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Molecular Genetic Mechanisms of the Development of Fruit and Seed Coloration in Plants

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Abstract—The diverse coloration of plant fruits and seeds is determined by the presence of two important types of pigments, carotenoids (red, orange, yellow) and anthocyanins (purple, blue, red). They belong to two groups of secondary metabolites (isoprenoids and flavonoids). Recently, increased interest in the study of genetic mechanisms controlling coloration traits in plants is observed due to the antioxidant and antimicrobial properties of certain pigments and their colorless precursors consumed with plant food. The genes encoding enzymes required for successive transformations of the initial organic molecules in the final pigment compounds are referred to as the group of structural genes. The factors activating the expression of the structural genes and controlling the synthesis of certain pigments at a particular time in certain part of the plant are referred to as regulatory biosynthesis genes. The data accumulated in the field of plant genetics indicate that the interspecific and intraspecific diversity by the coloration traits (observed at the phenotypical level) is associated with regulatory genes. The creation of rich collections and accurate genetic models by the coloration traits in dicotyledonous and monocotyledonous plants in previous years, as well as the development of molecular genetic methods of plant research, allowed to study in detail the mechanisms of the genetic regulation of the synthesis of pigment compounds at the molecular level. In this article, the peculiarities of regulating carotenoid biosynthesis are illustrated on the example of their production in fruits of the Solanaceae family. Genetic regulation of the synthesis of different flavonoid pigments is demonstrated on the example of the study of the seed coloration in the Poaceae family plants. The prospects of the practical use of regulatory genes controlling the fruit and seed coloration are discussed in the final part of the work; specific examples of their use in breeding of vegetable and cereal crops are given.

Keywords: plants, pigmentation, secondary metabolites, flavonoids, carotenoids, antioxidants, regulatory genes, marker-assisted selection, Solanaceae, Poaceae

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INTRODUCTION

Along with chlorophyll conferring the green color, a number of other organic pigments creating a wide spectrum (from yellow to bright red and blue–black tints) are developed by the plants. Carotenoids (yellow, orange, and red pigments) relating to isoprenoids and anthocyanins (red, blue, and purple pigments), compounds of a phenolic nature, are the most widespread classes of pigment compounds. Along with carotenoids, a yellow or orange tint can be conferred to different plant parts by aurones, flavones, flavonols, flavonol glycosides, and anthocyanidins that refer to the phenolic compounds (flavonoids), as well as anthocyanins. The reddish brown or dark brown color of the plant seeds is caused by the flavonoid compounds (proanthocyanidins and phlobaphenes). The typical edible root color in the beet is associated with the synthesis of specific pigments (betalains). Finally, the black color of the seeds in some plants (for example, sunflower) is caused by melanin–like plant pigments, which have not been sufficiently studied (Zaprometov, 1974; Britton, 1983; Strack et al., 2003; Jana and Mukherjee, 2014).

A high degree of variability in terms of the plant color is caused by the diversity of the genetic mechanisms determining both the type of accumulated pigment and the place of its synthesis. The phenotypic diversity by the coloration traits can be illustrated on the example of barley (Fig. 1a) and wheat (Fig. 1b). In particular, it was demonstrated that the same group of pigments (anthocyanins) during the synthesis in different tissues under the effect of tissue-specific regulatory mechanisms results in the development of different coloration traits (for example, the blue-grain and purple-grain traits in wheat (Fig. 1b).

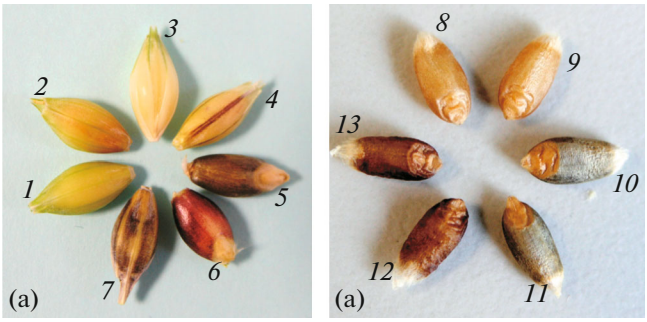

Fig. 1. Different types of caryopsis coloration in the isogenic lines of barley (a) and wheat (b) based on Bowman and Saratovskaya 29 varieties, respectively. *1*, Bowman variety; Bowman variety lines: *2*, with orange coloration of flowering scale due to violation in lignin synthesis; *3*, with white color of the scale and pericarp due to violation in chlorophyll synthesis; *4*, with red lemma midrib because of the synthesis of anthocyanins; *5*, *6*, with gray–blue and red (purple) grain coloration due to the synthesis of anthocyanins in aleurone layer and pericarp, respectively; *7*, with black coloration of pericarp and lemma due to unstudied pigments (presumably, melanin-like plant pigments); *8*, *9*, Saratovskaya 29 variety having reddish–brown tint of the grain due to the synthesis of proanthocyanidins in the seed coat; *10*, *11*, the line with gray–blue coloration of the grain due to the synthesis of anthocyanins in aleurone layer (blue grain trait); *12*, *13*, the line with purple grain coloration due to the synthesis of anthocyanins in pericarp (purple grain trait). (The barley seeds were kindly provided by Dr. A. Borner, IPK-Gatersleben, Germany; the wheat seeds, from the work collection of the Sector of Functional Genetics of Cereals, Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences; the photograph was taken by the authors).

The photoprotective function directed on the protection of the plant cell structures from the damaging effect of ultraviolet radiation is the main function of pigments. The function of pigments for the supply of visual signals is also important: the flower color is used to attract pollinator insects, while the fruit color is used to attract the seed spreader animals (Britton, 1983; Clegg and Durbin, 2000; Sasaki and Takahashi, 2002; Khlestkina, 2013).

For humans, the study of coloration in plants is of interest not only in terms of visual and aesthetic evaluation but also due to the effect of pigment compounds on the taste qualities of the consumed plant products. However, recently, the constantly growing attention paid to this area of study has been associated with the antioxidant and antimicrobial properties of certain enzymes and their colorless precursors consumed within plant food. These compounds prevent cancer, reduce the risk of cardiovascular diseases and atherosclerosis, increase immunity, improve the synthesis of visual pigments, activate metabolic processes, etc. (Middleton et al., 2000; Johnson, 2002; Lila, 2004).

