Variability of Rc (red coleoptile) Alleles in Wheat and Wheat-alien Genetic Stock Collections

E.K. KHLESTKINA1*, E.V. ANTONOVA2, L.A. PERSHINA1, A.A. SOLOVIEV3, E.D. BADAeva4, A. BÖRNER5 and E.A. SALINA1

1Institute of Cytology and Genetics (ICG), Siberian Branch of the Russian Academy of Sciences, Lavrentjeva Ave. 10, Novosibirsk, 630090, Russian Federation
2Institute of Plant and Animal Ecology (IPAE), Ural Division of the Russian Academy of Sciences, 8 Marta Str. 202, Yekaterinburg, 620144, Russian Federation
3Russian State Agrarian University – Moscow K.A. Timiryazev Agricultural Academy (MTAA), Temiryazev Str. 49, Moscow, 127550, Russian Federation
4Engelhardt Institute of Molecular Biology (IMB), the Russian Academy of Sciences, Vavilov Str. 32, Moscow, 119991, Russian Federation
5Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Corrensstr. 3, D-06466 Gatersleben, Germany

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Anthocyanin accumulation in vegetative organs has a relationship to stress resistance in plants. In wheat, ability to accumulate anthocyanins in the coleoptile is inherited and controlled by the Rc (red coleoptile) genes. The aim of the current study was to find potential sources of ‘strong’ Rc alleles conferring very high levels of anthocyanin production and to study the effect of genetic background on Rc expression. We measured the relative anthocyanin content (OD530) in the coleoptile of different wheat and wheat-alien genetic stocks and accessions to find potential sources of ‘strong’ Rc alleles conferring very high levels of anthocyanin production. The OD530 values varied from 0.514 to 3.311 in genotypes having red coleoptiles. The highest anthocyanin content was detected in coleoptiles of four Triticum dicoccoides accessions originating from Israel and the Russian T. aestivum cultivar ‘Novosibirskaya 67’, suggesting that their Rc alleles can be used to increase anthocyanin content in the coleoptile of wheat cultivars. It is also suggested that rye Rc alleles, such as that of Russian cultivar ‘Selenga’, can be used to increase anthocyanin content in triticale seedlings.

Keywords: Triticum aestivum, anthocyanin, genetic variability, stress resistance

Introduction

Accumulation of anthocyanin compounds in vegetative organs of different plant species is positively related to resistance to pathogens (Izdebski 1992; Bogdanova et al. 2002) and abiotic stress factors such as frost (Parker 1962, Singh et al. 1995; Chalker-Scott 1999), salinity (Dutt et al. 1991; Ramanjulu et al. 1993; Kaliamoorthy and Rao 1994; Tereshchenko et al. 2010), drought (Bahl et al. 1991; Chalker-Scott 1999; Farrant

* Corresponding author; E-mail: khlest@bionet.nsc.ru

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2000), UV (Feild et al. 2001; Ryan et al. 2002), irradiation exposure (Nagata et al. 2003, 2005), and heavy metals (Marrs and Walbot 1997; Gould et al. 2004). In wheat, plants with intensive anthocyanin pigmentation of the coleoptile, stem and anthers were shown to be resistant to *Ustilago tritici*. High anthocyanin content in these tissues negatively influenced fungal development (Bogdanova et al. 2002). In rye, anthocyanin pigmentation of the coleoptile and sheath of the first leaf correlated with resistance to *Fusarium nivale* and *Ophiobulus graminis* (Izdebski 1992). Salinity stress induced a significant increase in anthocyanin content of wheat coleoptiles, and between a pair of wheat near-isogenic lines, the line with more intensive anthocyanin pigmentation in normal conditions possessed higher salinity tolerance in stress conditions (Tereshchenko et al. 2010).

Ability to accumulate anthocyanins in the coleoptile is controlled by the *Rc* (red coleoptile) genes. The *Rc* loci were mapped on wheat chromosomes 7A (*Rc-A1*), 7B (*Rc-B1*), 7D (*Rc-D1*), and rye chromosome 4R (*Rc-R1*) (Khlestkina et al. 2002, 2009a). The aim of the current study was to find potential sources of ‘strong’ *Rc* alleles conferring very high levels of anthocyanin production and to study the effect of genetic background on *Rc* expression. Wheat genetic stock collections, intraspecific wheat (Kuspira and Unrau 1958) and wheat-alien (Silkova et al. 2006; Troubacheeva et al. 2008; Pershina et al. 2009) chromosome substitution lines and wheat-alien chromosome addition lines (Driscoll and Sears 1971; Friebe et al. 1993, 1995, 2000) are good models to investigate this issue, as they can be used in comparative analyses of gene expression in different genetic backgrounds. Furthermore, since common wheat relatives can be a potential source of useful genes, analysis of wheat-alien lines carrying *Rc* genes originating from different species may result in the discovery of more desirable alleles.

