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

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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 F1 hybrids. Heterosis enhanced Chl content, photosynthetic potential, photosynthetic productivity, and grain yield only in several F1 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.* 1999, 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 (Niziolek *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, Tarchevskii and Andrianova 1980, Kura-Hotta *et al.* 1987, Gaussoin *et al.* 1997) and distribution (Chaika *et al.* 1988, Chaika 1996) in pigment-protein complexes of photosynthetic membrane (PPC) and at different levels of plant organisation (Austin 1992, Baker 1996, Wohlhaftr *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 (Muraiyama *et al.* 1987, Maluszynski 1989, Vaishya *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 F1 hybrids.

Materials and methods

The objects of investigations were new lines of winter hexaploid *Triticale* and their F1 hybrids selected at the Research Institute of Agriculture and fodder (Agrarian Academy of Sciences, Zhodino, Minsk region, Belarus).

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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 scarring, 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 Lichtenhalber (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):

\[
P_{PH} = \frac{S_1}{2C} H_1 + \frac{S_2}{2C} H_2 + \frac{S_3}{2C} H_3 + ... + \frac{S_{n-1}}{2C} H_{n-1} + \frac{S_n}{2C} H_n
\]

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

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

where \( NP_{PR} \) - 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].

Photosynthetic 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 M MgCl\(_2\), and 0.0025 M K\(_2\)Fe(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. 1A). 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. 1B,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. 2B).

**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. 3C). 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. 3B). 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
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. 3F), by 27% for Chl content per single chloroplast (Fig. 3E), and up to 25% for Chl content in general PPC (Fig. 3D).

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 F₁ 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, F₁; Fig. 4C, F₁, F₁L, 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, F₁ (Fig. 4H, Q). Higher values of hybrid vigour in Chl content were detected for Ales×Mihas, F₁ and L-219×Mihas, F₁, 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, F₁, Fig. 4A, D, J, M), and 35% in Chl content per unit leaf area in seedlings (Fig. 4G). At the beginning of grain filling, mid-parent heterosis in Chl content per unit leaf area was 20% for Ales×Mihas, F₁ (Fig. 5A) and up to 35% for L-219×Mihas, F₁ (Fig. 5B). 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 F₁ hybrids studied had a middle values compared with analogous characters of parental Triticale lines (represented for L-219×Polus, F₁ and Dar Belarusi×CHD-888, F₁, Table 2).

