PHOTOSYNTHETICA 38 (3): 455-463, 2000

Organisation of photosynthetic apparatus of *Triticale* in relation to productivity

S.N. KABANOVA*, L.F. KABASHNIKOVA, E.V. SERDUCHENKO, L.N. KALITUHO, and M.T. CHAÏKA**

Institute of Photobiology, National Academy of Sciences of Belarus, Akademicheskaya str. 27, Minsk, 220072, Republic of Belarus

Abstract

Chlorophyll (Chl) content, photochemical activity of chloroplasts as well as photosynthetic and crop productivity were studied in different winter hexaploid *Triticale* (×*Triticosecale* Witt.) lines and their F_1 hybrids. Heterosis enhanced Chl content, photosynthetic potential, photosynthetic productivity, and grain yield only in several F_1 hybrids of *Triticale*. Indication in some genotypes of close correlations among morphological structure, Chl content, photochemical activity of chloroplasts, photosynthetic potential, and plant productivity may be used in breeding practice of *Triticale*.

Additional key words: chlorophyll; genotypes; grain yield; heterosis; hybrids; leaf area; photochemical activity of chloroplasts; plant height; productivity; seedling length.

Introduction

The interspecific man-made crop *Triticale* attracts great attention owing to high productivity of wheat and adaptability to environmental influences of rye (Quinones *et al.* 1972, Hoerlein and Valentine 1995). It seems to be an alternative feed grain and fodder crop (Gupta and Priyadarshan 1982, Royo *et al.* 1999).

The study of factors determining plant productivity is the main objective of current breeding programs (Clarke *et al.* 1998, Rozynek *et al.* 1998, Royo and Blanko 1999). One of these factors is the efficiency of photosynthetic apparatus (PSA) machinery (Baker and Ort 1992, Ishii 1993, Hudák 1997). Structure and functions of PSA both of wheat and rye is in general clear, but stays under progressive research (Niziołek *et al.* 1982, Tanaka *et al.* 1982, Ernst *et al.* 1990, Law and Crafts-Brandner 1999). In contrast, *Triticale* PSA organisation seems to be more complex and is not studied in detail.

As a marker of PSA activity, Chl content (Šesták 1977, Tarchevskiï and Andrianova 1980, Kura-Hotta *et al.* 1987, Gaussoin *et al.* 1997) and distribution (Chaïka *et al.* 1988, Chaïka 1996) in pigment-protein complexes of photosynthetic membrane (PPC) and at different levels of plant organisation (Austin 1992, Baker 1996, Wohlfahrt *et al.* 1999), *i.e.*, in single chloroplast, leaf, whole plant, or canopy, may be used.

Study of plant hybrids is important for possible use and prognosis of heterosis effect in practical agriculture (Murayama *et al.* 1987, Maluszynski 1989, Vaishlya *et al.* 1998). Therefore, the aim of the present work was: (*a*) to detect some structural and functional specifics of *Triticale* pigment apparatus, (*b*) to analyse correlations between Chl content at different levels of plant organisation (membrane, chloroplast, leaf, plant, canopy) and morphology, and (*3*) to find their relations to productivity in some winter hexaploid *Triticale* lines and their F_1 hybrids.

Materials and methods

The objects of investigations were new lines of winter hexaploid *Triticale* and their F_1 hybrids selected at the Research Institute of Agriculture and Fodder (Agrarian Academy of Sciences, Zhodino, Minsk region, Belarus).

Received 17 August 2000, *accepted* 26 October 2000.

*e-mail: Svetlana.Kabanova@uni-duesseldorf.de

**Deceased.

Acknowledgements: We thank Prof. S.I. Grib and Dr. V.N. Bushtevich (Research Institute of Agriculture and Fodder, Agrarian Academy of Sciences, Zhodino, Minsk Region, Belarus) for supply of *Triticale* seed material. We are also grateful to Prof. L.V. Khotyljova and Dr. L.A. Tarutina (Institute of Genetic and Cytology, Academy of Sciences, Minsk, Belarus) for their helpful comments on the work. This manuscript is a part of Ph.D. thesis of S.N.K.

Plants were grown in laboratory (climate room, 12-h photoperiod, 80 W m^{-2}, 22 °C) and field conditions (experimental area of the above Institute) in crop seasons 1993-95. Primary leaves in 10-d-old seedlings [phase 10 according to code of Zadoks *et al.* (1974) code], third leaves in whole plants at the stages of tillering and scrolling, and flag leaves at the stages of heading and grain filling (phases 26, 28 and 33, 35 according to Zadoks' code, respectively) were taken for measurements. *Triticale* lines and hybrids had a hexaploid number of chromosomes (2 n = 42), and similar type of leaf and habitus.

Total leaf area was detected by methods proposed by Forbes and Watson (1992) using software designed in the laboratory of photosynthetic apparatus physiology, Institute of Photobiology, National Academy of Sciences, Minsk, Belarus. Dry matter was determined after overnight incubation of leaflets at 80 °C and further cooling in vacuum. Chl content in PPC was determined according to Leong and Anderson (1986). Numbers of chloroplasts per cell and cells per unit leaf area were tested according to Meek (1976). Chl content per fresh mass of stems and ears as well as per unit leaf area was detected spectrophotometrically by the method of Lichtenthaler (1987). Calculation of Chl contents in 100 % acetone extracts was performed using coefficients proposed by Shlyk (1971). Photosynthetic potential and net photosynthetic productivity were detected by the method of Nichiporovich (1988):

$$P_{PH} = \frac{S_1}{2C} H_1 + \frac{S_1 + S_2}{2C} H_2 + \frac{S_2 + S_3}{2C} H_3 + \ldots + \frac{S_{n-1} + S_n}{2C} H_n \qquad (1)$$

where P_{PH} - photosynthetic potential [m^2 d^{-1} m^{-2}]; $S_1, S_2, S_3, \ldots, S_n$ - total leaf area in noted phase [m^2]; $H_1, H_2, H_3, \ldots, H_n$ - the time between phases [d]; C - total canopy area [m^2];

$$NP_{PR} = 2\frac{m_2 - m_1}{(S_1 + S_2)\ H} \qquad (2)$$

where NP_{PK} - net photosynthetic productivity [kg m^{-2} d^{-1}]; m_1 and m_2 - dry matter of plant at the beginning and the end of noted period [kg]; S_1 and S_2 - total leaf area of a single plant at the beginning and the end of noted period [m^2]; H - the time between phases [d].

