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Specifity of genetic determination of content of photosynthetic pigments in *Triticale*

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Abstract

Lines of winter hexaploid *Triticale* and their F_1 and F_2 hybrids differing in morphological structure, pigment contents, photosynthetic productivity, and grain crops were studied. F_1 hybrids received by crossing of *Triticale* lines contrasting in pigment contents showed in some cases a heterosis effect for chlorophyll (Chl) content per unit leaf area. Variation analysis demonstrated a polygenic control of *Triticale* pigment contents, and different rate of increase in F_2 generation. We found maternal type of heritability of Chl *b* content and Chl content in light-harvesting complex of photosystem 2.

Additional key words: chlorophyll, carotenoids, heritability.

Introduction

One of solutions of the problem of photosynthetic and crop productivity increase is genetic control of plant photosynthetic apparatus (PSA) formation (Austin 1982, Nichiporovich 1956, 1988, Nasyrov 1982, Chaïka *et al.* 1988, Chaïka 1996) as well as specifities of biosynthesis of photosynthetic pigments as its structural and functional components (Godnev 1963, Wettstein *et al.* 1974, 1995, Šesták 1977, Wang *et al.* 1977, Tarchevskiï and Andrianova 1980, Watanabe *et al.* 1993).

The success of cultivation of wheat-rye hybrid *Triticale* as an important alternative feed grain and fodder crop (Rao and Joshim 1979, Khotyljeva 1986, Gordeï 1992) stimulates detailed investigations of their PSA biogenesis and activity in general, and character of genetic determination of photosynthetic pigments in particular. Together with molecular genetic studies allowing to identify and characterise the specific genes responsible for photosynthetic functions, methods of quantitative genetics remain also helpful and informative (Russel 1998). The aim of present work was to determine contents of chlorophylls and carotenoids in winter hexaploid *Triticale* and to detect pigment content heritability and variation in *Triticale* lines and their F_1 and F_2 hybrids.

Materials and methods

Plants were grown in climate room (12-h photoperiod, irradiance of 80 W m^{-2}, temperature of 22 °C) or in field (experimental area of the Research Institute of Arable Farming and Fodders, Zhodino, Minsk Region, Belarus) during the season 1993 - 1995. *Triticale* lines had a hexaploid number of chromosomes (2n=42), and similar type of leaf and habitus. Dar Belarusi was selected from *Triticale* spring line K-346939 and winter *Triticale* line AD-206 at the Research Institute of Arable Farming and Fodders. CHD-888 was selected from winter *Triticale* line Lasko and winter rye line C1495/79 at the Institute of Selection and Acclimatisation of Plants, Radzikov, Poland.

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We analysed first leaves of 10-d-old seedlings (phase 10 according to Zadoks' code) (Zadoks *et al.* 1974), third leaves of whole plants at tillering as well as flag-leaves at earing (phases 26 and 33, respectively). The experiments were repeated three times. Content of Chl and Car per unit leaf area was determined in 100 % acetone extracts (Arnon 1949) with a spectrophotometer *Hitachi-150-20* (Tokyo, Japan). Leaf discs of 1.28 cm^2 were taken from the middle part of a leaf. Fifty plants of each genotype were used for the analysis. Pigment contents were calculated according to Shlyk (1971). Chl distribution in general pigment-protein complexes (PPC) was calculated basing on Leong and Anderson (1986). Heritability values (h^2) were detected according to Falconer (1970). Dominance degree percentage was found by a method proposed by Gustaffson and Dormling (1972). Inbreeding depression percentage was tested following Fisher (1965). Variation coefficients were calculated and correlation analysis was carried out according to Rokitskiĭ (1967), Falconer (1970), and Falconer and Douglas (1996).

Statistical analysis was made by *ANOVA* ($P \leq 0.05$) using software designed in the Laboratory of Mathematical Statistics (Institute of Genetics and Cytology, National Academy of Sciences, Minsk, Belarus). Statistical significance was assessed by Student's *t*-test.

Results

Pigment contents of parental winter hexaploid *Triticale* genotypes: According to previous results (Chaïka and Savchenko 1981, Kabashnikova 1987, Chernysheva and Bykov 1989, Dzyatkovskaya *et al.* 1991), maximal differences for Chl content in several cereal cultures appeared under stress and were less than 20 - 25 %. In *Triticale* seedlings significant differences in Chl and Car contents per unit leaf area and in PPC among contrasting genotypes we detected. Extreme values found for genotypes Dar Belarusi and CHD-888 reached 35 % for Chl *a*, 36 % for Chl *b*, and 35 % for Chl (*a*+*b*) (Fig. 1*A*), 10 % for Chl *a*/*b*, and 25 % for Car per unit leaf area (Fig. 1*B*); 27 % in light-harvesting complex of photosystem 2 (LHC2) (Fig. 1*C*), and 24 % for pigment contents in photosystems 1+2 (PS1+PS2) (Fig. 1*D*).