Typical dynamic of Chl accumulation during plant ontogeny both for lines and F₁ 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 1. Characteristics of Triticale lines at heading. Chl - chlorophyll; \( P_{\text{PH}} \) - photosynthetic potential; \( \text{NP}_{\text{PR}} \) - net photosynthetic productivity. Means ± standard error.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Chl in leaves [mg]</th>
<th>Chl in whole plant [mg]</th>
<th>Chl in canopy [g m⁻²]</th>
<th>( P_{\text{PH}} ) [m² d⁻¹ m⁻²]</th>
<th>( \text{NP}_{\text{PR}} ) [m² d⁻¹]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dar Belarusi</td>
<td>25.84 ± 0.07</td>
<td>52.04 ± 0.17</td>
<td>70.12 ± 0.34</td>
<td>9.98 ± 0.33</td>
<td>14.28 ± 0.08</td>
</tr>
<tr>
<td>Ales</td>
<td>26.02 ± 0.05</td>
<td>51.22 ± 0.15</td>
<td>69.14 ± 0.36</td>
<td>11.30 ± 0.73</td>
<td>16.14 ± 0.07</td>
</tr>
<tr>
<td>L-219</td>
<td>17.60 ± 0.08</td>
<td>36.95 ± 0.16</td>
<td>46.07 ± 0.93</td>
<td>9.66 ± 0.76</td>
<td>15.39 ± 0.07</td>
</tr>
<tr>
<td>Ruh</td>
<td>19.67 ± 0.07</td>
<td>35.02 ± 0.19</td>
<td>45.53 ± 0.86</td>
<td>9.26 ± 0.55</td>
<td>12.34 ± 0.08</td>
</tr>
<tr>
<td>Mihas</td>
<td>15.41 ± 0.04</td>
<td>33.98 ± 0.14</td>
<td>40.07 ± 0.45</td>
<td>9.12 ± 0.88</td>
<td>12.61 ± 0.05</td>
</tr>
<tr>
<td>Polus</td>
<td>15.05 ± 0.21</td>
<td>29.80 ± 0.07</td>
<td>28.59 ± 0.66</td>
<td>8.11 ± 0.73</td>
<td>12.71 ± 0.07</td>
</tr>
<tr>
<td>Zenit</td>
<td>14.94 ± 0.21</td>
<td>29.91 ± 0.06</td>
<td>28.76 ± 0.91</td>
<td>9.19 ± 0.68</td>
<td>13.03 ± 0.06</td>
</tr>
<tr>
<td>CHD-888</td>
<td>12.92 ± 0.09</td>
<td>20.21 ± 0.20</td>
<td>20.13 ± 0.63</td>
<td>9.01 ± 0.52</td>
<td>12.07 ± 0.05</td>
</tr>
</tbody>
</table>
Table 2. Characteristics of Triticale genotypes at heading. Chl - chlorophyll; $P_{PH}$ - photosynthetic potential; $NP_{PR}$ - net photosynthetic productivity. Means ± standard error.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Chl in leaves [mg]</th>
<th>Chl in whole plant [mg]</th>
<th>Chl in canopy [g m$^{-2}$]</th>
<th>$P_{PH}$ [m$^2$ d$^{-1}$ m$^{-2}$]</th>
<th>$NP_{PR}$ [g m$^{-3}$ d$^{-1}$]</th>
</tr>
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<td>12.61 ± 0.05</td>
</tr>
<tr>
<td>Ales × Mihas, F$_1$</td>
<td>30.00 ± 0.18</td>
<td>56.35 ± 0.21</td>
<td>72.01 ± 0.45</td>
<td>15.14 ± 0.37</td>
<td>18.03 ± 0.09</td>
</tr>
<tr>
<td>L-219</td>
<td>17.60 ± 0.08</td>
<td>36.95 ± 0.16</td>
<td>46.07 ± 0.93</td>
<td>9.66 ± 0.76</td>
<td>15.39 ± 0.07</td>
</tr>
<tr>
<td>L-219 × Mihas, F$_1$</td>
<td>24.89 ± 0.15</td>
<td>42.56 ± 0.13</td>
<td>50.07 ± 0.50</td>
<td>11.18 ± 0.24</td>
<td>16.10 ± 0.10</td>
</tr>
<tr>
<td>Polus</td>
<td>15.05 ± 0.21</td>
<td>29.80 ± 0.07</td>
<td>28.59 ± 0.66</td>
<td>8.11 ± 0.73</td>
<td>12.71 ± 0.07</td>
</tr>
<tr>
<td>L-219 × Polus, F$_1$</td>
<td>15.92 ± 0.14</td>
<td>32.28 ± 0.22</td>
<td>34.01 ± 0.30</td>
<td>8.50 ± 0.19</td>
<td>13.05 ± 0.07</td>
</tr>
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<td>Dar Belarusi</td>
<td>25.84 ± 0.07</td>
<td>52.04 ± 0.17</td>
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<td>20.21 ± 0.20</td>
<td>20.03 ± 0.63</td>
<td>9.01 ± 0.52</td>
<td>12.07 ± 0.05</td>
</tr>
<tr>
<td>Dar Belarusi × CHD-888, F$_1$</td>
<td>17.35 ± 0.19</td>
<td>35.62 ± 0.18</td>
<td>45.14 ± 0.44</td>
<td>9.74 ± 0.15</td>
<td>13.12 ± 0.08</td>
</tr>
</tbody>
</table>

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.

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. 2. Morphology of Triticale genotypes: A-C - seedling length; D-F - plant height; G-I - total leaf area; Genotypes: 2 - Ales; 4 - Mihas; 2×4 - Ales×Mihas, F$_1$; 7 - Dar Belarusi; 8 - CHD-888; 1×8 - Dar Belarusi×CHD-888, F$_1$; 3 - L-219; 6 - Polus; 3×6 - L-219×Polus, F$_1$.

