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Review

Genetics and chemistry of pigments in wheat grain – A review

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A B S T R A C T

Cereal grains contain many phytochemicals, some of which significantly influence the grain colour. Anthocyanins are accumulated in the aleurone or pericarp layer and give blue, purple or combination of these colours. Flavonoids, such as yellow C-glycosides of flavones, flavonols, flavanonols, proanthocyanidins and reddish-coloured phlobaphenes are mainly present in the outer layer of grains while carotenoids that are responsible for yellow grain are in the endosperm. Therefore, accumulation of these pigments in the grain can represent an important target in breeding programmes aimed at increasing the concentrations of bioactive components in grain and products. This review therefore summarises our current knowledge of anthocyanin and carotenoid pigments, their genetic control and variation in levels in different wheat lines.

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1. Introduction

Wheat is the most widely grown cereal crop in the world and bread wheat represents a staple food for human nutrition. The consumption of wholegrain wheat products is associated with a number of health benefits which may relate in part to the contents of phytochemicals. These show wide variation between wheat species and lines, as shown by analyses of bread wheat lines in the HEALTHGRAIN programme (Shewry et al., 2012; Shewry and Ward, 2012; Shewry and Hey, 2015). High levels of lipophilic carotenoids (lutein, zeaxanthin, β-carotene) are characteristic of einkorn and

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durum wheat (Lachman et al., 2013; Blanco et al., 2011). Anthocyanins give rise to pigmented grains, which vary widely in shade, and the combination of genes for different colours leads to very dark colour which in the literature is reported as "black colour" (Syed Jaafar et al., 2013; Garg et al., 2016). The important characteristics of black, purple, and blue grained wheats is that they contain natural anthocyanin compounds at higher levels than in red and white grained wheats.

Variation in colour components in the grain and grain products depends on genetic factors, growing conditions, and technological processes. Coloured wheat varieties may be a source of anthocyanins and carotenoids used for specific production of baking products, mainly made from whole grain.

The aim of this review is therefore to summarise the chemistry and genetic determination of the major pigments contained in colour-grained wheats.

2. Genetic determination of grain colour

The colour range for most grain cereals conforms with the "The Law of Homologous Series in Hereditary Variability," which was formulated in 1920 by N. I. Vavilov. It states that species and genera that are genetically closely related are usually characterized by a similar series of genetic variability. A similar range of grain colours to that in wheat therefore exists in rye, triticale, barley, oat, rice, maize (Abdel-Aal et al., 2006; Hills et al., 2007).

The expression of grain colour varies with the origin of the kernel tissue. In wheat the grain genetically consists of four types of tissue: pericarp, seed coat, embryo and endosperm. The pericarp and seed coat are maternal tissues derived from the carpel and integument, respectively. Because the purple colour of grain is expressed in the pericarp, it is not possible to observe segregation among the kernels inside the spike. In the case of the triploid endosperm, two doses of genetic information come from the maternal parent and one from the paternal parent. Because the aleurone layer is a part of the endosperm, the expression of blue aleurone or yellow endosperm colour depends upon the gene dose and therefore may result in the segregation of these colours among the kernels inside one spike or one plant. Because the genes for blue aleurone and purple pericarp are located on different chromosomes, a very wide range of grain colours can be observed in the F_2 generation determined by various combinations of genes. In addition, very dark grains, which result from a combination of genes for blue aleurone, purple pericarp, yellow endosperm, and red grain, could be present (Fig. 1).

Blue grain differs from purple grain not only in the composition of individual anthocyanins but also in their presence in individual layers which can be seen clearly on cross sections of kernels (Abdel-Aal and Hucl, 2003).

2.1. Red- and white-grained wheats

Red grain colour is common in most American and European wheats (Fig. 2a). It is controlled by one to three dominant alleles on the long arms of the three dominant *R-1* homologous genes located on the long arms of chromosomes 3A, 3B, and 3D (*R-A1*, *R-B1*, and *R-D1*, respectively). The alleles conferring red colour are designated *R-A1b*, *R-B1b* and *R-D1b*, and the alleles conferring white colour *R-A1a*, *R-B1a*, and *R-D1a* (McIntosh et al., 1998). A single locus expressing a dominant allele is sufficient to result in red colour. The degree of red colour is additive, the intensity depending on the number of R alleles. By contrast, white grain colour (Fig. 2b) is determined by the combination of three recessive alleles at *R-A1a*, *R-B1a*, and *R-D1a*.