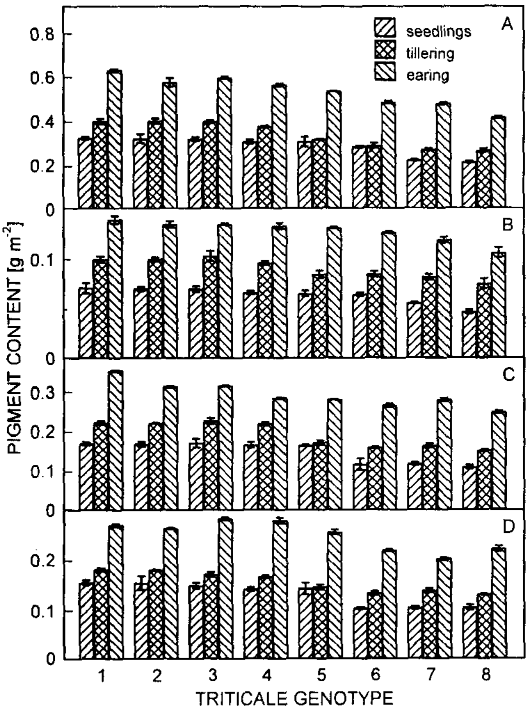

Fig. 1. Pigment contents: *A* - chlorophyll (Chl) and *B* - carotenoids (Car) per unit leaf area, *C* - Chl in light-harvesting complex (LHC2), *D* - Chl in photosystems (PS1+PS2) in seedlings of *Triticale* (*left*), at tillering stage (*middle*), or earing stage (*right*). *1* - Dar Belarusi; *2* - L-219; *3* - Ales; *4* - Mihas; *5* - Ruh, *6* - Polus; *7* - Zenit; *8* - CHD-888.

Analogous ranging for photosynthetic pigment contents among tested *Triticale* forms were found in the field conditions. At both tillering and earing, Dar Belarusi exceeded CHD-888 by 30 % in Chl *a*; by 36 % in Chl *b*; by 33 % in Chl (*a*+*b*) (Fig. 1*A*); by 15 % in Chl *a*/*b*. For Car content this difference was 29 % (Fig. 1*B*). In PPC of thylakoid membrane Dar Belarusi exceeded CHD-888 by 30 % for Chl content in LHC2, and by 20 % in pigments for PS1+PS2 (Fig. 1*C*,*D*), $P = 0.05$.

Thus, Dar Belarusi and CHD-888 differed most within the analysed photosynthetic pigment characteristics and were chosen as initial parental forms for hybridisation. We studied the following genotypes: Dar Belarusi, CHD-888, Dar Belarusi × CHD-888,F_1; CHD-888 × Dar Belarusi,F_1; Dar Belarusi × CHD-888,F_2; CHD-888 × Dar Belarusi,F_2.

Specifity of pigment content heritability and variation in F_1 and F_2 *Triticale* hybrids: To estimate the influence of inbreeding crossing on the analysed *Triticale* parent forms, we detected inbreeding depression percentage. Values of inbreeding depression both for Dar Belarusi and CHD-888 were less than 6 - 8 % and been observed during seedlings, tillering and earing.

Apart from inbreeding depression, heterosis or hybrid vigour is a phenomenon common for plant and animal F_1 hybrids that results in some cases in changed morphology and/or metabolic features compared with parents (Frankel 1983, Russel 1998). For hybrid Dar Belarusi × CHD-888, F_1 it was found 17 % mid-parent heterosis at tillering, and

15 % mid-parent heterosis at earing in Chl (*a*+*b*) content. For F_1 *Triticale* hybrid CHD-888 × Dar Belarusi we detected 13 % mid-parent heterosis at earing in Chl (*a*+*b*) content (Fig. 2).