### Materials and Methods

Thirty wheat and wheat-alien genetic stocks and rye cultivar-donors of the *Rc* genes in wheat-rye lines analyzed in the current study are described in Table 1. The seeds of these lines were placed on filter paper, moistened with distilled water and kept for 48 hours at 4°C without light to synchronize germination. Thereafter the temperature of the growth chamber was increased to 20°C, and after 5 days at a photoperiod of 12 h light/12 h darkness the coleoptile color was scored, and the relative anthocyanin contents in coleoptiles were measured. In rye cultivars, besides the coleoptile, the first leaf was colored. We also extracted and measured anthocyanins from the first leaf of the rye cultivars.

For anthocyanin extraction 150 mg of fresh coleoptiles were homogenized, dissolved in 1ml of 1% HCl/methanol at room temperature, and incubated at 4°C for 2 hours. The mixture was centrifuged at 10,000 g for 10 min and the supernatant was used for measurement of the relative anthocyanin content at 530 nm wavelength using a spectrophotometer «SmartSpec™Plus» (BioRad). Anthocyanin extractions and measurements were performed in triplicate. The significance of differences between genetic stocks was assessed using nonparametric Mann-Whitney U-tests (Mann and Whitney 1947); z – current
variate value for the normal distribution; $p$ – value. Statistical hypotheses were tested with the program Statistica 6.0 (StatSoft Inc., 2001).