The red pigment of the grain coat is formed from catechins and proanthocyanidins, which are synthesized via the flavonoid biosynthetic pathway (Himi et al., 2011) and are associated with a bitter flavour, a lower activity of hydrolytic enzymes, and better resistance to sprouting.

2.2. Yellow endosperm

Durum wheat has hard texture which, combined with its high protein content and gluten strength, makes it the wheat of choice for producing premium pasta products. Pasta made from durum is firm with consistent cooking quality. Durum kernels are amber-coloured with yellow endosperm, which gives semolina and pasta their golden colour. The contents of yellow pigments, lutein and zeaxanthin, have therefore been widely studied in *T. durum* (He et al., 2008). The yellow endosperm colour is determined mainly by two loci, *Psy1* and *Psy2*, located on chromosome groups 7 and 5, respectively (Pozniak et al., 2007). The most widely studied loci are *Psy1-A1* (7AL), *Psy1-B1* (7BL), *Psy1-D1* (7DL), *Psy2-A1* (5A) and *Psy2-B1* (5B) (Howit et al., 2009). Some hexaploid wheats also have yellow endosperm (Fig. 2c and d), but are not highly coloured.

2.3. Purple pericarp

Purple grain colour is conferred by the purple pericarp (*Pp*) genes, which were transferred to common wheat from tetraploid wheat (*Triticum turgidum* L. subsp. *abyssinicum* Vavilov) Ethiopia (Eticha et al., 2011). They result from the presence of anthocyanins in the pericarp of the grain. Two complementary genes were mapped in this tetraploid material: *Pp1* on the short arm of chromosome 7B and *Pp2* on chromosome 7A (Musilová et al., 2013). Dobrovolskaya et al. (2006) renamed the gene *Pp2* as *Pp3a* and located *Pp3b* to chromosome 2A. On the basis of mapping, the *Pp3*, *Pc*, *Pls* and *Plb* genes of *T. durum* are regarded as allelic to the *T. aestivum Pp3*, *Pc-B1*, *Pls-B1* and *Plb-B1* loci. However, the *T. durum* wheat *Pp* gene was mapped to the short arm of chromosome 7B (Khlestkina et al., 2010), whereas in hexaploid wheat it was reportedly located on the long arm (Dobrovolskaya et al., 2006). The genes *Pp1* and *Pp2* were also found in the hexaploid wheat variety 'Purple Feed', whereas the 'Purple' variety contained the *Pp1* and *Pp3* genes which were located on chromosome 2A. Later it was found that *Pp3* is composed of two alleles that have been named *Pp3a* and *Pp3b*. In crosses between the purple-grained wheats 'Purple' and 'Purple Feed' and the non-purple-grained 'Saratovskaya 29', a segregation ratio of 9 (purple) to 7 (non-purple) grains was obtained suggesting interactions of two dominant genes, *Pp1* and *Pp3*. The genes *Pp3a* and *Pp3b* were mapped to the centromeric region of chromosome 2A (Dobrovolskaya et al., 2006). Two complementary genes for purple grain colour were found in the variety 'Purple', one being mapped on the short arm of chromosome 7D 2.5 cM distal to the locus *Rc-D1* determining red coleoptile colour. This gene is in a similar position to the *Pp1* gene. It has been suggested that the *Pp* genes on chromosome 7B of tetraploid wheat and 7D chromosome in hexaploid wheat are orthologous and they were designated *Pp-B1* and *Pp-D1*, respectively (Tereshchenko et al., 2013). However, it is now known that cvs. 'Purple' and 'Purple Feed' have *Pp-D1* on chromosome 7DS but not *Pp-1* on chromosome 7B. A homoeologous set of *Pp1* genes is known (*Pp-A1* on 7AS, *Pp-B1* on 7BS and *Pp-D1* on 7DS). The *Pp1* and *Pp3* genes are complementary and encode different types of transcription factor (Gordeeva et al., 2015). The effects of combinations of *Pp3* and *Pp1* alleles on the transcription of *TaMyc1*, which encodes a MYC-like transcription factor, have been studied. In genotypes carrying the dominant *Pp3* allele, *TaMyc1* was strongly transcribed in the pericarp and at a lower level, also in the coleoptile, culm and leaf. It was found that the dominant allele *Pp-D1*