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# Grain yield and yield components of spring barley genotypes as the indicators of their tolerance to temporal drought stress

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**Abstract.** In 2011, a research project on breeding spring barley genotypes tolerant to temporary drought stresses was started. The authors' responsibility was to test the productivity of genotypes derived from different parental forms obtained as part of the project on drought resistance studied in a pot experiment. In the years 2011–2013, three consecutive series of experiments with approximately seventy genotypes each year were carried on. Two reference Polish varieties were included in each set. In the control treatment, plants were grown at the optimal soil moisture level of 13–15% weight by weight for the whole growing period. Drought stresses were introduced at the tillering stage (BBCH 23) for the period of 11 days or at full flag leaf stage (BBCH 45-47) for the period of 14 days. At both stress treatments, the moisture was maintained at the level of 5–6% weight by weight. Plants were harvested at full maturity stage. The grain and straw yields, yield components i.e. number of productive tillers, number of grains per spike and weight of 1000 grains were determined. Spring barley showed a higher tolerance to the drought stress at tillering stage than it did at flag leaf stage. Barley genotypes differed in their response to temporary drought stresses due to diverse ability for regenerating after the stress removal. The tolerance of the spring barley genotypes to drought stress imposed at tillering stage resulted from their ability to produce additional fertile tillers. The tolerance of the spring barley genotypes to temporal drought stress at flag leaf stage can be explained by compensation of the reduced grain number per spike through increasing the weight of 1000 grains.

**key words:** spring barley, drought tolerance, grain yield, yield components

## INTRODUCTION

Drought in Poland is the climatic phenomenon of increasing significance for agricultural production (Górski et al., 2008). Increasing temperature, and a number of sun-hours, even without significant changes in precipitation, cause the deepening of the already negative water balance, which is calculated as the difference of rainfall and potential evapotranspiration (Kozyra et al., 2009). According to European weather forecast for 2071–2100, the mean air temperature in Poland will probably increase by 3.5°C compared to 1961–1990 period. The simple model of the effect of climate warming on crop development showed that temperature increase by 1°C per 100 years fastens cereal crop maturity in Poland by 1 week (Górski et al., 2008). According to climate change models, a higher air temperature causes weather anomalies, which in turn bring about yield losses (Liszewska, Osuch, 1997). Moreover, more heterogenous distributions of rainfall during the whole year, and particularly during the vegetation period cause the plants to be exposed to frequent drought stresses (Górski et al., 2008; Kozyra et al., 2009).

Barley is an important cereal crop in Poland. It covers about 1 mln ha and takes about 12% of Poland's cropland. The spring form of this crop dominates strongly over the winter one. Due to short vegetation period extending for about 100 days and poorly developed root system, spring barley is very sensitive to drought stresses, even if they are temporary.

The phenomenon of decreasing spring barley yields under conditions of poor water supply is well known in the literature (Albrizio et al., 2010; Brestič, 1996; Cossani et al., 2009; Ferrante et al., 2008; Haddadin, 2015; Hossain et al., 2012, Jamieson et al., 1995; Savin, Nicolas, 1996; Zare et al., 2011). Drought stress reduces grain yield of barley through negatively affecting the yield components i.e. number of plants per unit area, number of spikes and grains per plant or unit area and single grain weight, which are determined at different stages of plant development (Ajalli, Salehi, 2012; Beigzadeh et al., 2013; Farooq et al., 2009; Francia et al., 2013; Haddadin, 2015; Hossain et al., 2012; Jamieson et al., 1995; Khaiti, 2012; Khokhar et al., 2012; Méndez et al., 2011; Samarah, 2005; Samarah et al.,

