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## EFFECT OF FORECROPS CROPS ON GAS EXCHANGE AND SELECTED AGRONOMIC CHARACTERISTICS OF WHEAT AND SPELT\*

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### ABSTRACT

In sustainable and organic farming methods, great importance is attached to environmentally friendly components of crop production techniques, particularly the forecrops. This study has assessed the effects of four forecrops, i.e. field pea, winter oilseed rape, spring barley and wheat (or spelt), on gas exchange parameters, foliage, grain yield and N uptake in common wheat and spelt. The study was based on a field experiment carried out in north-eastern Poland. The experimental factors were as follows: 1) winter wheat subspecies: common wheat and spelt; 2) cultivation of the above-mentioned cereals in stands after field pea, winter oilseed rape, spring barley and one after the other. A favourable effect of oilseed rape as a forecrops on the activity of the stomatal apparatus and the assimilation and transpiration rates was demonstrated. In the stands after cereals, wheat and spelt assimilated less CO<sub>2</sub> than after the other forecrops. However, the intercellular CO<sub>2</sub> concentration value after these crops was higher than after pea and oilseed rape. Wheat used water more efficiently during photosynthesis in fields after pea and oilseed rape than after cereals. In spelt, the forecrops had no significant effect on this parameter. The surface of leaves and their chlorophyll content (SPAD) in wheat and spelt in stands after pea and oilseed rape were greater than after barley and wheat (or spelt). Oilseed rape as a forecrops had a favourable effect on grain yield in both cereals. Wheat and spelt responded negatively to the cultivation of one after the other by a decrease in grain yield, with the decrease being greater in spelt than in wheat. In both cereals cultivated after all forecrops, a significant relationship was demonstrated between assimilation and the aperture, transpiration, chlorophyll content of leaves, grain yield and N uptake. The forecrops differentiated most gas exchange parameters more in wheat than in spelt.

**Keywords:** stomatal conductance, assimilation, transpiration, intercellular CO<sub>2</sub> concentration, chlorophyll content, yield, nitrogen uptake.

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## INTRODUCTION

Owing to the progress in crop cultivation and production techniques, and consequently improved yields and qualitative characteristics of grains, wheat has become the most commonly cultivated cereal worldwide. Grains of this cereal provide the body with energy, carbohydrates (including fibre), proteins, vitamins and minerals. Spelt is a wheat subspecies known since prehistoric times, which was once almost forgotten but which has been cultivated increasingly often since the early 20<sup>th</sup> century owing to its high grain nutritional values, which are higher than common wheat (BIEL et al. 2016).

Common wheat is a cereal sensitive to cultivation after various forecrops. It yields the best when cultivated after leguminous plants, multi-annual papilionaceous plants, oilseed rape, beet and potato. Leguminous plants, particularly lupins, pea, pigeon bean and soybean, have a favourable effect on the soil environment (FALIGOWSKA et al. 2019). They leave crop residues rich in nitrogen and other nutrients, with a narrow C:N ratio. This contributes to rapid changes in soil properties and an increase in its biological activity, thus accelerating the mineralisation process. Plants enrich the soil with nitrogen, which is used by succeeding plants (SIELING, CHRISTEN 2015, PSZCÓŁKOWSKA et al. 2018). Winter oilseed rape is an equally good forecrops. The residues left after its harvest are rich in nitrogen. The plant limits the soil transmission of those pathogens that mainly infect the stem base, which stimulates the growth of microorganisms antagonistic towards cereal pathogens and improves the soil structure (SIELING, CHRISTEN 2015). On the other hand, cereals can be unfavourable forecrops, particularly where wheat is cultivated after wheat. Wheat responds to cultivation in these stands by a decrease in yield and deterioration of its quality. The reasons for a lower yield vary and are complex. They are associated with an increase in weed infestation, excessive spread of pathogens, pests and harmful microorganisms that colonise the rhizosphere, a change in the activity of mycorrhizal fungi, environmental self-poisoning or deterioration in the physical, chemical and biological properties of the soil (BENNETT et al. 2012, SIELING, CHRISTEN 2015).