**Table 1.** Plant materials used in the current study

<table>
<thead>
<tr>
<th>Designation in Fig. 1</th>
<th>Description</th>
<th>Rc gene</th>
</tr>
</thead>
<tbody>
<tr>
<td>M808</td>
<td><em>T. aestivum</em> ‘Mironovskaya 808’ (Ukrainian cultivar maintained in IPK stock collection)</td>
<td>Rc-D1 (Khlestkina et al. 2002)</td>
</tr>
<tr>
<td>Golubka</td>
<td><em>T. aestivum</em> (Russian cultivar maintained in ICG stock collection)</td>
<td>Colorless coleoptile</td>
</tr>
<tr>
<td>N67</td>
<td><em>T. aestivum</em> ‘Novosibirskaya 67’ (Russian cultivar maintained in ICG stock collection)</td>
<td>Rc-D1 (Khlestkina et al. 2009b)</td>
</tr>
<tr>
<td>S29</td>
<td><em>T. aestivum</em> ‘Saratovskaya 29’ (Russian cultivar maintained in ICG stock collection)</td>
<td>Rc-A1 (Khlestkina et al. 2010)</td>
</tr>
<tr>
<td>S29(Onokh 2R(2D))</td>
<td><em>T. aestivum</em> ‘S29’(<em>S. cereale</em> ‘Onokhovskaya’) chromosome substitution line 2R(2D) (Silkova et al. 2006)</td>
<td>Rc-A1 (Khlestkina et al. 2009a, 2010)</td>
</tr>
<tr>
<td>Hope</td>
<td><em>T. aestivum</em> (US cultivar maintained in IPK stock collection)</td>
<td>Rc-A1, Rc-B1 (Gale and Flavell 1971)</td>
</tr>
<tr>
<td>PC394</td>
<td><em>T. aestivum</em> ‘Chinese Spring’ (Chinese cultivar; stock earlier used to create CS(Hope 7A), CS(Hope 7B) and CS-Imp 4R), maintained in IPK stock collection</td>
<td>Colorless coleoptile</td>
</tr>
<tr>
<td>CS(Hope 7A)</td>
<td><em>T. aestivum</em> chromosome substitution line ‘Chinese Spring’ (‘Hope’ 7A) developed by Dr. E.R. Sears (Kuspira and Unrau 1958)</td>
<td>Rc-A1 (Gale and Flavell 1971)</td>
</tr>
<tr>
<td>CS(Hope 7B)</td>
<td><em>T. aestivum</em> chromosome substitution line ‘Chinese Spring’ (‘Hope’ 7B) developed by Dr. E.R. Sears (Kuspira and Unrau 1958)</td>
<td>Rc-B1 (Gale and Flavell 1971)</td>
</tr>
<tr>
<td>CS-Imp 4R</td>
<td><em>T. aestivum</em> ‘CS’+<em>S. cereale</em> ‘Imperial’ chromosome addition line 4R (Driscoll and Sears 1971)</td>
<td>Rc-R1 (Khlestkina et al. 2009a)</td>
</tr>
<tr>
<td>P28</td>
<td><em>T. aestivum</em> ‘Pyrothrix 28’ (Kazakhstan cultivar); stock earlier used to create P28 (Hm 7H(7D)) (Troubacheeva et al. 2008; Pershina et al. 2009)</td>
<td>Colorless coleoptile</td>
</tr>
<tr>
<td>P28 (Hm 7H(7D))</td>
<td><em>T. aestivum</em> ‘Pyrothrix 28’ (<em>Hordeum marinum</em>) chromosome substitution line 7H(7D) (Troubacheeva et al. 2008; Pershina et al. 2009)</td>
<td>Rc-Hf1 (current study)</td>
</tr>
<tr>
<td>CS-Aesp 7S</td>
<td><em>T. aestivum</em> ‘CS’+<em>Ae. speltoides</em> chromosome addition line 7S (Friebe et al. 2000)</td>
<td>Rc on 7SS (Friebe et al. 2000)</td>
</tr>
<tr>
<td>CS-Aeln 7S</td>
<td><em>T. aestivum</em> ‘CS’+<em>Ae. longissima</em> chromosome addition line 7S (Friebe et al. 1993)</td>
<td>Rc on 7SŁ (Friebe et al. 1993)</td>
</tr>
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<td>CS-Aes 7S</td>
<td><em>T. aestivum</em> ‘CS’+<em>Ae. searsii</em> chromosome addition line 7S (Friebe et al. 1995)</td>
<td>Rc on 7SŁS (Friebe et al. 1995)</td>
</tr>
<tr>
<td>Designation in Fig. 1</td>
<td>Description</td>
<td>Rc gene</td>
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<tr>
<td>-----------------------</td>
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</tr>
<tr>
<td>CS/N</td>
<td><em>T. aestivum</em> ‘Chinese Spring’ (Chinese cultivar; stock earlier used to create CS-Aet 7D-1b; Pestsova et al. 2006), maintained in IPK stock collection</td>
<td>Colorless coleoptile</td>
</tr>
<tr>
<td>CS-Aet 7D-1b</td>
<td>Introggression line ‘Chinese Spring’-<em>Ae. tauschii</em> 7D (Pestsova et al. 2006)</td>
<td><em>Re</em>-D1 (Khlestkina et al. 2009b)</td>
</tr>
<tr>
<td>SN/N</td>
<td>Synthetic wheat <em>T. durum</em> × <em>Ae. tauschii</em> ‘Synthetic 6x’ (McFadden and Sears 1947), maintained in IPK stock collection</td>
<td><em>Re</em>-D1 (Khlestkina et al. 2009b)</td>
</tr>
<tr>
<td>Arbel 2</td>
<td><em>T. dicoccoides</em> accession, collected in Arbel, Israel in 2008</td>
<td>unknown</td>
</tr>
<tr>
<td>Arbel 15</td>
<td><em>T. dicoccoides</em> accession, collected in Arbel, Israel in 2008</td>
<td>unknown</td>
</tr>
<tr>
<td>Arbel 16</td>
<td><em>T. dicoccoides</em> accession, collected in Arbel, Israel in 2008</td>
<td>unknown</td>
</tr>
<tr>
<td>Gamla</td>
<td><em>T. dicoccoides</em> accession, collected in Gamla, Israel in 2008</td>
<td>Colorless coleoptile</td>
</tr>
<tr>
<td>Beit Oren</td>
<td><em>T. dicoccoides</em> accession, collected in Beit Oren, Israel in 2008</td>
<td>unknown</td>
</tr>
<tr>
<td>Imperial</td>
<td><em>S. cereale</em> (Canadian cultivar maintained in IPK stock collection)</td>
<td><em>Re</em>-R1 (Khlestkina et al. 2009a)</td>
</tr>
<tr>
<td>Onokhoiskaya</td>
<td><em>S. cereale</em> (Russian cultivar, maintained in ICG stock collection)</td>
<td>unknown</td>
</tr>
<tr>
<td>Selenga</td>
<td><em>Secale cereale</em> (Russian cultivar, maintained in MTAA stock collection)</td>
<td>unknown</td>
</tr>
<tr>
<td>131/731</td>
<td>Triticale originating from ‘Selenga’ (MTAA stock collection)</td>
<td>unknown</td>
</tr>
<tr>
<td>131/745</td>
<td>Triticale originating from ‘Selenga’ (MTAA stock collection)</td>
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<td>131/749</td>
<td>Triticale originating from ‘Selenga’ (MTAA stock collection)</td>
<td>unknown</td>
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<tr>
<td>131/797</td>
<td>Triticale originating from ‘Selenga’ (MTAA stock collection)</td>
<td>unknown</td>
</tr>
</tbody>
</table>