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2009). The values of yield components are genetically-based, but they can be strongly modified by the pattern of moisture conditions in the growing period (Ajalli, Salehi, 2012; Albrizio et al., 2010; Cossani et al., 2009, Francia et al., 2013; Hossain et al., 2012). Tillers and primordia of generative organs (spikes, spikelets and florets), which determine the number of grains per spike and unit area are initiated at tillering stage, and developed at the stage of stem elongation (García del Moral et al., 1991; Křen et al., 2014; Svobodová, Míša, 2004). Insufficient water and nutrients supply or poor effectiveness of photosynthesis during tillering or stem elongation can decrease the number of fertile florets and the number of grains per spike (Conry, Keane, 1994; Ferrante et al., 2008). Brestič (1996) noticed that the development of the florets into grains was decreased most considerably by the reduction of initiated florets under stress at the stem elongation stage as compared to stresses in the period of anthesis or grain filling only. In the meantime, according to Savin and Slafer (1991), environmental conditions around 20 days pre- and 10 days post-anthesis are considered as critical for grain yield determination. At heading stage, when in the case of barley anthesis takes place, sufficient moisture supply supports pollination and fertilization processes, and therefore initiation of grain primordia (Briggs et al., 1999). During pre-anthesis, the potential grain number per unit area (Fisher, 1985), and potential grain weight (Calderini et al., 2001) are defined. The final number of grains per unit area is set immediately after anthesis, while grain filling and accumulation of biomass of grains take place during the remaining post-anthesis period (Ugarte et al., 2007). At that time, good moisture and light conditions increase the effectiveness of photosynthesis, which is related to the plant assimilation area which developed at the previous stages. Finally, weight of 1000 grains depends on the physiological functionality of genotype and length of photosynthesis period (Bertholdsson, 1999; Przulj, Momcilovic, 2001). The number of spikes per unit area, i.e. number of fertile stems is determined by weather conditions during the whole growing period from the emergence through tillering and stem elongation up to the stages of spike development. Hence, although late-emerged tillers contribute less to grain yield than do tillers that emerged earlier (Lauer, 1991), there still exists a possibility for plant to re-growth after temporary stress abating and it is considered as one of the implications of adaptation responses to the varying water supply (Acevedo et al., 2002; García del Moral, 1991; García del Moral, 2003; Samarah, 2005; Svobodová, Míša, 2004).

Barley cultivars differ considerably in their response and adaptation to the drought stresses (Ajalli, Salehi, 2012; Beigzadeh et al., 2013; Hossain et al., 2012; Khaiti, 2012; Khokhar et al., 2012; Křen et al., 2014; Przulj, Momcilovic, 2001; Zare et al., 2011). These differences are partly attributed to different re-growth ability of plants after the stress removal. The regenerating ability is manifested by the strength of compensation of one yield component by another/other ones (García del Moral, 1991; García del Moral, 2003; Méndez et al., 2011). Therefore, understanding of relationships between yield components in yield compensation after temporal drought stress may help target the key traits that limit yield. Selecting different genotypes under environmental stress conditions is one of the main tasks of plant breeders for exploiting the genetic variations to improve the stress tolerant cultivars (Haddadin, 2015). Agronomic traits such as grain yield and its components are the major selection criteria for evaluating drought tolerance of barley (Hossain et al., 2012; Niazi-Fard et al., 2012). Available reports show that drought-tolerant species perform well under both drought and well-watered conditions (Ajalli, Salehi, 2012; Eivazi et al., 2013; Haddadin, 2015; Janfrozzadh, Niazi Fard, 2014; Samarah et al., 2009; Sharafi et al., 2011) and can be recommended to be used as parents for improvement of drought tolerance in other cultivars (Aghaei et al., 2010; Haddadin, 2015; Khokhar et al., 2012; Méndez et al., 2011). Therefore the comparative analysis of the yield components under stressed and unstressed conditions can be helpful in predicting stress tolerance of genotypes, and then in selection of more tolerant entries (Perlikowski et al., 2013; Plaut, 2003).

Based on the previous literature findings the hypothesis was defined as follows: the tolerance of spring barley genotypes to temporary drought stress results from their ability to regrow after the stress removal, which is related to phenomena of late tillering and compensation of yield losses by yield components.