Although the consequences of wheat cultivation after wheat and other cereals are quite well known and documented in scientific literature, most research concerns common wheat (JASKULSKA et al. 2013). On the other hand, the literature provides little information on spelt. There are no data either on the effect of forecrops on the course of physiological processes in these plants. This research was undertaken for two purposes: (1) to determine the effects of four selected forecrops (field pea, winter oilseed rape, spring barley and winter wheat/spelt) on gas exchange, aerial biomass, grain yield and N uptake for two wheat subspecies, i.e. common wheat and spelt; and (2) to determine the correlations between assimilation and transpiration and gas exchange indicators, foliage, N uptake and plant yielding.

## MATERIAL AND METHODS

The study was conducted in a carefully controlled field experiment carried out since the autumn of 2011 at a research facility of the University of Warmia and Mazury in Olsztyn (53°35'46"N 9°51'18" E) (Poland).

Experimental factors:

1. Winter wheat subspecies: common wheat and spelt;
2. Forecrops of common wheat and spelt: field pea, winter oilseed rape, spring barley, common wheat or spelt.

The following cultivars were grown in the experiment: common wheat Muszelka, the spelt wheat Rokosz field pea Batuta, winter oilseed rape SY Kolumb, and spring barley Mercada.

The study presents results from three wheat-growing seasons: 2012/2013, 2013/2014 and 2014/2015. They corresponded to the second, third and fourth year of the experiment. The results are presented as means from three years.

The experiment was carried out in four replications for all fields (forecrops – main crop) at the same time. The soil under the experimental fields was classified as typical lessive soil, composed of 64.7% of sand, 15.36% of coarse silt, 16.51% of fine silt and 3.43% of clay. It had slightly acidic pH (pH KCl 5.8-6.5), Corg. content of 8.6-9.3 g kg<sup>-1</sup>, total N content of 0.80-0.85 g kg<sup>-1</sup>, content of available forms of: P at 57.2-79.4 mg kg<sup>-1</sup> (medium to high), K at 9.46-136.1 mg kg<sup>-1</sup> (medium to high) and Mg at 33.6-45.6 mg kg<sup>-1</sup> (low).

The cereals were sown on optimal dates according to common crop production guidelines (17 September 2012, 21 September 2013, 18 September 2014), using 450 kernels per m<sup>2</sup>. The harvest was carried out in the full-grain ripeness stage (BBCH 89; late July/early August). After the harvest of the forecrops, straw was cut and removed from the field.

The doses of NPK mineral fertilizers applied in the experiment depended on the content of nutrients in the soil, expected grain yield and the forecrops. In the experiment, an average N dose for particular years amounted to 160 kg ha<sup>-1</sup> after oilseed rape, wheat and spelt. After pea, it was reduced to 130 kg ha<sup>-1</sup>. The P and K doses were not differentiated by the forecrops, and amounted to K – 91.3 kg ha<sup>-1</sup> and P – 35.2 kg ha<sup>-1</sup>. The herbicide Mustang was applied to control weeds, while Imput 460 EC reduced fungal diseases and Decis Mega 50 EW limited the occurrence of plant pests.

Measurements of gas exchanges were taken every year during the heading stage (BBCH 55-59) on 32 plots sown with wheat and spelt. They were performed on a fully developed, undamaged flag leaf, on ten randomly selected plants from each plot. The study was carried out on cloudless days, before noon (between 10:00 AM and 12:00 AM). The photosynthetically active radiation was 536 to 1071 μmol photon m<sup>-2</sup> s<sup>-1</sup>, the ambient CO<sub>2</sub> concentration was 386 do 406 μmol mol<sup>-1</sup>, and the vapour pressure was 13.2 do 16.3 kPa

at a field temp. of 20.0-24.2°C. The gas exchange was measured using a compact photosynthesis testing system Eijkelkamp LCi. The study included the following assays: stomatal conductance (gs), net assimilation rate (A), transpiration rate (E) and intercellular CO<sub>2</sub> concentration (Ci). The instantaneous water use efficiency (WUE) was calculated as A/E, the intrinsic water use efficiency (PWUE) was determined as A/gs and the stomatal limitation value (Ls) was  $1-c_i/c$ .

Measurements of the cereal leaf area were taken using a leaf area meter (CI – 202 Portable Laser Leaf Area Meter) in the heading stage (BBCH 55-59) on the three highest-set leaves on 10 stems from each plot. At the same time, chlorophyll concentration in the leaves was determined using a chlorophyll meter SPAD 502-Plus, Minolta. The measurements were carried out on the central part of each leaf. Each year, during the full-grain ripeness stage (BBCH 89), 100 stems with heads were collected from each plot. They were then dried to the air-dry weight and weighed. From the entire plot, grains of both cereals were collected in the full ripeness stage (BBCH 89), dried to the water content of 12%, and weighed. Total nitrogen content in the grains was determined by the Kjeldahl method. N uptake by the cereals was determined by converting the obtained value by the grain yield.