The large diversity of the biochemical composition and plant coloration is provided by a complex of genes encoding the enzymes required for successive transformations of the initial organic molecules in the final pigment compounds and their synthesis at a certain time in the required part of the plant. The genes encoding enzymes should be attributed to structural genes. The regulatory genes activating the expression of structural genes are another group of genes. The accumulated data indicate that the interspecific and intraspecific diversity in terms of the coloration traits (observed at the phenotypic level) is associated with the genes encoding the regulatory factors of the biosynthesis of pigment compounds. Duplicated copies frequently occur and rapidly evolve in the regulatory genes. The large diversity and noticeable variation of the allele frequencies are also typical for regulatory genes. Moreover, the combination of different alleles of different genes frequently occurs in the same genotype resulting in an even wider spectrum of manifestation at the phenotypic level in the appropriate species. When comparing different species of monocotyledonous and dicotyledonous plants, it becomes clear that tissue- and species-specific peculiarities of the regulation of the pigment compound's biosynthesis appeared rather quickly during evolution. As opposed to the regulatory genes, the structural genes can be attributed to a conservative part of the gene network of the plant's pigment biosynthesis (Khlestkina et al., 2008; Rausher, 2008; Khlestkina, 2010).

The peculiarities of regulating carotenoid biosynthesis were detected first of all due to the study of the accumulation of these compounds in the fruits of solanaceous plants (the Solanaceae family). The diversity of the genetic mechanisms providing the synthesis of different flavonoid pigments was revealed during the study of the coloration of seeds in cereals (the Poaceae family). Several examples and prospects of using the regulatory genes controlling the coloration in the selection process are presented in the final section of the review.

GENETIC REGULATION OF CAROTENOID ACCUMULATION

Carotenoids are a large and diverse group of yellow, orange, and red pigments belonging to tetraterpene isoprenoids (DOXP/MEP or MVA pathway) and having a polyisoprenoid (C40) chain of conjugated double bonds. Carotenoids are present in membranes of all photosynthesizing organisms and perform a number of important functions in the photosynthesis process: antenna (additional pigments in the process of solar energy absorption) and protective (quenchers of triplet chlorophyll and singlet oxygen; they prevent the reaction center from powerful energy flows at high light intensities and stabilize the lipid layer of the thylakoid membranes protecting it from overoxidation) (Strzhalka et al., 2003; Alekhina et al., 2005).

Among all plant families, the Solanaceae is the model for studying the evolution of secondary metabolite synthesis. The early studies of the process of

carotenoid biosynthesis were conducted by Porter and Lincoln, who, based on the biochemical analysis of intermediate products, suggested the scheme of the successive synthesis of carotenoids in 1950, according to which some carotenoids are used as intermediate products for the generation of other carotenoids. The nonmevalonate pathway (MEP pathway) of carotenoid biosynthesis was discovered in the mid-1980s (Flesch, Rohmer, 1988), according to which isoprenoids are synthesized in eubacteria, in the chloroplasts of the photosynthesizing tissues, as well as the chloroplasts of fruits and flowers (Ershov, 2005; Kopsell and Kopsell, 2006).

The molecular studies on the cloning of the genes involved in the process of carotenoid biosynthesis started in the 1990s allowed us to determine the key stages of the carotenoids' enzymatic transformation and their genetic determination. The MEP pathway of carotenoids' biosynthesis and structural genes determining its stages are presented in J. Hirschberg's work (2001) (Fig. 2).

The synthesis of carotenoids produced in plastids begins with combining two isoprenyl pyrophosphate (IPP) molecules and generating dimethylallyl pyrophosphate (DMAPP), which is transformed into geranylgeranyl pyrophosphate (GGPP), a precursor of the first biosynthetic pathway carotenoid (colorless phytoene). Phytoene (C_{40}) is produced as a result of the condensation of two GGPP (C_{20}) molecules with the involvement of the phytoene synthase (*PSY*) enzyme. The *PSY1* gene plays a key role at the initial stage of carotenoid synthesis. The *psy1* mutation is the reason for the development of a deficient enzyme, the low content of the carotenoids, and the development of yellow fruit pulp (*r* phenotype). The two *PSY* genes in tomatoes, the *PSY2* (which works only in chloroplast containing tissues) and *PSY3* genes (which presumably functions in the roots under stress conditions) are also well known (Kachanovsky et al., 2012).

As a result of dehydration, phytoene desaturase (PDS) and ζ-carotene desaturase (ZDS) enzymes catalyze the production of the color lycopene molecule from phytoene through ζ- carotene and prolycopene. The *tangerine* (*t*) mutation in the gene encoding carotenoid isomerase (CRTISO) violates the stage of prolycopene (tetra-cis-lycopene) transformation into lycopene (trans-forms) and leads to an increased prolycopene concentration and generation of fruits with a deep yellow coloring. Carotenoids of the phytoene–lycopene region are linear molecules. At the next stage of biosynthesis, carotenoids with three types of benzene rings (the β-, γ-, and ε-type) are generated from lycopene. Lycopene cyclases (catalyzing the reaction) are specific and their generation is determined by different genes. Thus, lycopene-β-cyclase (CYC-B) is under the control of the dominant *Beta* (*B*) gene; and lycopene-ε-cyclase (CYC-ε), under the *Delta* (*Del*) gene. Then xanthophylls is produced due to the enzy-