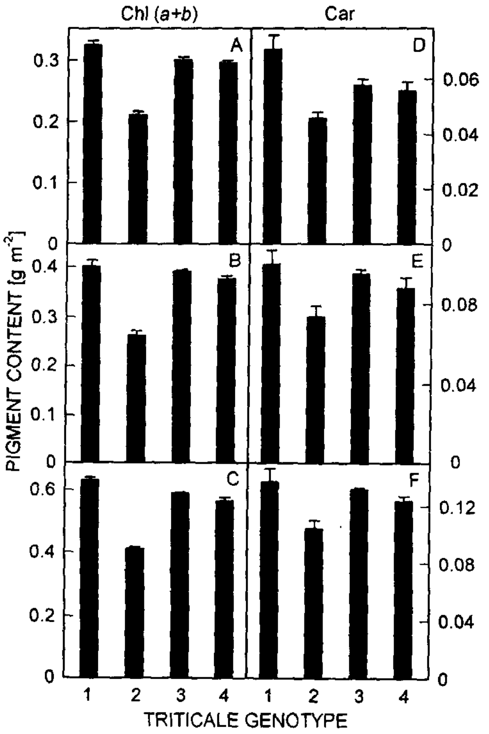

Fig. 2. Pigment contents per unit leaf area in *Triticale* lines and their F_1 hybrids: chlorophyll (Chl) and carotenoids (Car) in seedlings (*A, D*), at tillering (*B, E*), or earing (*C, F*) phases, respectively. *1* - Dar Belarusi; *2* - CHD-888; *3* - Dar Belarusi × CHD-888,F_1; *4* - CHD-888 × Dar Belarusi,F_1.

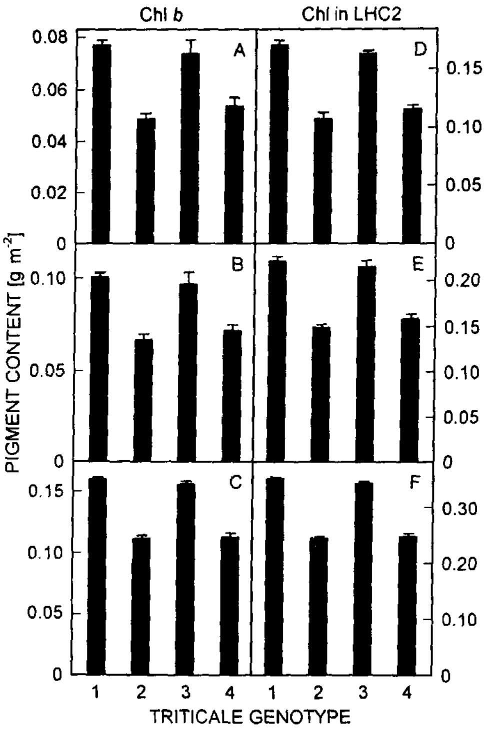

Fig. 3. Pigment contents per unit leaf area in *Triticale* lines and their F_1 hybrids: chlorophyll *b* (Chl *b*) and chlorophyll in light-harvesting complex of photosystem 2 (Chl in LHC2) in seedlings (*A, D*), at tillering (*B, E*), or earing (*C, F*) stages, respectively. *1* - Dar Belarusi; *2* - CHD-888; *3* - Dar Belarusi × CHD-888,F_1; *4* - CHD-888 × Dar Belarusi,F_1.

Analysis of direct and inverse F_1 hybrids of Dar Belarusi × CHD-888, and CHD-888 × Dar Belarusi showed a reciprocal effect for Chl *b* content per unit leaf area and Chl content in LHC2 (Fig. 3). For Chl *a* content per unit leaf area, Chl (*a*+*b*) content per unit leaf area, Chl *a*/*b*, Car content per unit leaf area, and Chl content in PS1+PS2 we did not detect any reciprocal effect. Indicated specifities of *Triticale* pigment formation were observed both in seedlings and whole plants, however, at earing the phenomenon was expressed more intensively.

The calculation of dominance degree for high to low pigment contents per unit leaf area showed that in seedling phase and at tillering the dominance percentage for high to low values for all analysed traits was increased in comparison to the end of vegetation (earing). The dominance for Chl *a* content per unit leaf area reached 45 - 69 % and 4 - 11 %, for Chl *b* content 50 - 72 % and 20 - 33 %, for Chl (*a*+*b*) content 48 - 70 % and 13 - 26 %, for Chl *a*/*b* 22 - 30 % and 10 - 11 %, for Car content per unit leaf area 40 - 45 % and 20 - 25 % at the 10-d-old seedlings, tillering, and earing stages, respectively. Dominance degrees for pigment contents in PPC were: for Chl content in LHC2 43 - 51 % at the stages of seedling and tillering, 15 - 20 % at the stage of earing; for pigment contents in PS1+PS2 37 - 39 % at the first ones, and 10 - 16 % at the second one, respectively.