Photochemical activity of chloroplasts was measured according to rate of ferricyanide reduction (Hill reaction). Chloroplast extraction procedure was made following proposals of Hanson and Grier (1973) with the following modifications of composition in extraction and reaction media: Extraction medium (pH 7.8) consisted of 0.05 M HEPES-NaOH, 0.4 M sucrose, 0.01 M KCl, 0.001 M EDTA, 0.004 mercaptoethanol, and 5 % *Carbowax 4000* (polyethylene glycol). Reaction mixture (pH 7.8) contained 0.05 M HEPES-NaOH, 0.01 M KCl, 0.001 $MgCl_2$, and 0.0025 M $K_3Fe(CN)_6$. Concentration of Chl in chloroplasts was 0.01 kg m^{-3}.

Correlation coefficients were calculated according to Falconer and Douglas (1996). Statistical analysis was made by ANOVA using software designed in the laboratory of mathematical statistics (Institute of Genetics and Cytology, National Academy of Sciences, Minsk, Belarus). Least significant differences among means were tested at the $p = 0.05$ level of probability. The experiments were repeated three times.

Results

Plant morphology: 10-d-old *Triticale* seedlings differed in length by 43 %. In *Triticale* lines Dar Belarusi, Ales, and L-219 maximum, and in Zenit and CHD-888 minimum lengths were found (Fig. 1*A*). In field conditions, plant height of Dar Belarusi was higher by 45 %, and total leaf area was higher by 50 % compared to CHD-888 (Fig. 1*B*,*C*). The studied hybrids, Ales×Mihas; L-219×Polus; L-219×Mihas; Dar Belarusi×Polus; Ruh×Mihas; L-219×Ales; Zenit×Mihas; Zenit×Ales; Dar Belarusi×CHD-888, did not reveal any heterosis effect both on seedling length, plant height, and total leaf area, and had average values compared to parental *Triticale* genotypes (represented for Ales×Mihas and L-219×Polus) (Fig. 2). Exception was indicated for Dar Belarusi×CHD-888, which had 15% mid-parent heterosis in seedling length (Fig. 2*B*).

Content and accumulation of Chl: Difference in Chl (*a*+*b*) content per unit leaf area was the most significant for 10-d-old seedlings of studied *Triticale* lines, and reached for contrast genotypes 35 % (Fig. 3*C*). Thus, Dar Belarusi, Ales, and L-219 are high Chl-containing lines, whereas Zenit and CHD-888 are low Chl-containing ones. The lines Ruh, Mihas, and Polus had middle Chl contents. Among high and low Chl-containing lines a consistent difference for Chl content per single chloroplast was found. The extreme value of this difference achieved 20 % for Dar Belarusi and CHD-888 (Fig. 3*B*). The above mentioned *Triticale* lines differed in Chl content in PPC. Dar Belarusi, Ales, and L-219 had a maximum Chl content in both light-harvesting complex of photosystem 2 (LHC2) and photosystems 1 and 2 (PS1+PS2). Minimum Chl content in PPC was found for

Zenit, Polus, and CHD-888, and was less than in high Chl-containing lines up to 27 % (Fig. 3*A*).

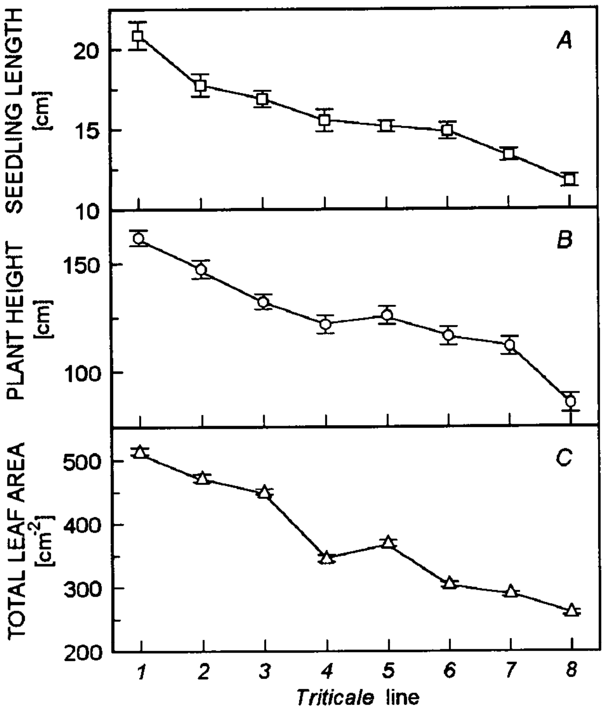

Fig. 1. Morphology of *Triticale* lines: *A* - seedling length; *B* - plant height; *C* - total leaf area. Lines: *1* - Dar Belarusi; *2* - Ales; *3* - L-219; *4* - Mihas; *5* - Ruh, *6* - Polus; *7* - Zenit; *8* - CHD-888.

Chl content in seedlings corresponded to that in whole plants. In field conditions, Dar Belarusi, L-219, and Ales prevailed over Zenit and CHD-888 by 33 % for Chl (*a*+*b*) per unit leaf area (Fig. 3*F*), by 27 % for Chl content per single chloroplast (Fig. 3*E*), and up to 25 % for Chl content in general PPC (Fig. 3*D*).

High Chl-containing *Triticale* lines exceeded the low Chl ones 1.5-2.0 times for Chl content in leaves, 1.2-2.5 times in whole plant, and 3.0-3.5 times in canopy, as well as up to 28 % for photosynthetic potential and by 20-25 % for net photosynthetic productivity (Table 1).

