EI, Khlestkina EK (2014b) The regulation of anthocyanin synthesis in the wheat pericarp. Molecules 19:20266-20279

Singh K, Ghai M, Garg M et al (2007) An integrated molecular linkage map of diploid wheat based on a *Triticum boeoticum* x *T. monococcum* RIL population. Theor Appl Genet 115:301–312

Tanaka Y, Brugliera F, Chandler S (2009) Recent progress of flower colour modification by biotechnology. Int J Mol Sci 10:5350–5369

Tereshchenko OY, Khlestkina EK, Gordeeva EI et al (2012a) Relationship between anthocyanin biosynthesis and abiotic stress in wheat. In: Börner A, Kobijlski B (eds) Proceedings of the 15th international EWAC conference, vol 15. European cereals genetics co-operative newsletter, Novi Sad, pp 72–75

Tereshchenko OY, Gordeeva EI, Arbuzova VS et al (2012b) The D genome carries a gene determining purple grain colour in wheat. Cereal Res Commun 40:334–341

Tereshchenko OY, Arbuzova VS, Khlestkina EK (2013) Allelic state of the genes conferring purple pigmentation in different wheat organs predetermines transcriptional activity of the anthocyanin biosynthesis structural genes. J Cereal Sci 57:10–13

Wang C, Shu Q (2007) Fine mapping and candidate gene analysis of purple pericarp gene *Pb* in rice (*Oryza sativa* L.). Chinese Sci Bull 52:3097–3104

Winkel-Shirley B (2001) Flavonoid biosynthesis. A colorful model for genetics, biochemistry, cell biology and biotechnology. Plant Physiol 126:485–493

Yang G, Li B, Gao J et al (2004) Cloning and expression of two chalcone synthase and a flavonoid 3′5′-hydroxylase 3′-end cDNAs from developing seeds of blue-grained wheat involved in anthocyanin biosynthetic pathway. J Integr Plant Biol 46:588–594

Zeven AC (1991) Wheats with purple and blue grains: a review. Euphytica 56:243–258

Zhao ZC, Hu GB, Hu FC et al (2012) The UDP glucose: flavonoid-3-*O*-glucosyltransferase (UFGT) gene regulates anthocyanin biosynthesis in litchi (*Litchi chinesis* Sonn.) during fruit coloration. Mol Biol Rep 39:6409–6415