Calculations of heritability (h^2) of *Triticale* pigments showed maxima for Chl *a*, Car content per unit leaf area and Chl *a*/*b* (Table 1). Chl (*a*+*b*) content per unit leaf area and Chl content in PS1+PS2 had a middle values of h^2, whereas Chl *b* content per unit leaf area and Chl content in LHC2 had a minimum heritability. A certain increase in h^2 values at tillering and earing in comparison to seedling stage for all studied characteristics was found. At earing compared to tillering, Chl *a* and Car contents per unit leaf had more increased heritability values, whereas for Chl *b* and Chl (*a*+*b*) contents per unit leaf area, Chl *a*/*b*, Chl content in PS1+PS2, and Chl content in LHC2 the h^2 values did not practically change. During whole plant ontogeny the heritability values of pigment traits for Dar Belarusi were higher than for CHD-888.

Chl and Car biosynthetic pathways are considered to be polygenically determined (Wettstein *et al.* 1974, Goodwin 1988, Suzuki *et al.* 1997). Character of change of variation coefficients of *Triticale* pigment contents was general in accordance with present explanations of polygenic inheritance mechanisms. Thus, F_1 *Triticale* hybrids during their development showed intermediate pigment contents characters between parental genotypes, and close to the last ones rates of variation; whereas in F_2 hybrids variation coefficients increased in comparison with parental forms, and F_1 hybrids together with similar to F_1 means of studied Chl and Car contents. The variation increase was different for each of studied pigment features.

Variation coefficients of Chl and Car contents per unit leaf area and in PPC were fairly small both for the *Triticale* seedlings and whole plants. Minimum increase (1.1 - 1.2 times) of variation coefficients in F_2 generation compared with parental forms was detected for Car content per unit leaf area (Table 2). Variation of Chl *a* in the second generation was increased 1.3 - 1.5 times, and Chl (*a*+*b*) 1.2 - 1.5 times compared with parent genotypes. Maximum increases of variation in F_2 were found for Chl *b* content per unit leaf area (2.6 times), Chl *a*/*b* (2.5 times), and for Chl content in LHC2 (2.4 times).

Table 1. Heritability values (h^2) of *Triticale* pigment contents. Means ± SE.

Stage	Cultivar	Chl *a*	Chl *b*	Chl (*a*+*b*)	Chl *a*/*b*	Car	Chl LHP2	Chl PS1+PS2
Seedling	Dar Belarusi	0.33±0.06	0.24±0.03	0.29±0.09	0.35±0.07	0.35±0.01	0.19±0.07	0.27±0.03
	CHD-888	0.30±0.09	0.19±0.05	0.20±0.04	0.29±0.11	0.36±0.02	0.16±0.03	0.22±0.07
Tillering	Dar Belarusi	0.51±0.02	0.42±0.03	0.45±0.02	0.48±0.01	0.50±0.01	0.37±0.11	0.43±0.04
	CHD-888	0.46±0.01	0.40±0.02	0.42±0.02	0.46±0.01	0.49±0.03	0.36±0.05	0.43±0.07
Earing	Dar Belarusi	0.72±0.01	0.44±0.03	0.48±0.02	0.51±0.01	0.60±0.02	0.41±0.09	0.42±0.11
	CHD-888	0.60±0.03	0.34±0.02	0.45±0.02	0.47±0.03	0.59±0.01	0.35±0.08	0.40±0.08

Table 2. Variations of pigment contents in parental and hybrid *Triticale* genotypes at the stage of earing, VP_1, VP_2, VF_1, and VF_2 coefficients of variation of pigment contents in Dar Belarusi, CHD-888, Dar Belarusi × CHD-888, F_1 and Dar Belarusi × CHD-888, F_2, respectively. Means ± SE.

Parameter	VP_1	VP_2	VF_1	VF_2	VF_2/VP_1	VF_2/VP_2
Chl *a*	2.33±0.25	2.87±0.30	2.96±0.31	3.53±0.29	1.5	1.3
Chl *b*	3.42±0.36	4.05±0.48	3.23±0.34	8.91±0.94	2.6	2.2
Chl (*a*+*b*)	2.24±0.24	2.78±0.33	2.94±0.31	3.34±0.35	1.5	1.2
Chl *a*/*b*	1.57±0.17	1.92±0.20	1.71±0.18	3.97±0.72	2.5	2.0
Car	1.55±0.03	1.80±0.21	1.61±0.17	1.92±0.20	1.2	1.1
Chl LHC2	2.38±0.25	3.11±0.48	3.24±0.34	5.84±0.64	2.4	1.9
Chl PS1+PS2	3.06±0.31	2.91±0.30	3.34±0.35	5.19±0.55	1.7	1.8