Based on differences noted we anticipated that heterosis in Chl content could appear in F_1 hybrids produced by crossing the most contrast for pigment content genotypes such as Dar Belarusi and CHD-888. Most of the studied *Triticale* hybrids during vegetation had in general middle or less, compared to parents, Chl contents in PPC, per single chloroplast, and per unit leaf area (represented for seedlings of L-219, Polus, L-219×Polus, F_1; Fig. 4*C,F,I,L,O,R*). We found a 15 % mid-parent heterosis in Chl content per unit leaf area for seedlings, and a 17 % one at heading for Dar Belarusi×CHD-888, F_1 (Fig. 4*H,Q*). Higher values of hybrid vigour in Chl content were detected for Ales×Mihas, F_1 and L-219×Mihas, F_1, and reached, compared to the middle parent value, 15-20 % in PPC and per single chloroplast in seedlings and at heading (represented for Ales×Mihas, F_1, Fig. 4*A,D,J,M*), and 35 % in Chl content per unit leaf area in seedlings (Fig. 4*G*). At the beginning of grain filling, mid-parent heterosis in Chl content per unit leaf area was 20 % for Ales×Mihas, F_1 (Fig. 5*A*) and up to 35 % for L-219×Mihas, F_1 (Fig. 5*B*). For these genotypes we found a 35-32 % mid-parent heterosis in Chl content in leaf, 33-35 % in whole plant, 30-34 % in canopy, 35-40 % for photosynthetic potential, and 20-23% for net photosynthetic productivity (Table 2). The mentioned characteristics for other F_1 hybrids studied had a middle values compared with analogous characters of parental *Triticale* lines (represented for L-219×Polus, F_1 and Dar Belarusi×CHD-888, F_1, Table 2).

Table 1. Characteristics of *Triticale* lines at heading. Chl - chlorophyll; P_{PH} - photosynthetic potential; NP_{PR} - net photosynthetic productivity. Means ± standard error.

Genotype	Chl in leaves [mg]	Chl in whole plant [mg]	Chl in canopy [g m^{-2}]	P_{PH} [m^2 d^{-1} m^{-2}]	NP_{PR} [g m^{-2} d^{-1}]
Dar Belarusi	25.84 ± 0.07	52.04 ± 0.17	70.12 ± 0.34	9.98 ± 0.33	14.28 ± 0.08
Ales	26.02 ± 0.05	51.22 ± 0.15	69.14 ± 0.36	11.30 ± 0.73	16.14 ± 0.07
L-219	17.60 ± 0.08	36.95 ± 0.16	46.07 ± 0.93	9.66 ± 0.76	15.39 ± 0.07
Ruh	19.67 ± 0.07	35.02 ± 0.19	45.53 ± 0.86	9.26 ± 0.55	12.34 ± 0.08
Mihas	15.41 ± 0.04	33.98 ± 0.14	40.07 ± 0.45	9.12 ± 0.88	12.61 ± 0.05
Polus	15.05 ± 0.21	29.80 ± 0.07	28.59 ± 0.66	8.11 ± 0.73	12.71 ± 0.07
Zenit	14.94 ± 0.21	29.91 ± 0.06	28.76 ± 0.91	9.19 ± 0.68	13.03 ± 0.06
CHD-888	12.92 ± 0.09	20.21 ± 0.20	20.03 ± 0.63	9.01 ± 0.52	12.07 ± 0.05

Typical dynamic of Chl accumulation during plant ontogeny both for lines and F_1 hybrids of *Triticale* was analogous and tended to increase of Chl content from the stage of tillering to the beginning of grain filling (Fig. 5).

Table 2. Characteristics of *Triticale* genotypes at heading. Chl - chlorophyll; P_{PH} - photosynthetic potential; NP_{PR} - net photosynthetic productivity. Means ± standard error.

Genotype	Chl in leaves [mg]	Chl in whole plant [mg]	Chl in canopy [g m^{-2}]	P_{PH} [m^2 d^{-1} m^{-2}]	NP_{PR} [g m^{-2} d^{-1}]
Ales	26.02 ± 0.05	51.22 ± 0.15	69.14 ± 0.36	11.30 ± 0.73	16.14 ± 0.07
Mihas	15.41 ± 0.04	33.98 ± 0.14	40.07 ± 0.45	9.12 ± 0.88	12.61 ± 0.05
Ales x Mihas, F_1	30.00 ± 0.18	56.35 ± 0.21	72.01 ± 0.45	15.14 ± 0.37	18.03 ± 0.09
L-219	17.60 ± 0.08	36.95 ± 0.16	46.07 ± 0.93	9.66 ± 0.76	15.39 ± 0.07
L-219 x Mihas, F_1	24.89 ± 0.15	42.56 ± 0.13	50.07 ± 0.50	11.18 ± 0.24	16.10 ± 0.10
Polus	15.05 ± 0.21	29.80 ± 0.07	28.59 ± 0.66	8.11 ± 0.73	12.71 ± 0.07
L-219 x Polus, F_1	15.92 ± 0.14	32.28 ± 0.22	34.01 ± 0.30	8.50 ± 0.19	13.05 ± 0.07
Dar Belarusi	25.84 ± 0.07	52.04 ± 0.17	70.12 ± 0.34	9.98 ± 0.33	14.28 ± 0.08
CHD-888	12.92 ± 0.09	20.21 ± 0.20	20.03 ± 0.63	9.01 ± 0.52	12.07 ± 0.05
Dar Belarusi x CHD-888, F_1	17.35 ± 0.19	35.62 ± 0.18	45.14 ± 0.44	9.74 ± 0.15	13.12 ± 0.08

Photochemical activity of chloroplasts: Some correlations between chloroplast photochemical activity in cereal species and photosynthetic efficiency were already found (Morgan and Austin 1986, Evans 1987, Bansal *et al.* 1993). In contrast, Barta and Hodges (1970) and Hanson and Grier (1973) found that chloroplast photochemical activity was not directly related to the net photosynthetic productivity.