*Notes: ICG = Institute of Cytology and Genetics, Novosibirsk; IPK = Leibniz Institute of Plant Genetics and Crop Plant Research, Gatersleben; MTAA = Moscow K.A. Timiryazev Agricultural Academy.*
Results

The relative anthocyanin contents in coleoptiles of the 30 lines chosen for analysis were compared using OD530 values varying from 0.149 in *T. dicoccoides* ‘Gamla’ to 3.311 in *T. dicoccoides* ‘Arbel 2’. In coleoptiles assessed visually as colorless, the OD530 values varied from 0.149 to 0.267, and in red coleoptiles from 0.514 to 3.311 (Fig. 1). The difference between the values obtained for colorless coleoptiles (in common wheat cultivars, ‘Chinese Spring’, ‘Golubka’, and ‘Pyrothrix 28’ and in *T. dicoccoides* ‘Gamla’) and red ones was significant ($z = 1.96, p < 0.05$).

In addition to anthocyanin pigmentation of the coleoptile rye cultivars ‘Imperial’, ‘Onokhoiskaya’ and ‘Selenga’ had pigmented first leaves (Fig. 1). We suggest that the *Rc* gene in rye may have a pleiotropic effect on coloration of the first leaf, but a similar effect does not occur in wheat, wheat-rye addition lines or triticale. In ‘Selenga’, the relative anthocyanin content in the first leaf was significantly lower than that in the coleoptile ($z = 1.96, p < 0.05$), whereas in ‘Imperial’ and ‘Onokhoiskaya’ the values obtained for coleoptiles and leaves were similar ($z = 0.22$ and $1.53, p > 0.05$).

Anthocyanin content in coleoptiles of wheat genotypes

The darkest coleoptile pigmentation was observed in four *T. dicoccoides* accessions and the common wheat cultivar ‘Novosibirskaya 67’. The relative anthocyanin content in their coleoptiles was as high as 2.224-3.311 (Fig. 1; within group variation significance is presented in Table 2).
In two wheat genotypes, ‘Saratovskaya 29’ and ‘Chinese Spring’(‘Hope’ 7A), carrying the same gene Rc-A1, the relative anthocyanin contents in coleoptiles were significantly different (0.534 and 2.021; \( z = 1.96, p < 0.05 \)). In three genotypes, ‘Mironovskaya 808’, ‘Novosibirskaya 67’ and a synthetic wheat T. durum × Ae. tauschii ‘Synthetic 6x’ carrying Rc-D1, the relative anthocyanin contents in coleoptiles varied from 1.125 to 2.398 (Fig. 1). The differences were also significant \( (z = 1.96, p < 0.05) \). Comparison of the synthetic T. durum × Ae. tauschii ‘Synthetic 6x’ and the introgression line ‘Chinese Spring’-Ae. tauschii 7D carrying the Rc-D1 allele from the synthetic line indicated a suppressive effect of the ‘Chinese Spring’ background on Rc expression. The relative anthocyanin contents in the synthetic wheat and the introgression line were 1.386 and 1.765, respectively, and the difference was significant \( (z = 1.96, p < 0.05) \) (Fig. 1).

In wheat ‘Hope’ carrying Rc-A1 and Rc-B1, the relative anthocyanin content in the coleoptile was similar to that in ‘Chinese Spring’(‘Hope’ 7B) \( (z = 0.65, p > 0.05) \), and significantly lower than that in ‘Chinese Spring’(‘Hope’ 7A) \( (z = 1.96, p < 0.05; Fig. 1) \).