Correlation analysis: Determination of photosynthetic pigment contents is a marker of PSA activity, in some cases directly correlated with plant potential and crop productivity (Tarchevskiї and Andrianova 1980, Chaïka *et al.* 1988). We found a significant high positive correlation for analysed *Triticale* forms Dar Belarusi and CHD-888 and their hybrid Dar Belarusi × CHD-888, F_1 between Chl content and mass of 1000 kernels or mass of kernels in plant. At earing the correlation coefficients for indicated genotypes were $r^2 = +0.82 - +0.87$ for Chl (*a*+*b*) content per unit leaf area and mass of 1000 kernels, and $r^2 = +0.58 - +0.76$ for Chl (*a*+*b*) content per unit leaf area and mass of kernels in plant. There was no positive correlation between Car content and *Triticale* crop characters.

Discussion

The pigment contents in studied *Triticale* lines both in seedlings and further stages confirm previous results (Chaïka and Savchenko 1981, Kabashnikova 1987, Dzyatkovskaya *et al.* 1991), and thus it is possible to use seedlings as model for studying pigments in field conditions. Chl and Car differences of 25 - 36 % in contrast *Triticale* genotypes are sufficient (Rokitskiї 1967) to further hybridisation and study of pigment genetic specifities. Small inbreeding depression (Fisher 1965), confirms correctness of choice of Dar Belarusi and CHD-888 as parental forms for hybridisation.

The genetic basis of heterosis or hybrid vigour is not yet explained. Heterosis is caused by various factors, such as different types of nuclear (Russel 1998) and cytoplasmic (Srivastava 1983) gene interactions or by the influence of variable environment (Falconer 1970). The analysed *Triticale* genotypes and their F_1 and F_2 hybrids have been developed in equal growing conditions that may rule out a role of environmental factors in their forming. Detection of mid-parent heterosis in Chl contents in studied F_1 *Triticale* hybrids corresponds with data of Krebs *et al.* (1996), who found heterosis in pigment content in maize, results of Gordeï (1992), who notified that frequency and effectivity of heterosis in *Triticale* considerably depended of crossing combinations and analysed features, and data of Synková *et al.* (1997), who observed that differences in pigment contents in *Lycopersicon esculentum* Mill were significantly dependent on plant age.

A reciprocal crossing (Klug and Gummings 1986) is widely used to determine the role of extranuclear effects in heritability by taking into account possible maternal inheritance phenomena. Maternal inheritance of Chl content in some higher plants was described by Anderson (1923), Demeres (1927), Karper and Conner (1931), and Robertson (1937). Analysis of green seedlings and seedlings with Chl deficiencies allowed to speculate about possible parallelism of Chl characters in heredity of sorghum and maize (Karper and Conner 1931), and to accept a "cytoplasmic" explanation of this phenomenon postulating the main role of female gamete in inheritance of Chl features (Demeres 1927). Our results of the reciprocal effect (maternal inheritance) for Chl *b* content per unit leaf area and Chl content in LHC2 showed a significant role of cytoplasmic, preferably chloroplast genome in heritability of *Triticale* pigments.

Chl *b* differs from Chl *a* by substituted methyl group in ring 2 (position 3) of its Mg-tetrapyrrol structure, and seems to be synthesised from precursor of Chl *a*, chlorophyllide *a* or direct from Chl *a via* hydroxymethyl intermediate by an oxygenase enzyme (Wettstein *et al.* 1995, Porra 1997). Chl *b* may also be formed from its precursor, chlorophyllide *b* before Chl *a* formation (Schoch *et al.* 1995), using Chl *a* as possible positive effector (Bendarik and Hoober 1985). Based on detection of Chl biosynthesis genes in chloroplast DNA of black pine (Wakasugi *et al.* 1994), and their characterisation in green plastids of other conifers (Karpinska *et al.* 1997) and *Chlorella vulgaris* (Wakasugi *et al.* 1997), we propose that *Triticale* chloroplast genome contains genes or groups of genes encoding some key enzymes of Chl *a* and/or Chl *b* biosynthesis pathways. Chloroplast genome probably influences on regulation of the Chl *b* biosynthetic relationships: *via* chlorophyllide *a*/Chl *a* or *via* chlorophyllide *b*. These hypothesis require further investigations. Cytoplasm with optimal PSA pigment formation may be used in *Triticale* breeding.