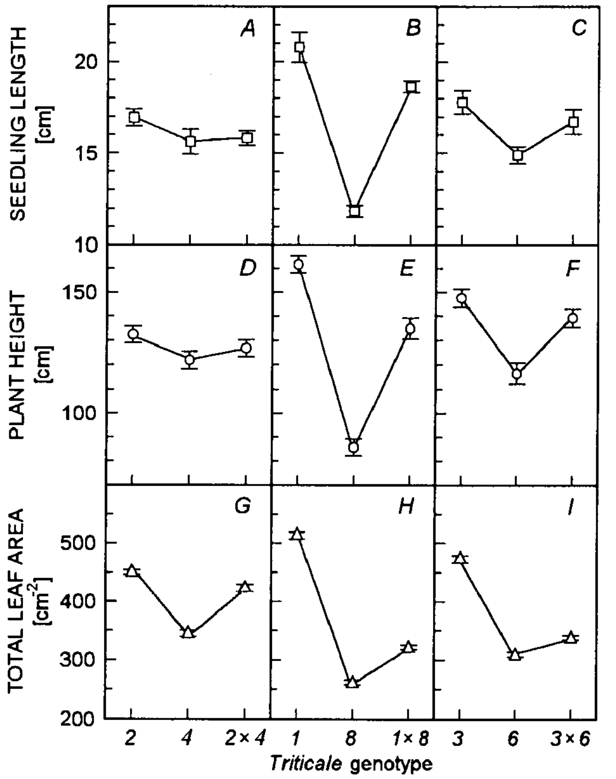

Fig. 2. Morphology of *Triticale* genotypes: *A-C* - seedling length; *D-F* - plant height; *G-I* - total leaf area; Genotypes: *2* - Ales; *4* - Mihas; *2x4* - AlesxMihas, F_1; *1* - Dar Belarusi; *8* - CHD-888; *1x8* - Dar BelarusixCHD-888, F_1; *3* - L-219; 6 - Polus; *3x6* - L-219xPolus, F_1.

Our results indicated that photochemical activity of chloroplasts tended to correspond to the distribution of Chl content in *Triticale* lines studied. Thus, high pig-

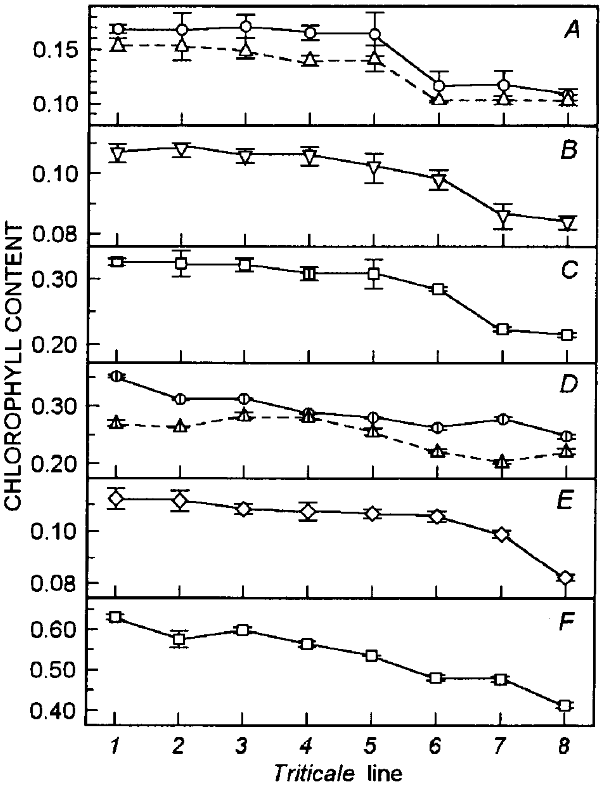

Fig. 3. Chlorophyll content in *Triticale* lines: *A* - in PPC (*solid curve* - in light-harvesting complex, *dashed curve* - in photosystems 1 and 2) in seedlings [g m^{-2}]; *B* - per single chloroplast in seedlings [ng m^{-2}]; *C* - per unit leaf area in seedlings [g m^{-2}]; *D* - in PPC (*solid curve* - in light-harvesting complex, *dashed curve* - in photosystems 1 and 2) at heading [g m^{-2}]; *E* - per single chloroplast, at heading [ng m^{-2}]; *F* - per unit leaf area at heading [g m^{-2}]. Lines: *1* - Dar Belarusi; *2* - Ales; *3* - L-219; *4* - Mihas; *5* - Ruh, *6* - Polus; *7* - Zenit; *8* - CHD-888.

ment-containing lines Dar Belarusi, Ales, and L-219 exceeded by 10-12 % Zenit and CHD-888 for electron transport rates during plant ontogenesis. The studied lines showed an increase of chloroplast photochemical activity at tillering to heading, and a decrease to the stage of grain filling. Rate of ferricyanide-dependent Hill activity of chloroplasts of *Triticale* F_1 hybrids had average values compared to corresponding parameter in parental genotypes at the first vegetation stages (tillering, scrolling), and exceeded this one at the end of vegetation (grain filling). Maximum heterosis effect compared to the middle parent in photochemical activity of chloroplasts at the stage of grain filling was registered for Ales×Mihas, F_1 87 % (Fig. 5*E*); for L-219×Mihas, F_1 35 % (Fig. 5*F*), and for Dar Belarusi×CHD-888, F_1 63 % (Fig. 5*G*). Other *Triticale* F_1 hybrids had a 20-25 % heterosis of the indicated feature (represented for L-219×Polus, F_1) (Fig. 5*H*).