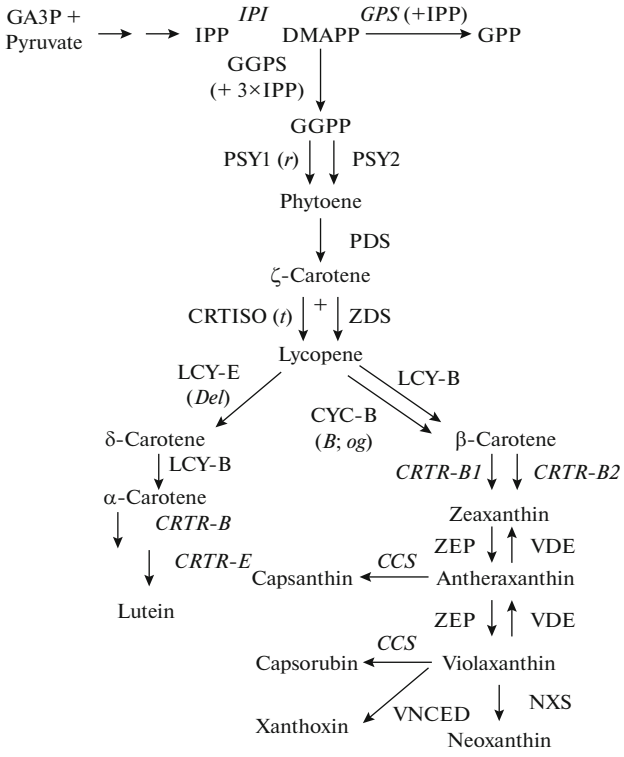

Fig. 2. MEP-pathway of carotenoid biosynthesis in tomato (Hirschberg, 2001). Enzymes and intermediate substances: CCS, capsanthin–capsorubin synthase; CRTISO, carotenoid isomerase; CRTR-B, β-ring hydroxylase; CRTR-E, ε-ring hydroxylase; CYC-B, chromoplast-specific lycopene-β-cyclase; DMAPP, dimethylallyl pyrophosphate; GA3P, geranylaldehyde-3-phosphate; GPP, geranyl pyrophosphate; GGPP, geranylgeranyl pyrophosphate; GGPS, geranylgeranyl pyrophosphate synthase; GPS, geranyl pyrophosphate synthase; IPI, IPP-isomerase; IPP, isopentyl pyrophosphate; LCY-B, lycopene-β-cyclase; LCY-E, lycopene-ε-cyclase; NXS, neoxanthin synthase; PDS, phytoene desaturase; PSY, phytoene synthase; VDE, violaxanthin diepoxidase; VNCED, 9-*cis*-epoxycarotenoid dioxygenase; ZDS, ζ-carotene desaturase; ZEP, zeaxanthin epoxidase. The tomato mutations changing the carotenoid biosynthesis are demonstrated in brackets: *B*, *Beta*; *Del*, *Delta*; *og*, *old-gold*; *r*, *yellow-flesh*; *t*, *tangerine*.

matic oxidation of α-carotene into lutein and β-carotene into zeaxanthin, violaxanthin, or neoxanthin (Hirschberg, 2001; Bramley, 2002; Liu et al., 2003).

Along with the genes that determine the stages of carotenoid synthesis, an important influence on their accumulation is exerted by the regulatory genes determining the mechanisms of the transcriptional (TF genes) and posttranscriptional (PTGS genes) regulation of the biosynthesis of the pigments and their degradation. Most of the genes encoding the transcription factors decelerate or completely suppress the fruit from maturing. Such factors include RIN-MADS (Vrebalov et al., 2002), CNR-SQUAMOSA (Manning, 2006), TAGL1-MADS BOX (Vrebalov et al., 2009), LeHB-1 HB zip (Lin et al., 2008), and SIAP2a (the

AP2 gene) (Chung et al., 2010; Karlova et al., 2011) (table).

The known regulatory genes in the Solanaceae have both a direct and indirect effect on carotenoid biosynthesis. Among them, the MADS Box Transcription family genes (such as the *AGAMOUS* genes) make an important contribution to regulating the biosynthesis. They are able to regulate the biosynthesis of the carotenoids through interaction with the promoters of the lycopene-β-cyclase (CYC-B) and carotenoid isomerase (CRTISO) genes. Two *AGAMOUS* members (*TAG1* and *TAGL1*) were described in tomatoes. The TAGL1 also regulates the pigmentation of the tomato fruits as a result of the direct activation of the *ACS2* ethylene biosynthesis gene (Itkin, 2009). It is known that another MADS-box (the *TDR4* gene) acts together with the *TAGL1* (described above) regulating the maturation of the tomato fruit (Nguyen et al., 2014).

The *RIN* locus belonging to the family of genes encoding the SEPALLATA and MADS-box transcription factors is among the most important regulators of fruit maturation. The *RIN* locus contains two tandem MADS-box genes, one of which (*LeMADS-RIN*) regulates maturation, while the other (*LeMADS-MC*) is responsible for the development of sepals and the indeterminacy of inflorescences (Vrebalov et al., 2002). The LeMADS-RIN regulatory activity is manifested in the ability to bind to the CArG-box elements of the promoter of the *ACS2* and *ACS4* genes (involved in maturation) and change their expression (Fujisawa et al., 2011). The ability of RIN to bind to the *PSY1* carotenogenesis gene was also demonstrated (Pan et al., 2010).

Recent studies have demonstrated that the *RIN* is involved in the synthesis of ethylene and signal transmission, cell wall modification, carotenoid accumulation, development of the aroma, and the transcriptional regulation of the genes encoding the transcription factors associated with maturation, including the *NOR*, *CNR*, *TDR4*, and *HB-1* genes (Fujisawa et al., 2011; Martel et al., 2011).

The *NOR* gene encodes the LENAC-NOR transcription factor. The *nor* mutation caused by a short deletion (2 bp) leads to a shift of the reading frame and generation of a nonfunctional protein (Giovannoni, 2004). The consequences of this mutation and *rin* mutation are similar. In the work of S. Osorio (2011), in which the role of monogenic rin and *nor* mutations in the regulation of ethylene biosynthesis and tomato maturation was in detail characterized at the level of transcripts, protein products, and metabolites; it was demonstrated that the *rin* and *nor* alleles act together in the process associated with controlling fruit maturation, and the *nor* effect is manifested in the stronger suppression of fruit maturation than the *rin* effect.

The CNR (Squamosa Promoter Binding Protein) is another transcription factor which reduces the catotenoid accumulation (Lin, 2008). A rare dominant allele of the *Cnr* gene was detected in tomatoes; it results in an immature phenotype with two distinctive features, including dense fruits with reduced cellular adhesion (the mealy structure of the pericarp) and the complete absence of carotenoid biosynthesis (Orfila et al., 2002). A decrease in ethylene synthesis, unpigmented pericarp, and increased fruit density are typical for plants carrying the *Cnr* allele. As opposed to mutations in other genes (*Nr*, *nor*, and *rin*) influencing maturation through the partial suppression of lycopene synthesis, the *cnr* gene mutation is associated with the complete suppression of the *PSY1* gene expression and carotenoid biosynthesis, even in the presence of ethylene (Manning, 2006).

The *LeHB-1* transcription factor gene encodes the protein of the HD-Zip class (table) (Lin et al., 2008). The *LeHB-1* is able to interact with the promoter of the *ACO1* ethylene biosynthesis gene, increasing its expression and the maturation process of tomato fruits.