The results were processed statistically through analysis of variance, in line with the constant model for factorial sets, at the level of significance  $\alpha = 0.05$ , and identifying homogeneous groups with the Tukey's test. Analyses of simple correlations between the assimilation rate (A) and transpiration rate (E) and stomatal conductance (gs), intercellular CO<sub>2</sub> concentration (Ci), the water use efficiency (WUE), photosynthetic water use efficiency (PWUE), chlorophyll content (SPAD), the leaf area (P), aerial plant weight (M), grain yield (Y) and N uptake were based on the Spearman's rank correlation test. All calculations were supported by the software program Statistica 12.5.

## RESULTS

The wheat leaves were characterised by greater stomatal conductance (by approx. 30%) and intercellular CO<sub>2</sub> concentration (by approx. 5%) than the spelt leaves (Table 1). As regards the assimilation and transpiration rates, no significant differences between these plants were noted. In both cereals, a favourable effect of the oilseed rape as a forecrops on the activity of stomatal apparatus, CO<sub>2</sub> assimilation and transpiration was demonstrated. In the field, after this crop, the aperture was greater in wheat and spelt by 30.4% and 141.2%, respectively; the assimilation rate by 63.7% and 24.1%, respectively; and the transpiration rate by 56.8% and 35.2%, respectively, than after the other forecrops. In wheat and spelt, the assimilation process and in spelt the transpiration process were slightly more intensive after pea than after barley and one after the other. In the stands

Table 1

Leaf gas exchange parameters in wheat and spelt

| Treatment | Stomatal conductance (gs) [mol (H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )] | Net assimilation rate (A) [μmol(CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )] | Transpiration rate (E) [mmol (H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )] | Intercellular CO <sub>2</sub> concentration (Ci) [μmol(CO <sub>2</sub> ) mol <sup>-1</sup> ] | WUE                     | PWUE                    | LS                       |
|-----------|---|--|---|--|-------------------------|-------------------------|--------------------------|
| W         | 0.60±0.03 <sup>a</sup>  | 15.92±0.22 <sup>a</sup>  | 3.80±0.27 <sup>a</sup>  | 237.8±2.98 <sup>a</sup>  | 4.19±0.29 <sup>a</sup>  | 26.1±0.38 <sup>b</sup>  | 0.268±0.02 <sup>b</sup>  |
| S         | 0.46±0.03 <sup>b</sup>  | 15.07±0.11 <sup>a</sup>  | 3.98±0.14 <sup>a</sup>  | 225.3±4.51 <sup>b</sup>  | 3.79±0.15 <sup>b</sup>  | 32.8±0.21 <sup>a</sup>  | 0.338±0.01 <sup>a</sup>  |
| WP        | 0.60 ±0.02 <sup>b</sup>   | 15.61±0.14 <sup>bc</sup>   | 3.09±0.23 <sup>c</sup>  | 239.0±3.48 <sup>b</sup>  | 5.05±0.35 <sup>a</sup>  | 26.0±0.09 <sup>c</sup>  | 0.268± 0.02 <sup>c</sup> |
| WR        | 0.73±0.02 <sup>a</sup>  | 22.48 ±0.36 <sup>a</sup>   | 5.22±0.31 <sup>a</sup>  | 223.0±2.23 <sup>c</sup>  | 4.30±0.40 <sup>a</sup>  | 30.8± 0.46 <sup>c</sup> | 0.344±0.01 <sup>b</sup>  |
| WB        | 0.52±0.05 <sup>b</sup>  | 13.52±0.09 <sup>d</sup>  | 3.44±0.19 <sup>c</sup>  | 243.5± 4.4 <sup>a</sup>  | 3.93±0.33 <sup>b</sup>  | 26.0±0.49 <sup>c</sup>  | 0.254±0.01 <sup>c</sup>  |
| WW        | 0.56 ±0.04 <sup>b</sup>   | 12.05±0.17 <sup>d</sup>  | 3.45±0.14 <sup>c</sup>  | 245.8±3.22 <sup>a</sup>  | 3.49±0.21 <sup>c</sup>  | 21.5±0.16 <sup>d</sup>  | 0.206±0.03 <sup>d</sup>  |
| SP        | 0.31±0.02 <sup>c</sup>  | 15.37±0.09 <sup>c</sup>  | 4.04±0.14 <sup>b</sup>  | 219.6±5.12 <sup>d</sup>  | 3.80±0.14 <sup>b</sup>  | 49.6±0.08 <sup>a</sup>  | 0.426±0.01 <sup>a</sup>  |
| SR        | 0.82±0.02 <sup>a</sup>  | 17.63±0.13 <sup>b</sup>  | 4.95± 0.09 <sup>a</sup>   | 218.7± 4.23 <sup>c</sup>   | 3.56±0.11 <sup>bc</sup> | 21.5±0.22 <sup>c</sup>  | 0.287± 0.01 <sup>c</sup> |
| SB        | 0.31±0.04 <sup>c</sup>  | 13.01±0.10 <sup>d</sup>  | 3.24±0.13 <sup>c</sup>  | 231.1± 3.98 <sup>b</sup>   | 4.02±0.13 <sup>b</sup>  | 42.0±0.31 <sup>b</sup>  | 0.353±0.01 <sup>b</sup>  |
| SS        | 0.40±0.06 <sup>c</sup>  | 14.25±0.19 <sup>d</sup>  | 3.70±0.12 <sup>bc</sup>   | 231.7±4.02 <sup>b</sup>  | 3.85±0.16 <sup>b</sup>  | 35.6±0.11 <sup>ab</sup> | 0.284±0.02 <sup>c</sup>  |