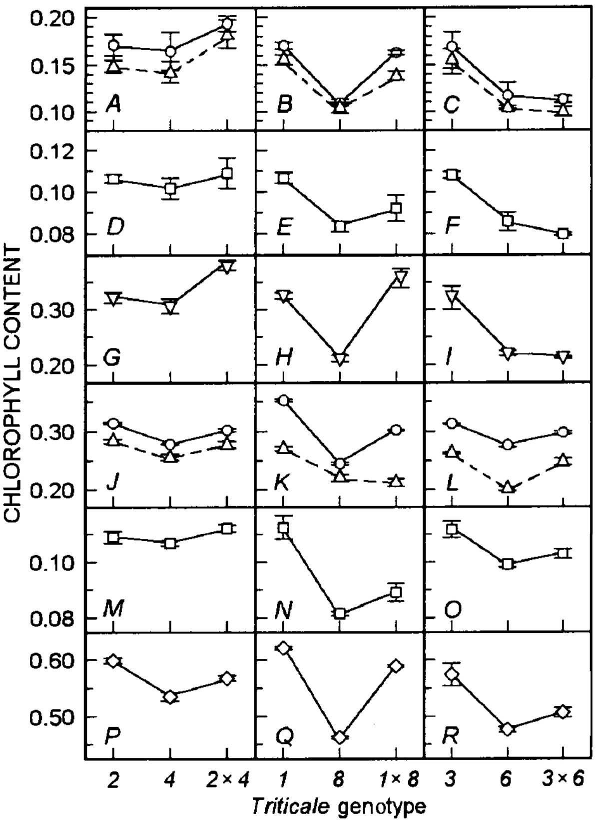

Fig. 4. Chlorophyll content in *Triticale* genotypes: *A*-*C* - in PPC (*solid curve* - in light-harvesting complex, *dashed curve* - in photosystems 1 and 2) in seedlings [g m^{-2}], *D*-*F* - per single chloroplast in seedlings [ng m^{-2}], *G*-*I* - per unit leaf area in seedlings [g m^{-2}], *J*-*L* - in PPC (*solid curve* - in light-harvesting complex, *dashed curve* - in photosystems 1 and 2) at heading [g m^{-2}], *M*-*O* - per single chloroplast at heading [ng m^{-2}], *P*-*R* - per unit leaf area at heading [g m^{-2}]. Genotypes: *2* - Ales; *4* - Mihas; *2*x4 - Ales×Mihas, F_1; *1* - Dar Belarusi; *8* - CHD-888; *1*x8 - Dar Belarusi×CHD-888, F_1; *3* - L-219; *6* - Polus; *3*x6 - L-219×Polus, F_1.

Plant productivity and crop characteristics: High Chl-containing *Triticale* lines Dar Belarusi, L-219, and Ales had higher mass of kernels per plant; mass of 1000 kernels, and grain yield than the middle (Ruh, Mihas, Polus) and low (Zenit and CHD-888) Chl-containing ones (Table 3). Among the F_1 hybrids of *Triticale*, only Ales×Mihas and L-219×Mihas had increased values of (*1*) mass of kernels per plant on 15-30 %; (*2*) mass of 1000 kernels on 12-15 %, and (*3*) grain yield on 13-15 % compared to the middle parent (Table 4). Other F_1 hybrids of *Triticale* had comparable values of indicated parameters to their parental lines (represented for L-219×Polus, F_1 and Dar Belarusi×CHD-888, F_1, Table 4).

Correlation analysis: At the first vegetation stages (tillering to scrolling) either in *Triticale* lines or in their F_1 hybrids significant high correlation coefficients ($p = 0.05$) were found between Chl content and some morphological characters. Thus, the correlations between Chl content in leaf and plant height for Ales, Dar Belarusi, CHD-888, Ales×Mihas, F_1, and Dar Belarusi×CHD-888, F_1 were 0.68-0.74, between Chl content per unit leaf area and total leaf area they were 0.72-0.80.

At the end of vegetation (heading to grain filling) higher correlations were found between some photosynthetic characters and crop parameters. Correlation coefficients for Dar Belarusi, L-219×Polus, F_1, Zenit×Ales, F_1, L-219×Mihas, F_1 for photosynthetic potential-mass of kernels per plant, and mass of 1000 kernels-net photosynthetic productivities were 0.53-0.59 and 0.45-0.52, respectively.

Significant high correlation coefficients ($r = 0.60$-0.75) among plant height, plant mass, total leaf area, and Chl content at different levels of plant organisation, and crop productivity were detected for Dar Belarusi, CHD-888, and their F_1 hybrid Dar Belarusi×CHD-888. A reliable positive correlation ($r = 0.29$-0.35) between chloroplast photochemical activity and mass of kernels per plant was found for Ales×Mihas, F_1 and L-219×Mihas, F_1 at the stages heading-grain filling.

Discussion

Differences in Chl content between contrast genotypes for most species are usually lower than 20-25 % (Singh *et al.* 1985, Medrano *et al.* 1989, Synková *et al.* 1997). They tend to be extreme mostly in stress conditions, such as increase of plant density in canopy (Kabashnikova 1987), different irradiance (Delong and Steffen 1997), or treatment with plant growth regulators (Gaussoin *et al.* 1997). Chl accumulation patterns in various species (Thompson *et al.* 1996, Benbella and Paulsen 1998) indicated a decrease of pigment content at grain filling.

Table 3. Crop characters of *Triticale* lines. Means ± standard error.

Genotype	Kernel mass per plant [g]	Mass of 1000 kernels [g]	Grain yield [g m^{-2}]
Dar Belarusi	13.80 ± 0.31	62.1 ± 2.3	983 ± 32
L-219	13.96 ± 0.26	59.0 ± 1.0	956 ± 41
Ales	11.86 ± 0.17	66.5 ± 1.7	899 ± 52
Ruh	10.22 ± 0.24	56.5 ± 2.2	831 ± 40
Mihas	9.79 ± 0.18	55.3 ± 2.2	792 ± 43
Polus	10.02 ± 0.21	55.7 ± 1.7	790 ± 51
Zenit	10.95 ± 0.18	47.5 ± 2.1	750 ± 42
CHD-888	10.70 ± 0.18	50.0 ± 1.7	780 ± 38

Our results, 35 % differences in Chl content per unit leaf area both in seedlings and whole plants, and a certain increase of Chl content at the beginning of grain filling allow to speculate about the formation of unique, typical for this hybrid cereal, mechanisms of photoregulation and hormonal regulation.