The *SlAp2a* tomato gene, which delays the maturation and accumulation of carotenoids, was described in the family of regulatory AP2/ERF factors (Chung et al., 2010). The *SlAp2a* is involved in regulating the ethylene and auxin signal pathway in the process of chloroplast differentiation. The *SlAp2a* suppresses the generation of ethylene in wild-type tomato fruits. The *ERF6* gene is another gene encoding the transcription factor from the AP2/ERF family; it regulates the accumulation of carotenoids. In tomatoes, the *SlERF6* controls the accumulation of translycopene and β-carotene. It is assumed that the regulators of ethylene synthesis and fruit maturation (*SlERF6* and *SlAp2a*) act together, performing a negative control of the ethylene signals during maturation (Lee et al., 2012).

The genes associated with the work of photoreceptors have a regulating effect on carotenoid accumulation. The *HP-1* and *HP-2* genes in the Solanaceae are a key regulator for controlling the cytokinin of the cell cycle, cell size, and the number of chloroplasts (Caspi et al., 2008). These genes are referred to as the family of the UV-damaged DNA-binding protein (table). The effect of mutants of the *high pigment* series (*hp-1*, *hp-1*^{w}, *hp-2*, *hp-2*^{j}, and *hp-2*^{dg}) is characterized by an increase in the number and sizes of the chloroplasts that is the basis for the increase in the carotenoid synthesis in tomato fruits during maturation (Kolotilin et al., 2007; Barry, 2009). The tomato plants carrying one such genotype mutation have a high level of anthocyanins and chlorophyll in the seedlings, short hypocotyls, and intensive pigmentation of leaves and fruits. The dark red fruits of the mutants are distinguished by a high level of carotenoids (primarily, lycopene), vitamins C and E, sugars, and some flavonoids (Palmieri et al., 1978; Kolotilin et al., 2007).

Other genes of light-dependent transcription factors (*LeHY5* and *LeCOP1LIKE*) belonging to the

Regulatory genes of flavonoid and carotenoid biosynthesis in members of mono- and dicotyledonous plants

Compounds	Family of regulatory factors	Genes in plant members	
		monocotyledonous	dicotyledonous
Flavonoids	MYB	***Hordeum vulgare* L.** *HvMpc1* (Shoeva et al., 2015); ***Oryza sativa* L.** *C* (Reddy et al., 1998; Saitoh et al., 2004); ***Triticum aestivum* L.** *Mpc1* (Li et al., 1999); ***Zea mays* L.** *C1*, *Pl1*, *P1* (Paz-Ares et al., 1987; Chandler et al., 1989; Gof et al., 1990; Petroni et al., 2000)	***Arabidopsis thaliana* L. Heinh.** *TT2*, *CPC*, *MYBL2* (Borevitz et al., 2000; Gonzalez et al., 2008; Dubos et al., 2008; Matsui et al., 2008); ***Petunia hybrida* L.** *AN2*, *AN4* (Quattrocchio et al., 1999, 2006); ***Vitis vinifera* L. Heinh.** *MYBA1*, *MYBA2*, *MYB5a* (Kobayashi et al., 2002; Deluc et al., 2006, 2008; Walker et al., 2007; Cutanda-Perez et al., 2009)
	bHLH	***Hordeum vulgare* L.** *Ant2* (Cockram et al., 2010); ***Oryza sativa* L.** *Pl* (Hu et al., 1996, 2000; Sakamoto et al., 2001); ***Triticum aestivum* L.** *TaMyc1* (Shoeva *et al.,* 2014); ***Zea mays* L.** *B*, *R*, *Lc*, *Sn*, *In1* (Burr et al., 1996; Chandler et al., 1989; Gof et al., 1990; Consonni et al., 1993; Petroni et al., 2000)	***Arabidopsis thaliana* L. Heinh.** *TT8* (Nesi et al., 2000); *GL3/EGL3* (Bernhardt et al., 2003; Heim et al., 2003; Zhang et al., 2003); ***Ipomoea tricolor* Cav.** *ItIVS* (Park, 2012); ***Petunia hybrida* L.** *AN1*, *JAF13* (Llyod et al., 1992; Quattrocchio et al., 1998; Spelt et al., 2000); ***Vitis vinifera* L. Heinh.** *MYC1*, *MYCA1* (Hichri et al., 2010; Matus et al., 2010)
	WD40	***Zea mays* L.** *PAC1* (Selinger, Chandler, 1999)	***Arabidopsis thaliana* L. Heinh.** *T TG1* (Walker et al., 1999); ***Petunia hybrida* L.** *AN11* (de Vetten et al., 1997); ***Vitis vinifera* L. Heinh.** *WDR1*, *WDR2* (Matus et al., 2010)
Carotenoids	ULT	No data	***Crocus sativus L.*** *CsULT1* (Ashraf et al., 2015);
	bHLH; bHLH/LZ		***Arabidopsis thaliana* L. Heinh.** *PIF1* (Toledo-Ortiz et al., 2010). ***Solanum lycopersicum* L.** *SlbHLH006*, *SlbHLH078*, *SlbHLH095* (Sun et al., 2015); ***Brassica rapa* ssp. *pekinensis*** *BrBIM1* (Jung et al., 2014)
	Zinc-coordinating DNA-binding domains		***Brassica rapa ssp. pekinensis*** *BrA20/AN1-like*, *BrZFP8* (Jung et al., 2014)
	GCC type transcriptional factor		***Citrus clementina*** *CcGCC1* (Rios et al., 2010)
	AP2/ERF transcription factor)		***Solanum lycopersicum* L.** *SlERF6* (Lee et al., 2012); ***Arabidopsis thaliana* L. Heinh** *RAP2.2* (Welsch et al., 2007), ***Solanum lycopersicum* L.** *SlAP2a* (Chung et al., 2010; Karlova et al., 2011)

Table. (Contd.)