W – wheat, S – spelt, WP – wheat after pea, WR – wheat after oilseed rape, WB – wheat after barley, WW – wheat after wheat, SP – spelt after pea, SR – spelt after oilseed rape, SB – spelt after barley, SS – spelt after spelt. Different letter within the same column (separately for cereals, and separately for forecrops) denote the differences between the treatments ( $P < 0.05$ )

after barley and after one another, the intercellular CO<sub>2</sub> concentration in the leaves of both cereals was similar. Its significantly lower concentration in relation to these stands was noted after pea (on average, by 2.3% in wheat and by 5.1% in spelt) and after oilseed rape (by 8.9% and 5.5%, respectively).

Wheat used water (WUE) more efficiently (by 10.6%) than spelt. This cereal made a better use of water in stands after pea and oilseed rape than in the stands after barley (by an average of 19%) and wheat (by 34%). In spelt, the WUE index exhibited no significant differences under the influence of the forecrops. In turn, higher intrinsic water use efficiency (PWUE) values were obtained for spelt than for wheat (by 25.7%). In wheat, no significant differences were found in the PWUE values between the stands after pea, oilseed rape and barley. This indicator reached lower values under the conditions of wheat cultivated after wheat. On the other hand, spelt used water more efficiently in the photosynthesis process after pea. The stand after oilseed rape had an adverse effect on the course of this process.

The stomatal limitation (Ls) reached significantly higher values in spelt (by an average of 26.1%) than in wheat. In wheat plants, the stomata limited CO<sub>2</sub> assimilation more after oilseed rape (in 34.4%), and in spelt plants – after pea (in 42.6%) than after the other forecrops. The smallest stomatal limitations were ensured by the stands of cultivation of wheat after wheat (20.6%) and spelt (28.4%), and also by stands of spelt cultivations following oilseed rape (28.7%).

Wheat and spelt were characterised by a similar assimilatory area (Table 2). However, more chlorophyll was found in the wheat leaves (by 13.5%). The leaves of both cereals were characterised by a significantly smaller area (by 9.0 and 5.7%, respectively) and their chlorophyll content

Table 2

Leaf area, chlorophyll content, aerial biomass, yield grain and N uptake by wheat and spelt