The purpose of the study was to segregate the barley genotypes into tolerant and sensitive to temporary drought stress groups on the base of individual plant yield and the following yield components: productive tillering (number of fertile tillers per plant), grain yield per spike, number of grains per spike, weight of 1000 grains (WTG) and harvest index (HI). Due to the constant number of plants per pot the grain yield per plant was considered as a measure of genotype productivity.

## MATERIALS AND METHODS

The pot experiment with spring barley was carried out in 2011–2013 years at the glasshouse of Grabow Experimental Station of the Institute of Soil Science and Plant Cultivation – State Research Institute in Pulawy, Poland (E 21$^{o}$39’, N 51$^{o}$21’). The total number of 206 genotypes, including 142 lines, their parental forms Maresi (Germany), CAM/B1/CI08887//CI05761 and Harmal (Syria), Georgia (Great Britain) and 60 cultivars registered and cultivated in Poland was tested against short-term drought stresses introduced at the tillering stage (BBCH 23, 31 days after sowings) for 11 days (S1) or at full flag leaf stage (BBCH 45-47, 50 days after sowings) for 14 days (S2). At the control treatment (C), soil moisture was maintained at the optimal level of 13–15% weight by weight for the whole vegetation period, and in the treatments S1 and S2, at the level of 5–6% weight by weight. The levels of moisture treatments were defined based on the soil water retention curve developed in the Institute of Agrophysics PAS in Lublin, Poland. The drought stress was maintained in the range of limited water availability and always above permanent wilting point. It allowed barley plants to show visual symptoms of turgidity loss after the drought stress applications, but they were able to recover after re-watering.

The two-factor experiment was set up each year at the second decade of April i.e. at optimal sowing time of spring barley in Eastern Poland, in three replicates (pots) with 10 plants per pot. Each pot was filled with 9 kg of mixture of loamy soil with sand in the 7:2 proportion, sufficiently supplied with all necessary nutrients according to fertilization recommendations of the Institute of Soil Science and Plant Cultivation State Research Institute. Drip irrigation of each pot was steered by a computer system (Adviser company, www.phu-adviser.pl), and corrected using an electronic balance.

The glasshouse provided with mobile glass roof and walls enabled plants to grow under conditions close to natural in the field, and protected them against rainfall. The mean air temperature inside the glasshouse at S1 stress equaled to 15.2°C and at S2 stress to 19.9°C. Air moisture varied on average between 71% and 75%, respectively. The air temperature and humidity inside the glasshouse were measured each second by the AR 236 recorder (www.sitaniectech.pl). After harvest, grain and straw yield, and number of fertile spikes per pot were determined. Then, based on selected randomly 10 main stems and 20 tillers number of grains per each spike, and 10 and 20 spike grain weight means were estimated. The other yield components were calculated according to the following formulas:

Grain yield per plant = grain yield per pot / number of plants per pot;

Grain yield per spike = grain yield per pot / number of spikes per pot;

Productive tillering (number of fertile tillers per plant) = number of spikes per pot / number of plants per pot;

Weight of 1000 grains (WTG) = (grain yield / number of grains) · 1000;

Number of grains per spike = (grain yield per spike / WTG) · 1000;

Harvest index (HI) = grain yield / (grain yield + straw yield).

The data was statistically analysed by k-Means method of cluster analysis and one-way ANOVA, separately for data referring to the stress at tillering stage and at flag leaf stage. Cluster analysis based on plant productive tillering, grain yield per pot, plant and spike, number of grains per spike and WTG allowed to segregate the tested genotypes into clusters of tolerant and sensitive to each stress. Then, by one-way ANOVA, the clusters of tolerant and sensitive genotypes were compared under control and stressed conditions and stressed treatments were tested against controls for the effects on yield and yield components. The means were compared by Tukey's HSD procedure at the $\alpha = 0.05$ significance level. The statistical analysis was performed using Statgraphics Centurion XVI statistical package.