Compounds	Family of regulatory factors	Genes in plant members	
		monocotyledonous	dicotyledonous
	MADS Box Transcription Factor		***Solanum lycopersicum* L.** *RIN-MADS* (Vrebalov et al., 2002), *TAGL1* (Vrebalov et al., 2009); ***Arabidopsis thaliana* L. Heinh.** *TDR4* (Manning et al., 2006); *SHP1/2* (Ferrandiz et al., 1999, 2000), ***Prunus persica* L.** *PpPLENA* (Tadiello et al., 2009)
	SBP-box (SQUAMOSA promoter binding protein-like)		***Solanum lycopersicum* L.** *CNR* (Manning et al., 2006)
	MYB	***Zea mays* L.** *Golden2* (Fitter et al., 2002) ***Oryza sativa* L.** *OsGLK1* **(**Nakamura et al., 2009)	***Solanum lycopersicum* L.** *Sl-GLK2* (Powell et al., 2012), ***Arabidopsis thaliana* L. Heinh.** *GLK* (Rossini et al., 2001)
	bZIP	No data	***Solanum lycopersicum* L.** *HY5*, *COP1-LIKE* (Liu et al., 2004)
	HB-ZIP		***Solanum lycopersicum* L.** *LeHB-1* (Lin et al., 2008)
	CRY		***Solanum lycopersicum* L.** *cry2* (Giliberto et al., **2005)**
	UV-damaged DNA-binding protein		***Solanum lycopersicum* L.** *hp-1* and *hp-2* (Liu et al., 2004)
	STAY-GREEN	***Oryza sativa* L.** *nyc1* (Cha et al., 2002); *ccr1* (Park et al., 2002)	***Solanum lycopersicum* L.** *gf* (Kerr, 1956), ***Capsicum annum*** *cl* (Akhtar et al., 1999)
	SET DOMAIN GROUP 8	No data	***Arabidopsis thaliana* L. Heinh.** *SDG8* (Cazzonelli and Pogson, 2010)

bZIP family are positive and negative regulators of a plant's pigmentation, respectively. The suppression of the *LeHYS* expression leads to a failure of tomato photomorphogenesis in the early development stages, violation of the thylakoid structure, and a reduction in carotenoid accumulation. In contrast, the repression of *LeCOP1LIKE* leads to increased photomorphogenesis, the development of dark green leaves, and an increase in carotenoid accumulation by 25–43% (Liu et al., 2004).

The *CRY2* gene, a member of another CRY family (Cryptochrome) is also a photoreceptor. The increased *Cry2* expression results in the increased accumulation of flavonoids and lycopene in transgenic tomato plants, which is a result of the transcription control and suppression of the *lycopene-β-cyclase* gene expression (Giliberto et al., 2005). The phenotype of such plants is similar to the plants with the *hp1* and *hp2* alleles, for which diminished hypocotyls and interstices, as well as brightly pigmented fruits with an increased level of lycopene and flavonoids, are also typical. However, the plants with increased *Cry2* gene expression have some negative qualities (late flowering observed under conditions of long and short days and the increased development of side shoots).

The accumulation of carotenoids and fruit coloration in the Solanaceae is also regulated by the *green–flesh* gene. The *Gf* locus encodes the regulatory STAY-GREEN factor (Barry et al., 2008). The *gf* mutants are not able to destroy chlorophyll at the beginning of maturation but accumulate carotenoids (which results in the brown color of the mature fruits). Mutations violating the chlorophyll degradation were identified in some higher plants: the *gf* mutation in tomatoes, the *cl* (*chlorophyll retainer*) mutation in pepper, and the *nyc1*

(*nonyellow coloring 1*) mutation in rice are indicated above (Akhtar et al., 1999; Park et al., 2007).

We note that regulation of carotenoid accumulation is very complicated and not fully understood; at present, it is being studied at many scientific centers.

REGULATORY GENES OF FLAVONOID PIGMENT SYNTHESIS

Flavonoids are a group of natural biologically active compounds (derivatives of benzo-γ-pyrone), which are based on a phenylpropane skeleton consisting of C_6-C_3-C_6-carbonic units. The C_3-fragment binding benzene rings can be presented by several states with a different oxidation degree. Each of these states corresponds to a separate flavonoid class. A huge diversity of flavonoid compounds is reached by means of the coordinated effect of more than 20 enzymes, which act alternately and synthesize initially chalcones and then give rise to different classes and different members within each class (Khlestkina et al., 2014). Most of the classes include pigment compounds or precursors of other flavonoid pigments. For example, flavones, flavonol glycosides, and aurones differ by yellow and/or orange coloration, while phlobaphenes (derivatives of flavan-4-ols) and proanthocyanidins (derivatives of catechins and leukoanthocyanidins) give a reddish brown tint to the plant tissues. Anthocyanidins and their derivatives (anthocyanins) provide a wide gamma of pigments (from pink to purple) (Britton, 1983; Winkel-Shirley, 2001). Flavonoid compounds (especially, anthocyanins) have a photoprotective effect; in addition, many flavonoid compounds are able to counteract the oxidative stress (arising due to the effect of unfavorable environmental conditions) or to prevent its development (thus protecting different cellular structures from destruction). Some flavonoids have antimicrobial properties (Khlestkina, 2013).

Understanding the pathway of flavonoid compound biosynthesis and its regulation was first developed through the study of cereals, namely, maize (*Zea mays* L.), which since the middle of the 20th century, when B. McClintock discovered mobile elements in it (1956)), became the main model for many directions of plant genetics for many years.

The three main groups of regulatory factors (MYB, MYC (bHLH), and WD40) generating the MBW complex required for activating structural genes are involved in regulating flavonoid biosynthesis. The genes encoding two of these three factors were first described in maize. In 1987, the MYB-like R2R3 type transcription factors regulating the biosynthesis of flavonoid pigments anthocyanins were discovered (Paz-Ares et al., 1987). The R2R3-MYB proteins are responsible for the light-dependent regulation of biosynthesis in a MBW complex (Taylor and Briggs, 1990). In maize, the R2R3-MYB factors are encoded by the *Colorless 1* (*C1*), *Purple 1* (*P1*), and *Purple leaf 1* (*Pl1*) genes (Paz-Ares et al., 1987; Goff et al., 1990; Petroni et al., 2000). The homologous genes isolated later from other species of monocotyledonous and dicotyledonous plants are presented in the table.