| Treatment | Leaf area (cm <sup>2</sup> ) | Chlorophyll content (SPAD) | Aerial biomass of 100 stems (g) | Grain yield (t ha <sup>-1</sup> ) | N uptake (kg ha <sup>-1</sup> ) |
|-----------|------------------------------|----------------------------|---------------------------------|-----------------------------------|---------------------------------|
| W         | 20.1±2.1 <sup>a</sup>        | 46.3±3.32 <sup>a</sup>     | 135.8±9.7 <sup>a</sup>          | 7.83±0.53 <sup>a</sup>            | 128.3±8.9 <sup>a</sup>          |
| S         | 19.8±1.1 <sup>a</sup>        | 40.8±2.06 <sup>b</sup>     | 125.5± 8.5 <sup>b</sup>         | 6.03±0.42 <sup>b</sup>            | 109.7±4.8 <sup>b</sup>          |
| WP        | 21.3±1.3 <sup>a</sup>        | 47.8±3.5 <sup>a</sup>      | 134.2±8.0 <sup>ab</sup>         | 8.03±0.99 <sup>b</sup>            | 140.9±10.5 <sup>a</sup>         |
| WR        | 20.7±1.9 <sup>a</sup>        | 47.5± 4.1 <sup>a</sup>     | 135.6±9.1 <sup>a</sup>          | 8.20±0.69 <sup>a</sup>            | 131.9± 9.9 <sup>a</sup>         |
| WB        | 19.5±2.1 <sup>b</sup>        | 45.3±4.1 <sup>b</sup>      | 139.5±10.7 <sup>a</sup>         | 7.67±0.63 <sup>c</sup>            | 121.2±8.5 <sup>b</sup>          |
| WW        | 18.7±2.2 <sup>b</sup>        | 44.7± 3.7 <sup>b</sup>     | 133.7±9.6 <sup>ab</sup>         | 7.43±0.45 <sup>c</sup>            | 119.2±8.0 <sup>bc</sup>         |
| SP        | 20.2 ±0.9 <sup>a</sup>       | 42.4±1.6 <sup>c</sup>      | 129.1±7.5 <sup>ab</sup>         | 6.35±0.18 <sup>c</sup>            | 127.5± 3.8 <sup>b</sup>         |
| SR        | 20.5±1.0 <sup>a</sup>        | 42.4±0.8 <sup>c</sup>      | 122.9±8.8 <sup>b</sup>          | 6.57± 0.57 <sup>d</sup>           | 116.6± 5.6 <sup>c</sup>         |
| SB        | 19.7±1.2 <sup>b</sup>        | 39.2±2.1 <sup>d</sup>      | 124.6±9.7 <sup>b</sup>          | 5.66±0.15 <sup>f</sup>            | 102.7±4.2 <sup>d</sup>          |
| SS        | 18.7±1.3 <sup>b</sup>        | 39.3±3.1 <sup>d</sup>      | 125.2±8.2 <sup>b</sup>          | 5.53±0.39 <sup>f</sup>            | 91.9±4.9 <sup>d</sup>           |

Explanations see Table 1.

(by 5.6 and 7.4%) in the fields after barley and after one another, in relation to the undifferentiated stands after pea and oilseed rape.

The aerial weight of wheat stems was significantly greater (by 8.2%) than that of spelt stems. In both cereals, the previous crops had no significant effect on its value. The yield of wheat was higher by almost 30% than the yield of spelt. Oilseed rape proved to be the most favourable forecrops for both cereals. The yield of wheat and spelt grains that was obtained in this sequence was higher by 8.6 and 17.3%, respectively, than from the least productive fields after cereals. Moreover, nitrogen uptake with the wheat grain yield was greater by 17% than with the spelt grain yield. In both cereals, the highest N uptake was ensured by the stands after pea and oilseed rape, and it was significantly lower after cereals as previous crops (in wheat by 11.9%, and in spelt by 20.3%).

The correlation analysis demonstrated that assimilation in both cereals was positively correlated with the activity of the stomatal apparatus, transpiration, chlorophyll content of the leaves, grain yield and N uptake, and additionally in wheat with the WUE indicator and in spelt with the intercellular CO<sub>2</sub> concentration after all forecrops (Table 3). Moreover, assimilation in wheat was significantly positively correlated with the PWUE indicator in the stands after pea and after wheat, and with the indicator Ls, leaf area and aerial biomass after pea and oilseed rape. In this cereal, a negative correlation was noted between assimilation and intercellular CO<sub>2</sub> concentration after all previous crops, and the area of the leaves after barley and wheat. In spelt, a decrease in assimilation was accompanied by a decrease in the leaf area after barley and spelt. In this cereal, a negative correlation was demonstrated between assimilation and the intrinsic water use efficiency after pea, barley and spelt and between assimilation and plant weight after oilseed rape and spelt.