Fig. 3. Chlorophyll content in Triticale lines: A - in PPC (solid curve - in light-harvesting complex, dashed curve - in photosystems 1 and 2); B - per single chloroplast in seedlings [ng m$^{-2}$]; C - per unit leaf area in seedlings [ng m$^{-2}$]; D - in PPC (solid curve - in light-harvesting complex, dashed curve - in photosystems 1 and 2) at heading [ng m$^{-2}$]; E - per single chloroplast, at heading [ng m$^{-2}$]; F - per unit leaf area at heading [ng 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 Belarus, 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 compared to the middle parent in photochemical activity of chloroplasts at the stage of grain filling was registered for Ales×Mihas, F1 87 % (Fig. 5E); for L-219×Mihas, F1 35 % (Fig. 5F), and for Dar Belarus×CHD-888, F1 63 % (Fig. 5G). Other triticale F1 hybrids had a 20-25 % heterosis of the indicated feature (represented for L-219×Polus, F1) (Fig. 5H).

Plant productivity and crop characteristics: High Chl-containing triticale lines Dar Belarus, 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 F1 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 F1 hybrids of triticale had comparable values of indicated parameters to their parental lines (represented for L-219×Polus, F1 and Dar Belarus×CHD-888, F1, Table 4).

Correlation analysis: At the first vegetation stages (tillering to scrolling) either in triticale lines or in their F1 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 Belarus, CHD-888, Ales×Mihas, F1, and Dar Belarus×CHD-888, F1 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 Belarus, L-219×Polus, F1, Zenit×Ales, F1, L-219×Mihas, F1 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 Belarus, CHD-888, and their F1 hybrid Dar Belarus×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, F1 and L-219×Mihas, F1 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 (Gausson 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.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Kernel mass per plant [g]</th>
<th>Mass of 1000 kernels [g]</th>
<th>Grain yield [g m⁻²]</th>
</tr>
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<tbody>
<tr>
<td>Dar Belarus</td>
<td>13.80 ± 0.31</td>
<td>62.1 ± 2.3</td>
<td>983 ± 32</td>
</tr>
<tr>
<td>L-219</td>
<td>13.96 ± 0.26</td>
<td>59.0 ± 1.0</td>
<td>956 ± 41</td>
</tr>
<tr>
<td>Ales</td>
<td>11.86 ± 0.17</td>
<td>66.5 ± 1.7</td>
<td>899 ± 52</td>
</tr>
<tr>
<td>Ruh</td>
<td>10.22 ± 0.24</td>
<td>56.5 ± 2.2</td>
<td>831 ± 40</td>
</tr>
<tr>
<td>Mihas</td>
<td>9.79 ± 0.18</td>
<td>55.3 ± 2.2</td>
<td>792 ± 43</td>
</tr>
<tr>
<td>Polus</td>
<td>10.02 ± 0.21</td>
<td>55.7 ± 1.7</td>
<td>796 ± 51</td>
</tr>
<tr>
<td>Zenit</td>
<td>10.95 ± 0.18</td>
<td>47.5 ± 2.1</td>
<td>750 ± 42</td>
</tr>
<tr>
<td>CHD-888</td>
<td>10.70 ± 0.18</td>
<td>50.0 ± 1.7</td>
<td>780 ± 38</td>
</tr>
</tbody>
</table>

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

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</tr>
<tr>
<td>Ales × Mihas, F₁</td>
<td>12.15 ± 0.21</td>
<td>69.5 ± 2.0</td>
<td>965 ± 36</td>
</tr>
<tr>
<td>L-219</td>
<td>13.96 ± 0.26</td>
<td>59.0 ± 1.0</td>
<td>956 ± 41</td>
</tr>
<tr>
<td>L-219 × Mihas, F₁</td>
<td>15.66 ± 0.17</td>
<td>65.2 ± 1.5</td>
<td>1012 ± 43</td>
</tr>
<tr>
<td>Polus</td>
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</tbody>
</table>

Speculations of constructing the ideotype of crop plants had to take into account that plants with optimum photosynthetic and crop productivity have not maximized their morphology and physiology (Austin 1992). We found that Triticale lines with high potential 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 Buzzell 1977, Hesketh et al. 1981, Hobbs and Mahon 1985), leaf mass (Suresh 1985).
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 CO₂ 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, Chaika 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 F₁ 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 F₁ Triticale hybrids (Ales×Mihas, L-219×Mihas) corresponds with the results of Gordei (1992) that frequency and effectivity of heterosis in Triticale considerably depended on crossing combinations and analysed features. Since the most of F₁ 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, F₁ and L-219×Mihas, F₁ with notified direct relation between chloroplast photochemical activity and plant productivity may be used in further Triticale breeding.
References


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