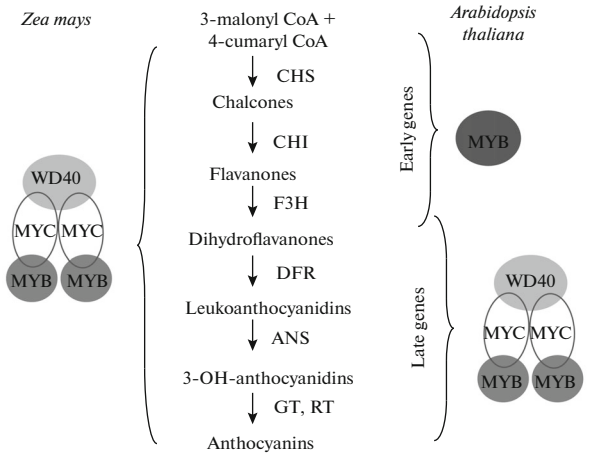

Fig. 3. Biosynthesis of anthocyanins and proanthocyanidins and its regulation in members of monocotyledonous (*Zea mays*) and dicotyledonous (*Arabidopsis thaliana*) plants. Enzymes: ANS, anthocyanidin synthase; CHI, chalcone–flavanone isomerase; CHS, chalcone synthase; DFR, dihydroflavanone 4-reductase; F3H, flavanone-3-hydroxylase; GT, glycosyltransferase; RT, rhamnosyl transferase. Transcription factors: MYB, MYC, WD40. Modified according to Petroni, Tonelli (2011).

MYC-like factors containing the bHLH domain (the main helix–loop–helix domain) in its structure are responsible for determining the tissue specificity of anthocyanin biosynthesis in a MBW complex (Taylor and Briggs, 1990). The first genes encoding MYC-like B/R type factors (according to the name of the appropriate loci (*B* and *R*)) were also discovered in maize (Chandler et al., 1989). Later, other members of this family were isolated from the genome of maize and other plants based on homology (table). The WD40 factor is required for stabilizing the MBW complex; the first member of this group in plants (*An11*) was described in petunia (de Vetten et al., 1997); its homolog from the genome of maize (*PAC1*) (Selinger and Chandler, 1999) and other plant species was isolated later (table).

As opposed to maize (in which the structural genes of anthocyanin biosynthesis are jointly regulated by means of the MBW complex) (Fig. 3), the *Arabidopsis thaliana* genes are divided into early and late genes of biosynthesis. The early genes are expressed in the absence of pigment synthesis due to activation by means of a certain MYB factor, while the late genes are expressed, as well as the maize genes (involving the MBW complex) (Fig. 3). The assumptions that these peculiarities reflect the typical differences between monocotyledonous and dicotyledonous plants were not justified when it became clear that specific pecu-

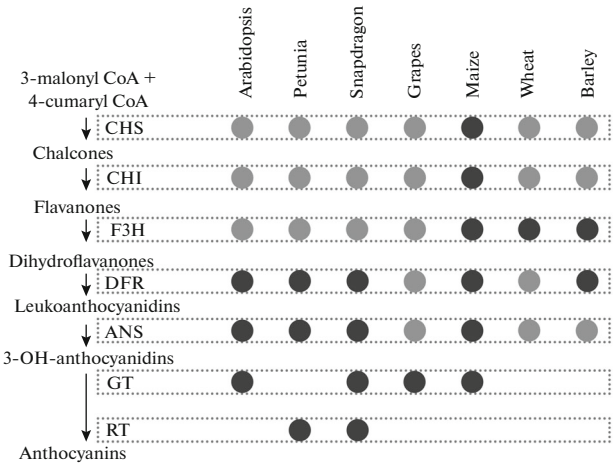

Fig. 4. Activity of structural genes of anthocyanin biosynthesis in tissues colored (dark rings) or uncolored (light rings) by anthocyanins in members of dicotyledonous and monocotyledonous plants. ANS, anthocyanidin synthase; CHI, chalcone–flavanone isomerase; CHS, chalcone synthase; DFR, dihydroflavanone 4-reductase; F3H, flavanone-3-hydroxylase; GT, glycosyltransferase; RT, rhamnosyl transferase. Summarized according to: Dooner, 1983; Cone et al., 1986; Ludwig et al., 1989; Martin et al., 1991; Quattrocchio et al., 1993; Boss et al., 1996; Pelletier and Shirley, 1996; Gonzalez et al., 2008; Khlestkina et al., 2008; Petroni and Tonelli, 2011; Tereshchenko et al., 2013; Shoeva et al., 2015.

liarities are also present among the smaller taxa. The activity of the structural genes in different plant species (depending on whether it is associated with the presence of the anthocyanin pigment) is schematically designated in Fig. 4. Different groups of genes are coexpressed (jointly regulated) in different plant species; there is no clear division between early and late genes; certain genes in the biosynthesis pathway (for example, *F3h* in wheat) are sometimes separately regulated (Fig. 4).

Besides the species-specific peculiarities of the regulation of anthocyanin biosynthesis, there are peculiarities of the regulation of the synthesis of the same pigments in different tissues in the same plant species. For example, only the pericarp coloration (among all the traits of anthocyanin coloration) is controlled by two complementary dominant genes encoding the MYC- and MYB-like factor, while the involvement of only those genes that are localized in the seventh homeologous group of chromosomes and correspond to the MYB-factor was detected in regulating the coloration of other plant parts (Fig. 5). According to the concept about the involvement of the MBW complex in activating the structural genes of anthocyanin biosynthesis, it is difficult to assume that such complex is only involved in the pigment synthesis in pericarp, while in the MYB factor is sufficient in other tissues. The possible variation of the allelic diversity among different MYC- and MYB-coding loci is the most probable explanation. Indeed, the study of the MYC-encoding *Pp3* gene (Shoeva et al., 2014) demonstrated that it has copies in the common wheat chromosomes 2B and 2D that are not expressed in pericarp but are active in the other plant parts (independently of the presence/absence of coloration) (Fig. 6). The *Myc3* and *Myc4* gene products are potential candidates involved in the development of the regulatory MBV complex in the coleoptile, stem, and other plant parts. The fact that the loci in chromosomes 2B and 2D have never been detected during the analysis of segregated populations may indicate that nonfunctional *Myc3* and *Myc4* gene alleles are either rare or do not exist, while the *Myc1* (*Pp3*) has allelic diversity at the phenotypic level and therefore registered during the analysis of segregated populations (Dobrovolskaya et al., 2006; Khlestkina et al., 2010).