The found correspondence between seedling length and plant morphology as well as between arrangement of Chl content in seedlings and whole plants confirmed the conclusions of Chaïka *et al.* (1988) and Mattsson (1997). They recommend to use seedlings as an early test in laboratory for predicting the photosynthetic efficiency of whole plants in a field.

Table 4. Crop characters of *Triticale* genotypes. Means ± standard error.

Genotype	Kernel mass per plant [g]	Mass of 1000 kernels [g]	Grain yield [g m^{-2}]
Ales	11.86 ± 0.17	66.5 ± 1.7	899 ± 52
Mihas	9.79 ± 0.18	55.3 ± 2.2	792 ± 43
Ales × Mihas, F$_1$	12.15 ± 0.21	69.5 ± 2.0	965 ± 36
L-219	13.96 ± 0.26	59.0 ± 1.0	956 ± 41
L-219 × Mihas, F$_1$	15.66 ± 0.17	65.2 ± 1.5	1012 ± 43
Polus	10.02 ± 0.21	55.7 ± 1.7	790 ± 51
L-219 × Polus, F$_1$	12.91 ± 0.14	55.3 ± 2.0	901 ± 35
Dar Belarusi	13.80 ± 0.31	62.1 ± 2.3	983 ± 32
CHD-888	10.70 ± 0.18	50.0 ± 1.7	780 ± 38
Dar Belarusi × CHD-888, F$_1$	12.14 ± 0.25	57.3 ± 2.3	924 ± 51

Speculations of constructing the ideotype of crop plants had to take into account that plants with optimum photosynthetic and crop productivity have not maximised their morphology and physiology (Austin 1992). We found that *Triticale* lines with high poten-tial and real productivity tended (*1*) to the highest values of morphological characteristics (plant height and total leaf area), and (*2*) to forming more efficient PSA with increased Chl content per membrane, chloroplast, leaf, plant, and canopy together with more effective chloroplast photochemical functions able to produce improved grain yield.

Nevertheless, the interrelations of Chl content, photosynthetic activity, and final grain yield formation are not yet clearly delineated. Direct correlations were found between Chl concentration and leaf photosynthetic efficiency (Buttery and Buzzel 1977, Hesketh *et al.* 1981, Hobbs and Mahon 1985), leaf mass (Suresh *et al.* 1997), or final yield (Singh *et al.* 1985). On the contrary, Gratani *et al.* (1998) reported about discordance between Chl content and photosynthetic rate during one year. According to Moss (1976), it was difficult to detect associations between photosynthesis and economic yield. Moreover, Elmore (1980) failed to find a correlation between CO_2 exchange rates and crop yield, and Medrano *et al.* (1989) did not observe any relationship between Chl content and plant production parameters.

Thus, the found close correlations among morphological structure, Chl content, and crop productivity confirmed known facts that content of photosynthetic pigments may be one of the test factors predicting potential plant productivity (Buttery and Buzzell 1977, Hesketh *et al.* 1981, Singh *et al.* 1985, Chaïka *et al.* 1988). Nevertheless, this does not rule out further research for more complete understanding of these photosynthetic characters.

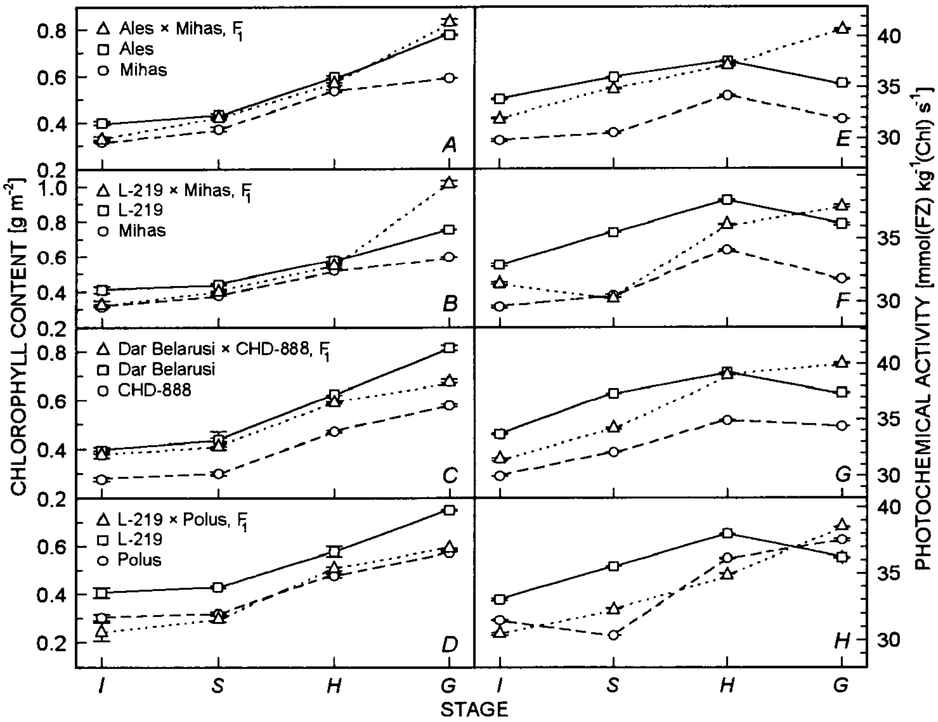

Fig. 5. Accumulation of chlorophyll (*a*+*b*) per unit leaf area [g m^{-2}] (*A*-*D*) and photochemical activity of chloroplasts according to ferricyanide (FZ) reduction (*E*-*H*) in *Triticale* lines and F_1 hybrids: *T* - tillering; *S* - scrolling; *H* - heading; *G* - beginning of grain filling.

The heterosis effect is caused by numerous factors, and the main ones are controlled by various types of nuclear (Maluszynski 1989), mitochondrial and chloroplast (Srivastava 1983) gene interactions, as well as by the environmental influence (Frankel 1983). Since the studied lines and hybrids of *Triticale* were grown at the same conditions, it is not necessary to take into account the role of environmental changes for revealing the effect of heterosis.