Chl *b* is one of the main components of light-harvesting complex of photosystem 2 of thylakoid membrane (Paulsen 1993). This may substantiate maternal inheritance for Chl content in LHC2. The reciprocal effect for this character at earing may be connected with possible activation of additional genes and/or gene groups and combinations to more effective expression of these characters at the end of vegetation.

Dominance degree for all examined pigment features reflect the incomplete dominance for high to low pigment contents in our *Triticale* genotypes. Detected relatively high heritabilities indicate a significant contribution of genes in variation of Chl and Car content of *Triticale* populations. Dar Belarusi had higher than CHD-888 heritability coefficients (h^2), and is more appropriate for selection for pigment characters.

Observed increased dominance for seedling and tillering phases than for earing as well as increased h^2 values at tillering and earing than in seedlings for all studied pigment characters may be used in practical agriculture. Small means of variation coefficients both for seedlings as whole plants evidence for low variation of pigment traits in the analysed genotypes. The increase of variation coefficients in F_2 compared with parental forms and F_1 was different for each analysed pigment feature, and illustrated the segregation on studied pigment traits. Similarly, Lemesh (1989) observed higher variation coefficients for Chl *b* than for Chl *a* in the second generation of maize hybrids. Maximum increase of variation in F_2 wheat hybrids for Chl *a*/*b* and Chl content in LHC2 was found by Watanabe *et al.* (1993).

Results of our analysis of variation coefficients of pigment traits demonstrated a polygenic control of Chl formation that agreed with other results. Thus, Chl synthesis is encoded by numerous structural and regulatory genes (Wettstein *et al.* 1974, Wakasugi *et al.* 1994, Suzuki *et al.* 1997). Genes for biosynthesis of Chl and Car in *Rhodopseudomonas capsulata* are genetically intimately related and tightly clustered (Britton 1988). Relatively small variation coefficients for *Triticale* pigment contents and their insignificant increase in second generation of hybrids may be explained by possible specifical clustering of genes controlling Chl and Car formation. The study of gene effects on the formation of *Triticale* pigments and/or providing increase of variation of Chl *b* in preference to Chl a in F_2 generation may be the aim of further investigations.

Our correlation analysis confirmed results of Tarchevskiï and Andrianova (1980) evidence that Chl content in some cases represents breeding interest as one of the possible test factors of high crop productivity. Thus, relatively high heritability and significant small variation in *Triticale* pigment contents together with their correlation with some crop parameters may be a practical goal of present agriculture.

References

Anderson, E.G.: Maternal inheritance of chlorophyll in maize. - Bot. Gaz. **76**: 411-418, 1923.

Arnon, D.I.: Cooper enzymes in isolated Chloroplasts. Polyphenoloxidase in *Beta vulgaris*. - Plant Physiol. **24**: 1-15, 1949.

Austin, R.B., Morgan C.L., Ford, M.A., Bhagwat, S.G.: Flag leaf photosynthesis of *Triticum aestivum* and related diploid and tetraploid species. - Ann. Bot. **49**: 177-189, 1982.

Bendarik, F., Hoober, K.J.: Biosynthesis of a chlorophyllide *b*-like pigment in phenanthroline-treated *Chlamydomonas reinhardtii* y-1. - Arch. Biochem. Biophys. **240**: 369-379, 1985.

Britton, G.,: Biosynthesis of carotenoids. - In: Goodwin, T.W. (ed.): Plant Pigments. Pp. 133-182. Academic Press, London - Toronto 1988.

Chaïka, M.T.: [Chlorophyll biosynthesis and biogenesis of photosynthetic apparatus.] - Timiryaz. Chteniya **54**: 1-71, 1996. [In Russ.]

Chaïka, M.T., Laman, N.A., Grib, S.I.: [Investigation of connection between growth and photosynthesis together with productive process during selection of cereals.] - In: Tarchevskiï, I.A. (ed.): Fotosintez i Produktsionnyï Protsess. Pp. 5-28. Nauka, Moskva 1988. [In Russ.]

Chaïka, M.T., Savchenko, G.E.: Biosintez Khlorofilla v Protsesse Razvitiya Plastid. [Biosynthesis of Chlorophyll During Plastid Development.] - Nauka i Tekhnika, Minsk 1981. [In Russ.]

Chernysheva, S.B., Bykov, O.D.: [Genotypical diversity and drought resistance of wheat cultivars for some photosynthetic parameters.] - Nauch. Trudy Prikl. Bot. Genet. Selekts. **27**: 100-105, 1989. [In Russ.]