## RESULTS

The main purpose of the study was to segregate spring barley genotypes with respect of their tolerance to drought stress. Therefore, as the first step of statistical analysis cluster method was considered. Based on grain yield and yield components, the clusters grouping genotypes tolerant and sensitive to the stresses were recognized. The cluster analysis was performed separately for the results obtained under early and the late drought stress. The analysis of barley response to the stress at the tillering stage (S1) showed that 69% of tested genotypes decreased grain yield significantly, and they were recognized as sensitive ones (Fig. 1). The other 31% significantly increased grain yield, therefore they were recognized as tolerant. The barley genotypes exposed to later stress (S2) mostly (86%) responded to the stress by the significant reduction of grain yield. Only 14% of tested genotypes tolerated drought stress at the later development stage (Fig. 1).

The analysis of the response of barley genotypes grain yield to the drought stress at tillering and flag leaf stages was performed in the response type groups. The means of the analyzed yield components are presented in tables 1-4 below.

### Stress at tillering stage (S1)

On the whole plant level, two yield components decided upon the response type of studied genotypes to drought stress (Table 1). The number of fertile tillers was the "positive" component, since it improved drought tolerance. On the other hand, the weight of 1000 grains, which always decreased under the stress conditions, was the "negative" component, since it lessened drought stress tolerance. In the group of tolerant genotypes, positive effect of drought of increasing tiller number prevailed over the negative effect of decreasing WTG.

The tolerant genotypes responded to the drought stress at tillering stage by increased productivity as a result of higher number of productive tillers per single plant (Table 1). They also showed a tendency to reduced productivity of a single spike due to decreased weight of 1000 grains. However, in the control treatment under optimal moisture conditions, they showed a smaller productivity and harvest index than did sensitive ones, due to a smaller number of fertile tillers and smaller grain yield of a singular spike and weight of 1000 grains. Genotypes which were sensitive to the drought stress decreased productivity of both single

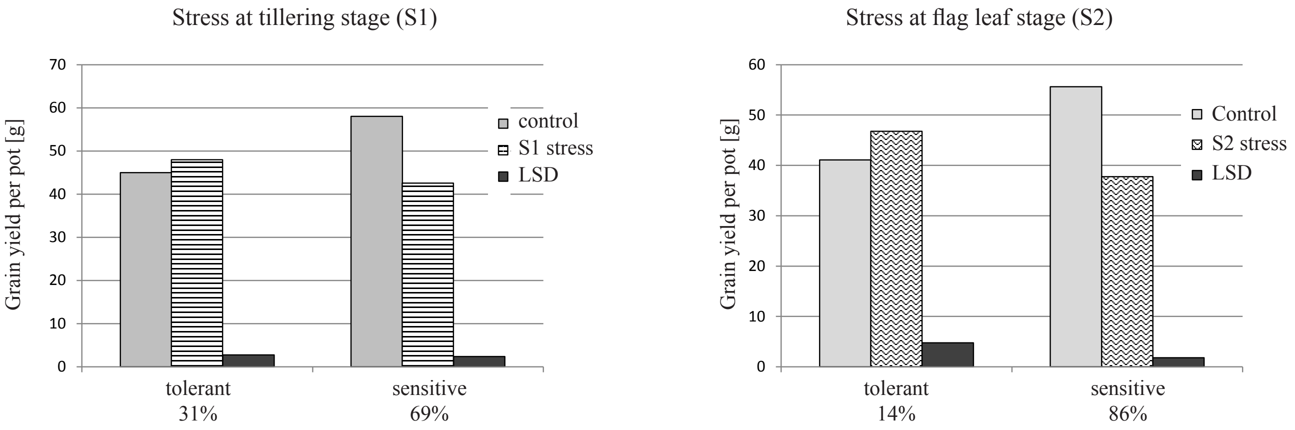

Fig. 1. Grain yield of spring barley genotypes in groups of tolerance to drought stresses at tillering and flag leaf stages.