### Anthocyanin content in coleoptiles of wheat wheat-alien genotypes

Common wheat cultivar ‘Pyrothrix 28’ has colorless coleoptiles whereas wheat-barley chromosome substitution line ‘Pyrothrix 28’ (H. marinum 7Hm(7D)) has light-red coleoptiles. The OD\(_{530}\) value difference between colorless coleoptiles of ‘Pyrothrix 28’ and red coleoptiles of the wheat-barley chromosome substitution line was significant \( (z = 1.96, p < 0.05) \). Similarly, wheat ‘Chinese Spring’ has colorless coleoptiles whereas wheat-Aegilops chromosome addition lines ‘Chinese Spring’ + Ae. speltoides 7S, ‘Chinese Spring’ + Ae. longissima 7S and ‘Chinese Spring’ + Ae. searsii 7S have light-red coleoptiles (OD\(_{530}\) value difference between ‘Chinese Spring’ and the addition lines was significant, \( z = 1.96, p < 0.05 \)).

Common wheat cultivar ‘Saratovskaya 29’ and wheat-rye chromosome substitution line ‘Saratovskaya 29’ (‘Onokhoiskaya’ 2R(2D)) had light-red coleoptiles with similar anthocyanin contents (0.534 and 0.566, respectively, \( z = 0.22, p > 0.05 \)). Rye ‘Onokhoiskaya’ had red coleoptiles with OD\(_{530}\) (1.700) differing significantly from those of ‘Saratovskaya 29’ and ‘Saratovskaya 29’ (‘Onokhoiskaya’ 2R(2D)) \( (z = 1.96, p < 0.05) \). The OD\(_{530}\) values in rye ‘Imperial’ (1.261) and the addition line ‘Chinese Spring’ + ‘Imperial’ 4R (0.743) differed significantly from that in ‘Chinese Spring’ \( (z = 1.96, p < 0.05) \) but not from each other \( (z = 1.53, p > 0.05) \). The Rc gene of rye ‘Selenga’ inherited by the...
triticale lines (Table 1, Fig. 1) maintained its expression level in the triticale lines (z varied from 0.22 to 1.53, p > 0.05).

**Discussion**

The darkest coleoptile pigmentation was observed in four *T. dicoccoides* accessions and the common wheat cultivar ‘Novosibirskaya 67’ (OD_{530} as high as 2.224–3.311; Fig. 1). These wild emmer accessions may be potential donors of ‘strong’ *Rc* alleles for bread wheat, and may be useful for increasing stress resistance in seedlings. Earlier, the *Rc* allele conferring a high level of anthocyanin content initially originating from tetraploid wheat *T. aethiopicum* was introduced from cultivar ‘Purple Feed’ to ‘Saratovskaya 29’ (Arbuzova et al. 1998), and recently it was shown that the near-isogenic line obtained had a fivefold higher anthocyanin content in the coleoptile and higher salinity tolerance at the seedling stage in comparison with ‘Saratovskaya 29’ (Tereshchenko et al. 2010). The ‘Novosibirskaya 67’ *Rc-D1* allele conferring a relative anthocyanin content in the coleoptile as high as 2.398 (Fig. 1) may also have potential for improvement of stress resistance at the seedling stage. Furthermore, in ‘Novosibirskaya 67’, the *Rc-D1* gene is closely linked with genes determining intensive anthocyanin pigmentation of the stem, leaves and anthers (Khlestkina 2009b). Thus, this cultivar may be used as a source of a gene cluster determining strong anthocyanin pigmentation in different plant organs, which again may be important for plant defence.

In three wheat genotypes analyzed in this study, ‘Mironovskaya 808’, ‘Novosibirskaya 67’ and a synthetic wheat *T. durum* × *Ae. tauschii* ‘Synthetic 6x’, anthocyanin pigmentation of the coleoptile was controlled by *Rc-D1* (Khlestkina et al. 2002, 2008, 2009b). However, the relative anthocyanin contents in their coleoptiles were different (Fig. 1). The variation may be explained by allelic diversity at the *Rc-D1* locus, similar to that at the *Rc-A1* locus observed in ‘Saratovskaya 29’ and ‘Chinese Spring’ (‘Hope’ 7A) in the present study (Fig. 1) and earlier at the transcriptional level (Khlestkina et al. 2010).