Demeres, M.: A second case of maternal inheritance of chlorophyll in maize. - Bot. Gaz. **84**: 139-155, 1927.

Dzyatkovskaya, E.N., Kakhnovich, L.V., Khodorenko, L.A., Petrenko, A.V.: [Specifities of pigment-protein complexes accumulation in barley seedlings with different productivity.] - Fiziol. Rast. **4**: 662-665, 1991. [In Russ.]

Falconer, D.S.: Heritability. - In: Falconer, D.S. (ed.): Introduction to Quantitative Genetics. Pp. 164-185. Oliver and Boyd, Edinburg - Glasgow 1970.

Falconer, D.S., Douglas, S.: Introduction to Quantitative Genetics. - Longman, Harlow 1996.

Fisher, R.A.: The Theory of Inbreeding. - Oliver and Boyd, Edinburgh 1965.

Frankel, R.: Heterosis: Reappraisal of Theory and Practice. - Springer-Verlag, Berlin - Heidelberg 1983.

Godnev, T.N.: Khlorofill, ego Stroenie i Obrazovanie v Rastenii. [Chlorophyll, its Structure and Formation in Plant.] - Nauka i Tekhnika, Minsk 1963. [In Russ.]

Goodwin, T.W.: Plant Pigments. - Academic Press, London - Toronto 1988.

Gordeï, I.A.: [Specifities of productive features formation and heredity of alloploic populations of new *Triticale* forms.] - In: Gordeï, I.A. (ed.): *Tritikale*: Geneticheskie Osnovy Sozdaniya. [*Triticale*: Genetic Bases of Formation.] Pp. 148-207. Nauka i Tekhnika, Minsk 1992. [In Russ.]

Gustaffson, A., Dormling, L.: Dominance and overdominance in phytotron analysis of monohybrid barley. - Hereditas **2**: 183-215, 1972.

Kabashnikova, L.F.: Osobennosti Organizatsii Fotosinteticheskogo Apparata u Sortov Yachmenya Raznoï Produktivnosti. [Specifities of Photosynthetic Apparatus Organisation in Barley Cultivars with Different Productivity.] - Ph.D. Thesis. Institute of Photobiology, Minsk 1987. [In Russ.]

Karper, R.E., Conner, A.B.: Inheritance of chlorophyll characters in sorghum. - Genetics **16**: 291-308, 1931.

Karpinska, B., Karpinski, S., Haellgren, J.E.: The chlB gene encoding a subunit of light-independent protochlorophyllide reductase is edited in chloroplasts of conifers. - Curr. Genet. **31**: 343-347, 1997.

Khotyljeva, L.V.: *Tritikale*: Sozdanie i Perspektivy Ispol'zovanija. [*Triticale*: Creation and Perspectives of Using.] - Nauka i Tekhnika, Minsk 1986. [In Russ.]

Klug, W.S., Gummings, M.R.: Concepts of Genetics. - Merril Publishing Co., Columbus - Sydney 1986.

Krebs, D., Synková, H., Avratovščuková, N., Kočová, M., Šesták, Z.: Chlorophyll fluorescence measurements for genetic analysis of maize cultivars. - Photosynthetica **32**: 595-608, 1996.

Lemesh, V.A.: Nasledovanie Fotosinteticheskih Priznakov u Mezhlineïnykh Gibridov Kukuruzy. [Heredity of Photosynthetic Features in Interlinear Maize Hybrids.] - Ph.D. Thesis. Institute of Genetics and Cytology, Minsk 1989. [In Russ.]

Leong, T.Y., Anderson, J.M.: Light-quality and irradiance adaptation of the composition and function of the pea thylakoid membrane. - Biochim. biophys. Acta **850**: 57-63, 1986.

Nasyrov, Yu.S.: [Genetics of photosynthesis in relation to selection problems.] - Sel'skohoz. Biol. **6**: 834-839, 1982. [In Russ.]

Nichiporovich, A.A.: [Photosynthesis and theory of high crops.] - Timiryaz. Chteniya **15**: 1-93, 1956. [In Russ.]

Nichiporovich, A.A.: Fotosinteticheskaya Deyatel'nost' Rasteniï kak Osnova ikh Produktivnosti v Biosfere i Zemledelii. [Plant Photosynthetic Activity as the Basis of Their Productivity in Biosphere and Agriculture.] - Nauka, Moskva 1988. [In Russ.]

Paulsen, H.: Assembly and reconstruction of chlorophyll *a/b*-containing complexes. - In: Sundquist, C., Ryberg, M. (ed.): Plastids: Synthesis and Assembly. Pp. 335-354. Academic Press, San-Diego - Toronto 1993.