The detection of peculiarities of regulating pigment synthesis became possible not only due to the rapid development of molecular genetic methods of plant study but also due to the creation of accurate genetic models by the coloration traits in previous years. The isogenic lines also refer to the most suitable models for the study of functions of the genes (Khlestkina, 2014). By means of the wheat isogenic lines created at the Institute of Cytology and Genetics (Siberian Branch, Russian Academy of Sciences) by V.S. Koval', it was established that the factor belonging to the MYB family is involved in regulating proanthocyanidin biosynthesis in the wheat seed coat and is encoded by the *R-A1*, *R-B1*, and *R-D1* genes localized in chromosomes 3A, 3B, and 3D (Himi et al., 2005; Himi and Noda, 2005). When using a set of wheat isogenic lines with different combinations of the dominant and recessive alleles of the *Pp* genes (the two initial lines obtained by V.S. Arbuzova at the Institute of Cytology and Genetics (Siberian Branch, Russian Academy of Sciences) became the core of the collection), the regulatory interaction between the MYB- and MYC-coding regulatory genes was also established (Shoeva et al., 2014; Gordeeva et al., 2015).

GENES OF PIGMENT SYNTHESIS IN PLANT BREEDING

Based on the known DNA sequences and the works on sequencing the studied alleles influence on carotenoid accumulation in tomato plants, the following recommendations were developed for the DNA-typing of the alleles of the regulatory factors extending the period of fruit preservation (*rin* (*ripening-inhibitor*), *nor* (*nonripening*), nor^A (*alcobaca*)); alleles of the structural genes (*PSY1* (*r*) (encodes phytoene synthase, PSY1), *t* (*tangerine*) (encodes carotenoid isomerase, CRTISO), *B* (*Beta*) (lycopene-β-cyclase, CYCB), *Del* (*Delta*) (lycopene-ε-cyclase, LCY-ε), *og* (*old-gold*), and og^c (*old-gold crimson*)); and alleles of the genes indirectly regulating the accumulation of the *hp-1* and $hp\text{-}2^{dg}$ (*hp*, *high pigment*) carotenoids favoring an

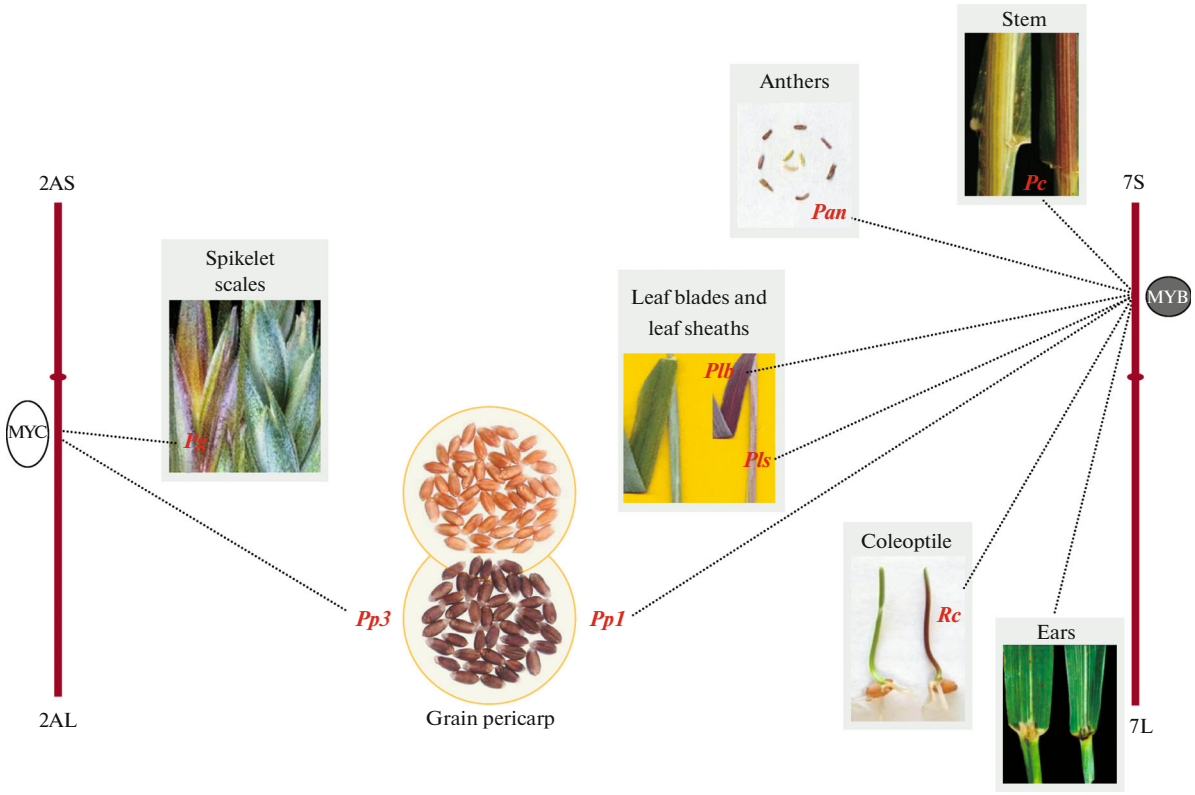

Fig. 5. Chromosomal localization of wheat genes determining anthocyanin coloration and encoding regulatory factors of MYC- and MYB-type. *Pan*, *purple anthers*; *Pc*, *purple culm*; *Pg*, *purple glume*; *Plb*, *purple leaf sheath*; *Pp*, *purple pericarp*; *Ra*, *red auricle*; *Rc*, *red coleoptiles*. Summarized according to: Khlestkina et al., 2002, 2009, 2010, 2014; Shoeva et al., 2014; Himi, Taketa, 2015.