In both cereals, transpiration exhibited a positive correlation with the aperture (with the exception of the field where wheat was cultivated after wheat, and the stand where spelt was cultivated after barley), WUE and Ls indicators in the fields after barley, and the grain yield and N uptake in the fields after pea and barley. Additionally, in wheat cultivated after pea, the increase in transpiration was accompanied by an increase in the Ls indicator and the plant weight, but a decrease in PWUE and in intercellular CO<sub>2</sub> concentration. In the stand after oilseed rape, transpiration was positively correlated with the PWUE indicator, intercellular CO<sub>2</sub> concentration and the plant weight, and negatively correlated with the WUE indicator. In the field after barley, a negative correlation was demonstrated between the transpiration and PWUE, while a positive correlation was demonstrated with the grain yield and N uptake. Under the conditions of wheat cultivation in succession, transpiration was positively correlated with the WUE, PWUE, Ls and SPAD indicators, and negatively correlated with the intercellular CO<sub>2</sub> concentration and the area of the leaves. In spelt, transpiration exhibited a positive

Table 3

Spearman rank order correlations matrix between assimilation, transpiration and examined traits of wheat and spelt ( $n=12$ )

| Traits | Assimilation (A) |         |         |         |         |         | Transpiration (E) |         |         |         |         |         |         |         |        |         |
|--------|------------------|---------|---------|---------|---------|---------|-------------------|---------|---------|---------|---------|---------|---------|---------|--------|---------|
|        | wheat            |         |         | spelt   |         |         | wheat             |         |         | spelt   |         |         |         |         |        |         |
|        | P                | R       | B       | W       | S       | B       | R                 | P       | B       | W       | S       | R       | P       | B       | S      |         |
| gs     | 0.916*           | 0.777*  | 0.626*  | 0.774*  | 0.949*  | 0.984*  | 0.900*            | 0.503*  | 0.676*  | 0.823*  | 0.887*  | 0.362   | 0.974*  | 0.875*  | 0.329  | 0.965*  |
| A      | 1                | 1       | 1       | 1       | 1       | 1       | 1                 | 1       | 0.568*  | 0.507*  | 0.844*  | 0.831*  | 0.879*  | 0.788*  | 0.859* | 0.569*  |
| E      | 0.568*           | 0.507*  | 0.844*  | 0.831*  | 0.879*  | 0.788*  | 0.859*            | 0.569*  | 1       | 1       | 1       | 1       | 1       | 1       | 1      | 1       |
| WUE    | 0.613*           | 0.422*  | 0.793*  | 0.827*  | 0.009   | -0.113  | 0.204             | 0.333   | -0.216  | -0.566* | 0.517*  | 0.560*  | -0.415* | -0.690* | 0.636* | -0.072  |
| PWUE   | 0.873*           | -0.277  | -0.225  | 0.868*  | -0.937* | -0.022  | -0.919*           | -0.419* | -0.483* | 0.865*  | -0.604* | 0.622*  | -0.948* | -0.929* | 0.248  | -0.922* |
| Ci     | -0.914*          | -0.635* | -0.420* | -0.967* | 0.944*  | 0.978*  | 0.578*            | 0.639*  | -0.750* | 0.644*  | 0.043   | -0.753* | 0.842*  | 0.691*  | 0.184  | 0.959*  |
| LS     | 0.931*           | 0.528*  | 0.092   | -0.933* | -0.937* | -0.978* | -0.494*           | -0.650* | 0.453*  | 0.096   | 0.386*  | 0.660*  | -0.909* | -0.787* | 0.787* | -0.959* |
| SPAD   | 0.658*           | 0.462*  | 0.644*  | 0.995*  | 0.904*  | 0.630*  | 0.926*            | 0.517*  | -0.212  | -0.287  | 0.201   | 0.839*  | 0.989*  | -0.095  | 0.926* | -0.746* |
| P      | 0.778*           | 0.748*  | -0.626* | -0.967* | 0.125   | 0.244   | 0.874*            | 0.499*  | 0.001   | -0.369  | -0.180  | -0.688* | -0.342  | 0.559*  | 0.568* | 0.958*  |
| M      | 0.794*           | 0.831*  | 0.054   | 0.260   | -0.155  | -0.574* | 0.174             | -0.487* | 0.626*  | 0.361*  | -0.280  | -0.238  | -0.077  | -0.916* | 0.448* | -0.861* |
| Y      | 0.556*           | 0.667*  | 0.515*  | 0.442*  | 0.787*  | 0.813*  | 0.653*            | 0.540*  | 0.866*  | 0.410   | 0.810*  | 0.411   | 0.773*  | 0.486*  | 0.727* | 0.877*  |
| N      | 0.651*           | 0.512*  | 0.449*  | 0.505*  | 0.667*  | 0.714*  | 0.608*            | 0.487*  | 0.802*  | 0.499   | 0.786*  | 0.386   | 0.652*  | 0.437   | 0.700* | 0.781*  |