Detection of heterosis effect in Chl content, chloroplast activity, and crop productivity only in two F_1 *Triticale* hybrids (Ales×Mihas; L-219×Mihas) corresponds with the results of Gordeï (1992) that frequency and effectivity of heterosis in *Triticale* considerably depended on crossing combinations and analysed features. Since the most of F_1 hybrids of *Triticale* have not realised their significantly high photochemical activity into a more increased grain crop, they may be physiologically not stable. Thus, more detailed understanding of regulatory mechanisms of *Triticale* lines and hybrids ontogenesis requires further complex genetical, biochemical, and physiological investigations.

Lines and hybrids such as Ales×Mihas, F_1 and L-219×Mihas, F_1 with notified direct relation between chloroplast photochemical activity and plant productivity may be used in further *Triticale* breeding.

References

Austin, R.B.: Plant productivity and genetic variation in photosynthesis. - In: Barber, J., Guerrero, M.G., Medrano, H. (ed.): Trends in Photosynthetic Research. Pp. 319-337. Athenaeum Press, Andover 1992.

Baker, N.R.: Environmental constrains on photosynthesis: An overview of some future prospects. - In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 469-475. Kluwer Academic Publ., Dordrecht – Boston - London 1996.

Baker, N.R., Ort, D.R.: Light and photosynthetic performance. - In: Barber, J., Thomas, H. (ed.): Crop Photosynthesis: Spatial and Temporal Determinants. Pp. 290-310. Elsevier, Amsterdam - Tokyo 1992.

Bansal, K.C., Uprety, D.C., Abrol, Y.P.: Genetic variation in photosynthetic characteristics in wheat: causes and consequences. - In: Abrol, Y.P., Govindjee (ed.): Photosynthesis: Photoreactions to Plant Productivity. Pp. 527-545. Kluwer Academic Publ., Dordrecht – Boston - London 1993.

Barta, A.L., Hodges, H.F.: Characterization of photosynthesis in cold hardening winter wheat. - Crop Sci. **10**: 535-538, 1970.

Benbella, M., Paulsen, G.M.: Efficacy of treatments for delaying senescence of wheat leaves: II. Senescence and grain yield under field conditions. - Agron. J. **90**: 332-338, 1998.

Buttery, B.R., Buzzell, R.I.: The relationship between chlorophyll content and rate of photosynthesis in soybeans. - Can. J. Plant Sci. **57**: 1-5, 1977.

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.: [Relation of growth and photosynthesis to production process during selection of cereals.] - In: Nichiporovich, A.A. (ed.): Fotosintez i Produktsionnyï Protsess. Pp. 262-267. Nauka, Moskva 1988. [In Russ.]

Clarke, F.R., Baker, R.J., DePauw, R.M.: Interplot interference distorts yield estimates in spring wheat. - Crop Sci. **38**: 62-66, 1998.

Delong, J.M., Steffen, K.L.: Photosynthetic function, lipid peroxidation, and α-tocopherol content in spinach leaves during exposure to UV radiation. - Can. J. Plant Sci. **77**: 453-459, 1997.

Elmore, C.D.: The paradox of no correlation between leaf photosynthetic rates and crop yields. - In: Hesketh, J.D., Jones, J.W. (ed.): Predicting Photosynthesis for Ecosystem Models. Vol. II. Pp. 155-167. CRC Press, Boca Raton 1980.

Ernst, D., Apfelböck, A., Bergman, A., Weyrauch, C.: Rhythmic regulation of the light-harvesting chlorophyll *a*/*b* protein and the small subunit of ribulose-1,5-bisphosphate carboxylase mRNA in rye seedlings. - Photochem. Photobiol. **52**: 29-33, 1990.

Evans, J.R.: The relationship between electron transport components and photosynthetic capacity in pea leaves grown at different irradiances. - Aust. J. Plant Physiol. **14**: 157-170, 1987.

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

Forbes, J.C., Watson, R.D.: Plants in Agriculture. - Cambridge University Press, Cambridge 1992.

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

Gaussoin, R.E., Branham, B.E., Flore, J.A.: Carbon dioxide exchange rate and chlorophyll content of turfgrasses treated with flurprimidol or mefluidide. - J. Plant Growth Regul. **16**: 73-78, 1997.

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

Gratani, L., Pesoli, P., Crescente, M.F.: Relationship between photosynthetic activity and chlorophyll content in an isolated *Quercus ilex* L. tree during the year. - Photosynthetica **35**: 445-451, 1998.

Gupta, P.K., Priyadarshan, P.M..: *Triticale*: present status and future prospects. - Adv. Genet. **21**: 256-345, 1982.

Hanson, W.D., Grier, R.E.: Rates of electron transfer and of non-cyclic photophosphorylation for chloroplasts isolated from maize populations selected for differences in juvenile productivity and in leaf widths. - Genetics **75**: 247-257, 1973.

Hesketh, J.D., Ogren, W.L., Hageman, M.E., Peters, D.B.: Correlations among leaf CO_2-exchange rates, areas and enzyme activities among soybean cultivars. - Photosynth. Res. **2**: 21-30, 1981.

Hobbs, S.L.A., Mahon, J.D.: Genetic, environmental and interactive components of photosynthesis in peas. - In: Hebblethwaite, P., Heath, M., Dawkins, T. (ed.): The Pea Crop – a Basis for Improvement. Pp. 307-315. Butterworth, London 1985.

Hoerlein, A.J., Valentine, J.: *Triticale* (×*Triticosecale*). - In: Williams, J.T. (ed.): Cereals and Pseudocereals. Pp. 186-203. Chapman and Hall, London - Madras 1995.

Hudák, J.: Photosynthetic apparatus. - In: Pessarakli, M. (ed.): Handbook of Photosynthesis. Pp. 27-48. Marcel Dekker, New York - Basel - Hong Kong 1997.