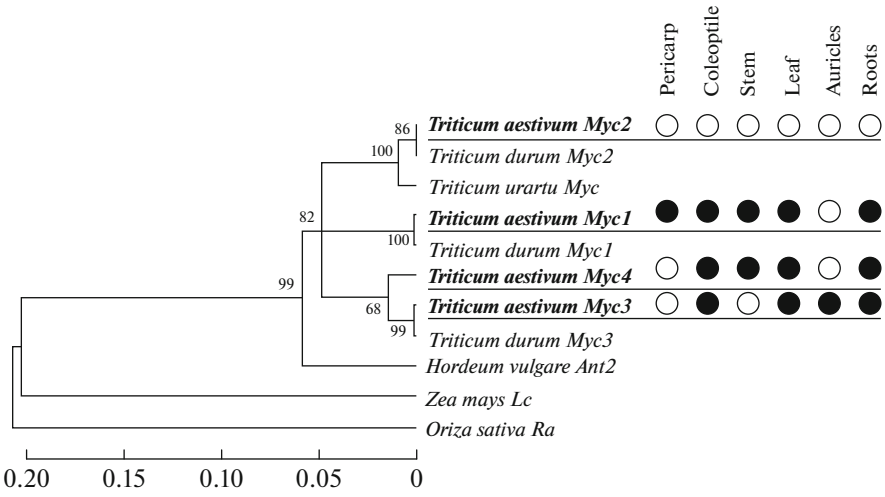

Fig. 6. Similarity of MYC-factors in different cereal species (Shoeva et al., 2014) and transcriptional activity of copies of wheat *Myc* gene in different parts of wheat plant (●, gene is expressed; ○, not expressed).

increase in the number and size of plastids, as well as the *gf-3* and *gf-5* (*gf*, *green flesh*) genes modifying the process of chlorophyll destruction (Kil'chevskii et al., 2014). These methodical recommendations were used at the Institute of Genetics and Cytology (National Academy of Sciences, Belarus) for the creation of forms of tomatoes with high quality fruits at the stage of form selection for crossing and selecting the breeding material in F_2 generations with the desired gene combination.

Fig. 7. Scheme of creation of tomato hybrids combining genes of continuous period of fruit preservation (*rin*, *nor*, and nor^A) and increased carotenoid content (*B*, og^c, *t*, *gf-3*) (Kil'chevskii et al., 2014).

The combination of the genes extending the preservation period of tomato fruit with the genes controlling the content of the carotenoids is of great practical interest in selecting the quality of tomato fruit; this allows us to create forms with an increased content of lycopene and carotene, as well as a simultaneous continuous period of fruit storage. The use of efficient molecular genetic methods, in combination with the traditional methods of tomato selection, will favor an increase in the efficiency of the selective process. Based on the molecular genetic analysis of the studied collection, F_1 hybrids with the genes involved in the process of carotenoid biosynthesis and transformation, as well as the genes controlling the fruit maturation, were created (Fig. 7).

Homozygous forms with a different combination of the structural and regulatory genes were selected at the next stage of the work. For further selective genotype improvement, the obtained homozygous plants were involved in hybridization with the samples carrying the $hp\text{-}2^{dg}$ and *gf-3* alleles (Fig. 8). The homozygous forms for three pairs of alleles in the F_2 generation were then selected.

The created material was estimated by the traits of carotenoid accumulation, as well as the duration of the storage and productivity period, and valuable forms

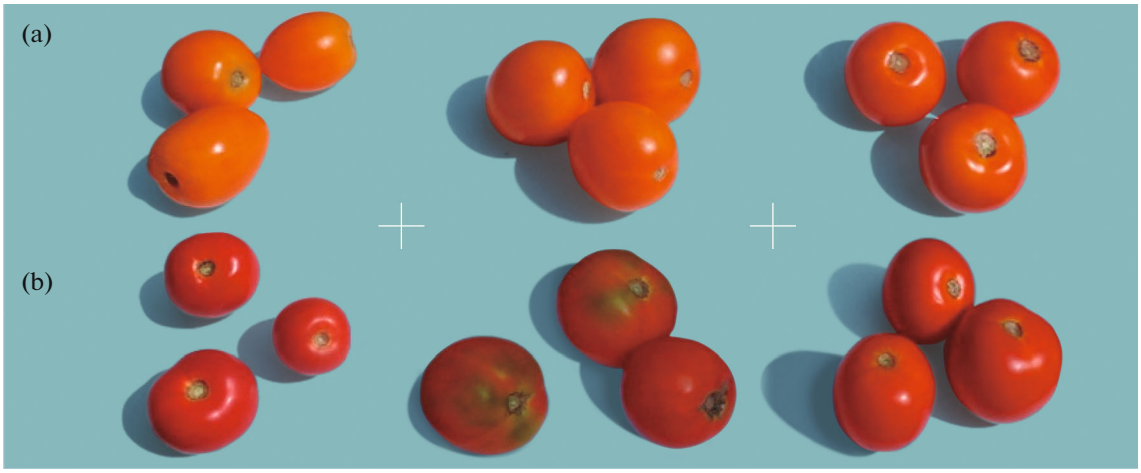

Fig. 8. F_1 tomato hybrids with allele combinations: a, *B/rin*, *B/rin/gf*, *B/rin/hp*; b, og^c/*nor*, og^c/*nor/gf*, og^c/*nor/hp* (Kilchevsky et al., 2014).

for breeding on fruit quality were selected. The detailed description of the conducted work is presented in the fourth volume of the collective monograph of the Institute of Genetics and Cytology (National Academy of Sciences of Belarus) (Kil'chevskii et al., 2014).

The use of regulatory genes of carotenoid biosynthesis for obtaining a grain rich in vitamin A (Al-Babili and Beyer, 2005) and the use of a number of regulatory genes controlling the synthesis of flavonoid pigments in different parts of caryopsis are promising directions in cereals. For example, the synthesis of proanthocyanidins in the seed coat is associated with resistance to wheat pre-harvest sprouting (Freed et al., 1976), while the presence of anthocyanins in pericarp can favor better seed longevity (Gordeeva and Khlestkina, 2013). In addition, the grain containing anthocyanins in the aleurone layer or pericarp (Fig. 1) can be used for producing bran and wholegrain products with an increased content of antioxidants. In spite of the fact that the pigmentation of some organs itself can be an excellent marker during selection by other traits, it is also expedient to use markers for the directed transfer of the genes controlling the coloration. For example, the time of receiving the final genotype can be reduced by half, while the number of occupied genotypes for the breeding material can by reduced greatly, during wheat selection by means of DNA markers by the trait of the anthocyanin coloration of pericarp (Gordeeva et al., 2015).

Thus, the timely creation of genetic collections by the coloration traits in dicotyledonous and monocotyledonous plants, in combination with the development of molecular genetic methods of plant study allowed us to detect peculiarities of genetic regulation of the plant's flavonoid and carotenoid synthesis and to characterize at a molecular level the key genes involved in biosynthesis of these compounds. The characteristics of the isolated genes will allow us to control at a molecular level and to accelerate the process of selection by the coloration traits that are important for increasing the nutritional value of the products produced from the plant's fruit and seeds.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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