In common wheat cultivar ‘Hope’, anthocyanin pigmentation on the coleoptile was previously shown to be controlled by *Rc-A1* and *Rc-B1*, with the anthocyanin content in ‘Hope’ similar to that in the chromosome substitution line ‘Chinese Spring’ (‘Hope’ 7A) and higher than that in ‘Chinese Spring’ (‘Hope’ 7B) (Gale and Flavell 1971). However, in the ‘Hope’ stock we analyzed in the current study, the relative anthocyanin content in the coleoptile was similar to that in ‘Chinese Spring’ (‘Hope’ 7B) and significantly lower than that in ‘Chinese Spring’ (‘Hope’ 7A). This may suggest that the ‘Hope’ stock used in the current study had probably lost its *Rc-A1* allele.

Substitution of common wheat cultivar ‘Pyrotrix 28’ chromosome 7D with barley *H. marinum* chromosome 7Hm resulted in coleoptile coloration of the substitution line ‘Pyrotrix 28’(*H. marinum* 7Hm(7D)). It can be suggested that *H. marinum* chromosome 7Hm carries a red coleoptile allele at the orthologous locus *Rc-H*"l. This gives additional support to the conclusion made earlier by Pershina et al. (2009) that *H. marinum* chromosome 7Hm possesses an ability to compensate for absence of chromosome 7D of common wheat. Because it, as well as the *Aegilops Rc-S1* alleles originating from *Ae. longissima,*
Ae. speltoides and Ae. searsii, confers only weak anthocyanin pigmentation (Fig. 1), Rc-Hm1 cannot be assumed as a source of strong enrichment of coleoptile color. Nevertheless, these alleles provide convenient morphological markers for the presence of the respective alien chromosomes (7S, 7Ss, 7Sl, or 7Hm).

Wheat-rye chromosome substitution line ‘Saratovskaya 29’(‘Onokhoiskaya’ 2R(2D)) carries the wheat Rc-A1 gene from ‘Saratovskaya 29’ and the rye structural anthocyanin biosynthesis gene F3h-R1 (encoding flavanone 3-hydroxylase; Khlestkina et al. 2009a). The anthocyanin contents in coleoptiles of ‘Saratovskaya 29’ and ‘Saratovskaya 29’(‘Onokhoiskaya’ 2R(2D)) were similar, whereas that in rye ‘Onokhoiskaya’ coleoptiles was significantly higher (Fig. 1). These results suggest that intensity of the coleoptile anthocyanin pigmentation is mainly determined by the regulatory gene Rc (which is different in ‘Onokhoiskaya’ in comparison with the other 2 lines) and is less affected by the structural F3h gene which may even have alien origin.

It was interesting to know whether the effect of the rye Rc gene can be modified in the wheat genetic background. We compared the relative anthocyanin contents in coleoptiles of wheat ‘Chinese Spring’ (colorless coleoptile), ‘Imperial’ rye (red coleoptile controlled by the Rc-R1 gene; Khlestkina et al. 2009a) and the wheat-rye chromosome addition line ‘Chinese Spring’+‘Imperial’ 4R carrying the Imperial Rc-R1 gene in ‘Chinese Spring’ background. The anthocyanin contents in coleoptiles of ‘Imperial’ and the addition line ‘Chinese Spring’+‘Imperial’ 4R differed significantly from that in ‘Chinese Spring’ but not from each other. Similarly, the Rc gene of rye ‘Selenga’ inherited by the triticale lines (Table 1, Fig. 1) maintained its expression level in the triticale lines (Table 1, Fig. 1). Thus, intensity of anthocyanin pigmentation in the coleoptiles of wheat-rye addition lines and triticale is determined by the rye Rc allele rather than effected by wheat genetic background. However, comparison of the synthetic T. durum × Ae. tauschii ‘Synthetic 6x’ and the introgression line ‘Chinese Spring’-Ae. tauschii 7D carrying the Rc-D1 allele from the synthetic line indicated a suppressive effect of the ‘Chinese Spring’ background on Rc expression (Fig. 1).

From the results presented we concluded that the four Triticum dicoccoides accessions originating from Israel and the Russian wheat cultivar ‘Novosibirskaya 67’ are good sources of germplasm to increase anthocyanin content in the coleoptiles of wheat, while rye Rc alleles such as that of the Russian cultivar ‘Selenga’ can be used to increase anthocyanin content in triticale seedlings. Comparative analyses of different genetic stocks showed that although anthocyanin level in coleoptiles is determined by particular Rc alleles, their effects can be modified by genetic background.

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