Forecrops: P – pea, R – oilseed rape, B – barley, W – wheat, S – spelt; gs – stomatal conductance, A – assimilation, WUE – instantaneous water use efficiency, PWUE – intrinsic water use efficiency, Ci – intercellular CO<sub>2</sub> concentration, LS – stomatal limitation value, SPAD – chlorophyll content, P – leaf area, M – above-ground biomass, Y – grain yield, N – nitrogen uptake



correlation with the intercellular CO<sub>2</sub> concentration (with the exception of the field after barley), chlorophyll content (SPAD) in the fields after pea and barley, the area of the leaves (with the exception of the field after pea), the plant biomass in the stand after barley, the grain yield and N uptake (with the exception of the field after oilseed rape), SPAD in the fields after pea and barley, and the plant weight in the stand after barley. In this cereal in the fields after pea and oilseed rape, an increase in transpiration resulted in a decrease in the value of WUE, PWUE and Ls indicators; after oilseed rape, there was also a decrease in the plant weight, and under the conditions of barley cultivation after barley there was a decrease in the PWUE, Ls and the weight of plants.

## DISCUSSION

The primary function of the stomata is to prevent water loss and enable the flow of CO<sub>2</sub> between the atmosphere and the plant. The stomatal apparatus is very sensitive to changes in environmental conditions. Under environmental stress conditions (e.g. water or nutrient scarcity), the stomata are closed, which restricts the fixation of CO<sub>2</sub> from the atmosphere to the cell interior. This is one of the main reasons for a decrease in plant productivity. On the other hand, closing the stomata protects a plant against water loss (REDDY et al. 2004).

The authors found no effects of wheat subspecies on the assimilation and transpiration rates. Wheat, however, was characterised by a greater activity of stomatal apparatus and higher intercellular CO<sub>2</sub> concentration than spelt. The intercellular CO<sub>2</sub> concentration is necessary to increase the photosynthesis rate; however, it is determined by the plant species and habitat conditions (KU et al. 1977), which is partially confirmed by the authors' study, in which the intercellular CO<sub>2</sub> concentration reached higher values in wheat than in spelt. However, in the same study, gas exchange was determined by the forecrops. In both cereals, a favourable effect of the oilseed rape as a previous crop on the aperture and the assimilation and transpiration rates was proven. Nevertheless, the intercellular CO<sub>2</sub> concentration after oilseed rape and after pea was lower than after cereals (particularly in wheat). In wheat, the oilseed rape as a previous crop, and in spelt preceded by pea caused the greatest limitations to obtaining CO<sub>2</sub> (Ls). This probably resulted from the more intensive metabolism of plants cultivated after these crops (including the activity of Rubisco, the basic photosynthesis enzyme) and, thus, a greater role in the productivity of non-stomatal factors than after cereals (YANG et al. 2009). Studies by PSZCZÓŁKOWSKA et al. (2018) and by SIELING and CHRISTEN (2015) demonstrated that wheat cultivated after favourable forecrops such as oilseed rape or pea developed better and gained greater height and weight. These plants leave a good stand, which

is rich in nitrogen and other elements, with a favourable structure that provides roots of the succeeding plants with optimal conditions for the development as well as water and nutrient uptake (EVANS et al. (2003). This was confirmed in the current study, where N uptake by wheat and spelt cultivated after oilseed rape and pea was greater than after cereals. Nitrogen can affect the stomatal apparatus regulation and the photosynthetic apparatus efficiency through increasing the chlorophyll content of the leaves (DAMATTA et al. 2002). In the analysed study, wheat and spelt cultivated after oilseed rape and pea were characterised by a greater assimilatory area and chlorophyll content than after cereals. An increase in the SPAD value with an increase in N fertilisation was also noted by JANUSAUSKAITE et al. (2017). Under favourable environmental conditions, physiological processes run more intensively and smoothly. The above was confirmed by WANG et al. (2018), who demonstrated that gas exchange and leaf chlorophyll content were affected by P supply and different cultivars, and by JANUSAUSKAITE et al. (2017), who found an increase in transpiration and the WUE index under conditions of abundant N fertilisation. The analysed cereals in fields, cultivated after oilseed rape and pea, exhibited greater nutrient content than those cultivated successively, which was also noted by a previous study (WANIC et al. 2019).