Porra, R.: Recent progress in porphyrin and chlorophyll biosynthesis. - Photochem. Photobiol. **65**: 492-516, 1997.

Rao, R., Joshim, V.: Inheritance of elements of productivity of hexaploid *Triticale*. - Z. Pflanzenzücht. **62**: 230-236, 1979.

Robertson, D.W.: Maternal inheritance in barley. - Genetics **22**: 104-113, 1937.

Rokitskiï, P.F.: Vvedenie v Statisticheskuyu Genetiku. [Introduction to Statistical Genetics.] - Vysshaya Shkola, Minsk 1967. [In Russ.]

Russel, P.J.: Genetics. - Benjamin/Cummings Publ. Co., Menlo Park - Amsterdam 1998.

Schoch, S., Helfrich, M., Wiktorsson, B., Sundqvist, C., Ruediger, W., Ryberg, M.: Photoreduction of zinc protopheophorbide *b* with NADPH-protochlorophyllide oxidoreductase from etiolated wheat (*Triticum aestivum*). -

Eur. J. Biochem. **229**: 291-298, 1995.

Šesták, Z.: Photosynthetic characteristics during ontogenesis of leaves. I. Chlorophylls. - Photosynthetica **11**: 367-448, 1977.

Shlyk, A.A.: [Determination of chlorophyll and carotenoids in green leaves extracts.] - In: Shlyk, A. (ed.): Biokhimicheskie Metody v Fiziologii Rasteniĭ. [Biochemical Methods in Plant Physiology.] Pp. 154-170. Nauka, Moskva 1971. [In Russ.]

Srivastava, H.K.: Heterosis and intergenomic complementation: mitochondria, chloroplast and nucleus. - In: Frankel, R. (ed.): Heterosis: Reappraisal of Theory and Practice. Pp. 261-286. Springer, Berlin 1983.

Suzuki, J.Y., Bollivar, D.W., Bauer, C.E.: Genetic analysis of chlorophyll biosynthesis. - Annu. Rev. Genet. **31**: 61-89, 1997.

Synková, H., Wilhelmová, N., Holá, D., Haisel, D., Šesták, Z.: Comparison of chlorophyll fluorescence kinetics and photochemical activities of isolated chloroplasts in genetic analysis of *Lycopersicon esculentum* Mill. hybrids. - Photosynthetica **34**: 427-438, 1997.

Tarchevskiĭ, I.A., Andrianova, U.E.: [Pigment content as an index of photosynthetic apparatus efficiency in wheat.] - Fiziol. Rast. **2**: 341-349, 1980. [In Russ.]

Wakasugi, T., Toshiyki, N., Kapoor, M., Siguta, M., Ito, M., Ito, S., Tsudzuki, J., Nakashima, K., Tsudzuki, T., Suzuki, Y., Hamara, A., Ohta, T., Inamura, A., Yoshinaga, K., Sugiura, M.: Complete nucleotide sequence of Chloroplast genome from the green alga *Chlorella vulgaris*: The existence of genes possibly involved in Chloroplast division. - Proc. nat. Acad. Sci. USA **94**: 5967-5972, 1997.

Wakasugi, T., Tsudzuki, J., Ito, S., Nakashima, K., Tsudzuki, T., Sugiura, M.: Loss of all *ndh* genes as determined by sequencing the entire chloroplast genome of the black pine *Pinus thunbergii*. - Proc. nat. Acad. Sci. USA **91**: 9794-9798, 1994.

Wang W., Boynton, J.E, Gillham, N.W.: Genetic control of chlorophyll biosynthesis: effect of increased δ-aminolevulinic acid synthesis on the phenotype of y-1 mutant of *Chlamydomonas*. - Mol. gen. Genet. **152**: 7-12, 1977.

Watanabe, N., Ogawa, A., Furuta, I.: Diversity of chlorophyll *a/b* ratio in durum wheat accessions and its association with photosynthetic rate. - J. Genet. Breed. **47**: 205-210, 1993.

Wettstein, D. von, Goudh, S., Kannangara, G.: Chlorophyll biosynthesis. - Plant Cell **7**: 1039-1057, 1995.

Wettstein, D. von, Kahn, A., Nielsen, O.F.: Genetic regulation of chlorophyll synthesis analysed with mutants of barley. - Science **184**: 800-802, 1974.

Zadoks, J.C., Chang, T.T., Konzak, C.F.: A decimal code for the growth stages of cereals. - Weed Res. **14**: 415-421, 1974.