Ishii, R.: Leaf photosynthesis in rice in relation to grain yield. - In: Abrol, Y.P., Mohanty, P., Govindjee (ed.): Photosynthesis: Photoreactions to Plant Productivity. Pp. 561-569. Kluwer Academic Publ., Dordrecht – Boston - London 1993.

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.]

Kura-Hotta, M., Satoh, K., Katoh, S.: Relationship between photosynthesis and chlorophyll content during leaf senescence of rice seedlings. - Plant Cell Physiol. **28**: 1321-1329, 1987.

Law, R.D., Crafts-Brandner, S.J..: Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. - Plant Physiol. **120**: 173-181, 1999.

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

Lichtenthaler, H.K.: Chlorophylls and carotenoids – pigments of photosynthetic membranes. - In: Colowick, S.P., Kaplan, N.O. (ed.): Methods in Enzymology. Vol. 148. Pp. 350-382. Academic Press, San Diego – New York – Berkeley – Boston – London – Sydney – Tokyo - Toronto 1987.

Maluszynski, M.: Current options for cereal improvement: doubled haploids, mutants and heterosis. - In: Maluszynski, M. (ed.): Proceedings of the First FAO/IAEA Research Coordination Meeting on "Use of Induced Mutations in Connections with Haploids and Heterosis in Cereals." Pp. 129-147. Kluwer Academic Publ., Dordrecht 1989.

Mattsson, A.: Predicting field performance using seedling quality assessment. - New Forests **13**: 227-252, 1997.

Medrano, H., Pol, A., Delgado, E.: Plant production, photosynthesis rate and related characters in doubled-haploid lines of *Nicotiana tabacum* selected by photosynthetical efficiency. - In: Barber, J., Malkin, R. (ed.): Techniques and New Developments in Photosynthesis Research. Pp. 481-484. Plenum, New York - London 1989.

Meek, G.A.: Practical Electron Microscopy for Biologists. - Unwin Brothers, Surrey 1976.

Morgan, C.L., Austin, R.B.: Analysis of fluorescence transients of DCMU-treated leaves of *Triticum* species to provide estimates of the densities of photosystem II reaction centres. - Photosynth. Res. **7**: 203-219, 1986.

Moss, D.N.: Studies of increasing photosynthesis in crop plants. - In: Burris, R.H., Black, C.C. (ed.): CO_2 Metabolism and Plant Productivity. Pp. 31-41. University Park Press, Baltimore – London – Tokyo 1976.

Murayama, S., Miyazato, K., Nose, A.: Studies on dry matter production of F_1 hybrid in rice. I. Heterosis in the single leaf photosynthetic rate. - Jap. J. Crop Sci. **56**: 198-203, 1987.

Nichiporovich, A.A.: [Plant Photosynthetic Activity as the Basis of Their Productivity in Biosphere and Agriculture.] – In: Nichiporovich, A.A. (ed.): Fotosintez i Produktsionnyĭ Protsess. Pp. 5-28. Nauka, Moskva 1988. [In Russ.]

Niziołek, S., Bielawski, W., Nalborczyk, E.: Photosynthesis in detached rye leaves at normal and low oxygen concentration. II. Incorporation of $^{14}CO_2$ into amino acids. - Acta biochim. pol. **29**: 339-347, 1982.

Quinones, N.A., Larter, E.N., Samborski, D.J.: The inheritance of resistance of *Puccinia recondita* in hexaploid *Triticale*. - Can. J. Cytol. **14**: 495-505, 1972.

Royo, C., Blanko, R.: Growth analysis of five spring and five winter *Triticale* genotypes. - Agron. J. **91**: 305-311, 1999.

Royo, C., Voltas, J., Romagosa, I.: Remobilization of pre-anthesis assimilates to the grain for grain only and dual purpose (forage and grain) *Triticale*. - Agron. J. **91**: 312-316, 1999.

Rozynek, B., Guentner, T., Hesemann, C.U.: Gel electrophoretic investigations of prolamins in eu- and allo-plasmatic octoploid primary *Triticale* forms. - Theor. appl. Genet. **96**: 46-51, 1998.

Šesták, Z.: Photosynthetic characteristics during ontogenesis of leaves. 1. Chlorophylls. - Photosynthetica **11**: 367-448, 1977.

Shlyk, A.A.: [Determination of chlorophylls and carotenoids in green leaf extracts.] - In: Shlyk, A. (ed.): Biokhimicheskie Metody v Fiziologii Rasteniĭ. Pp. 154-170. Nauka, Moskva 1971. [In Russ.]

Singh, B.B., Shrivastava, M.K., Lalchand, K: Relationships among leaf chlorophyll, bean yield and other characters in field grown soybean cultivars. - Photosynthetica **19**: 240-243, 1985.

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.

Suresh, K., Rao, K.L.N., Nair, T.V.R.: Genetic variability in photosynthetic rate and leaf characters in *Brassicaceae* coenospecies. - Photosynthetica **33**: 173-178, 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.

Tanaka, K., Kakuno, T., Yamashita, J., Horio, T.: Purification and properties of chlorophyllase from greened rye seedlings. - J. Biochem. (Tokyo) **92**: 1763-1773, 1982.

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

Thompson, J.A., Schweitzer, L.E., Nelson, R.L.: Association of specific leaf weight, an estimate of chlorophyll, and chlorophyll concentration with apparent photosynthesis in soybean. - Photosynth. Res. **49**: 1-10, 1996.

Vaishlya, O.B., Ladygin, V.G., Sokolov, V.A., Semenova, G.A.: Characterization of photosynthetic apparatus of pea chlorophyll mutants and their heterotic F_1 hybrids with standard genotype (cv. Torsdag). - Photosynthetica **35**: 428-433, 1998.

Wohlfahrt, G., Bahn, M., Cernusca, A.: The use of ratio between the photosynthesis parameters $P_{(ml)}$ and $V_{(cmax)}$ for scaling up photosynthesis of C_3 plants from leaves to canopies: a critical examination of different modeling approaches. - J. theor. Biol. **200**: 163-181, 1999.

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