The successive cultivation of cereals results in many adverse changes in the soil environment. The vegetation of cereals (particularly wheat) under such conditions causes stress in plants, which is manifested by poorer emergence, a less developed root system (plants take up less water and nutrients), poorer growth and development, and the formation of plants with poorer foliage with a lower chlorophyll content (LALARUKH et al. 2014). This was confirmed in the current study, which demonstrated that in stands where the cereals were cultivated in succession, the plants formed leaves with a smaller area and lower chlorophyll content. GRANIER et al. (2000) found that, fewer cells develop in the leaves of plants subjected to stress, and those present do not grow to full size. The plants exhibit greater activity of the enzyme chlorophyllase, which results in a lower chlorophyll content (MAFAKHERI et al. 2010). A decrease in the chlorophyll content of leaves may restrict the assimilation process and, ultimately, the productivity of plants (CABRERA-BOSQUET et al. 2009). Literature data indicate that plants, when under the influence of stress, often suffer from the lack of water and of nutrients as well, which can change the course of basic physiological processes. Under such conditions, they close their stomata, which contributes to a decrease in CO<sub>2</sub> diffusion and is the main cause of the decrease in assimilation rate (REDDY et al. 2004). The present research reveals that the cultivation of wheat and spelt one after the other in succession and after barley disturbs the course of gas exchange. After these forecrops, lower activity of stomatal apparatus as well as lower assimilation and transpiration rates were noted. In the stand of wheat after wheat, the WUE and PWUE indicators decreased as well. In the fields after cereals, however, the intercellular CO<sub>2</sub> concentration increased, which may indicate the insufficiency

of the photosynthetic apparatus, which has not been able to make use of the excess CO<sub>2</sub> (SAEIDI, ABDOLI 2015). A decrease in the photosynthesis rate may also result from reasons not related to the stomatal limitation but to other processes, e.g. a reduced activity of certain Calvin cycle enzymes, photosynthetic electron transport inhibition or limited phosphorylative capacity (SAEIDI, ABDOLI 2015). It should be noted here that the response of spelt to the cultivation after cereals was weaker than that of wheat. This confirms the literature data on the greater tolerance of cultivation under unfavourable habitat conditions (ŻUK-GOŁASZEWSKA et al. 2015).

It was demonstrated in our experiment that assimilation was positively correlated with stomatal conductance, transpiration, the chlorophyll content of leaves and the grain yield in both cereals after all previous crops. The positive correlation between the grain yield and assimilation and SPAD was confirmed by JANUSAUSKAITE et al. (2017), between stomatal conductance and the grain yield by BAHAR et al. (2009), and between assimilation and stomatal conductance and the grain yield by GONZALEZ et al. (2010). However, OLSZEWSKI et al. (2014) found no significant correlation between the grain yield and assimilation in two spring wheat cultivars, while KULIG et al. (2010) found no significant relationship between the SPAD and the grain yield.

## CONCLUSION

The results demonstrated that gas exchange, foliage, yield and N uptake were determined by the wheat subspecies and the previous crop. It was shown that wheat plants compared with spelt plants were characterised by more intensive gas exchange, a better-developed stomatal apparatus, a higher N uptake and a greater biomass and grain yield. In both cereals, a favourable effect of the oilseed rape as a forecrops on the activity of the stomatal apparatus and the assimilation and transpiration rate was demonstrated. However, in terms of water use efficiency in the photosynthesis process, the leaf area, chlorophyll content of leaves, grain yield and N uptake, pea as a previous crop was equal to oilseed rape. Most of the gas exchange parameters were decreased in the stands where wheat and spelt were cultivated after barley and after one another. The forecrops had a stronger effect on the course of physiological processes in wheat than in spelt. However, spelt responded more forcefully than wheat to the cultivation in stands after barley and after one another by a reduction in grain yield and lower N uptake. In both cereals cultivated after the analysed previous crops, a significant relationship was demonstrated between assimilation and the aperture, transpiration, chlorophyll content of leaves, grain yield and N uptake.

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