Table 1. Effect of drought stress at tillering stage (S1) on grain yield per plant and its components of barley genotypes.

| Treatment | Grain yield per plant [g] | | Number of fertile tillers per plant | | Grain yield per spike [g] | | Number of grains per spike | | WTG [g] | | Harvest index | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Genotypes tolerant to S1 stress | | | | | | | | | | | | |
| Control | 4.50 b | B | 4.9 b | B | 0.93 a | B | 20.2 a | A | 46.4 a | B | 0.48 b | B |
| S1 stress | 4.80 a | A | 5.5 a | A | 0.88 a | B | 20.1 a | A | 44.3 a | A | 0.51 a | B |
| LSD (α = 0.05) | 0.277 | | 0.28 | | 0.074 | | 1.35 | | 2.65 | | 0.013 | |
| Genotypes sensitive to S1 stress | | | | | | | | | | | | |
| Control | 5.80 a | A | 5.7 a | A | 1.02 a | A | 20.4 a | A | 50.1 a | A | 0.53 a | A |
| S1 stress | 4.26 b | B | 5.5 a | A | 0.79 b | A | 17.2 b | B | 46.2 b | A | 0.54 a | A |
| LSD (α = 0.05) | 0.240 | | 0.23 | | 0.042 | | 0.79 | | 2.08 | | 0.014 | |
| LSD (α = 0.05) for the difference between genotypes tolerant and sensitive to S1 stress | | | | | | | | | | | | |
| Control | 0.326 | | 0.268 | | 0.058 | | 0.954 | | 2.39 | | 0.013 | |
| S1 stress | 0.243 | | 0.288 | | 0.055 | | 1.14 | | 2.68 | | 0.020 | |

Control – control treatment (no drought stress); S1 – stress at tillering stage; WTG – weight of 1000 grains; LSD – Least Significant Difference; smaller letters for comparisons of the treatments inside the genotype groups; uppercase for comparisons of the genotype groups inside the treatments

Table 2. Effect of drought stress at tillering stage (S1) on a spike yield components of barley genotypes.

| Treatment | Grain yield per spike [g] | | | | | | No. of grains per spike | | | | WTG [g] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | main stem | | a tiller | | total tillers | | main stem | | a tiller | | main stem | | a tiller | |
| Genotypes tolerant to S1 stress | | | | | | | | | | | | | | |
| Control | 1.19 a | B | 0.85 a | A | 3.31 a | B | 23.9 a | A | 19.8 a | B | 50.0 a | A | 42.9 a | A |
| S1 stress | 1.12 a | A | 0.82 b | A | 3.68 a | A | 23.2 a | A | 18.8 a | A | 48.1 a | A | 43.5 a | A |
| LSD (α = 0.05) | 0.084 | | 0.068 | | 0.372 | | 1.29 | | 1.13 | | 2.58 | | 2.72 | |
| Genotypes sensitive to S1 stress | | | | | | | | | | | | | | |
| Control | 1.25 a | A | 0.80 a | A | 4.55 a | A | 23.9 a | A | 20.7 a | A | 52.1 a | A | 38.6 a | B |
| S1 stress | 0.96 b | B | 0.60 b | A | 3.30 b | B | 20.1 b | B | 17.6 b | B | 48.2 b | A | 34.1 b | B |
| LSD (α = 0.05) | 0.051 | | 0.047 | | 0.307 | | 0.81 | | 0.55 | | 1.77 | | 2.18 | |
| LSD (α = 0.05) for the difference between genotypes tolerant and sensitive to S1 stress | | | | | | | | | | | | | | |
| Control | 0.067 | | 0.060 | | 0.398 | | 0.94 | | 0.76 | | 2.17 | | 2.45 | |
| S1 stress | 0.068 | | 0.228 | | 0.313 | | 1.15 | | 0.82 | | 2.31 | | 2.83 | |

Control – control treatment (no drought stress); S1 – stress at tillering stage; WTG – weight of 1000 grains; LSD – Least Significant Difference; smaller letters for comparisons of the treatments inside the genotype groups; uppercase for comparisons of the genotype groups inside the treatments plant and single spike due to decreased WTG and number of grains per spike.

The more detailed analysis at a single plant level considered the main shoot and the tillers. Water shortage at tillering stage reduced productivity of both main stems and the tillers of all tested barley genotypes exposed to the stress (Table 2). In the case of tolerant genotypes, the productivity of a singular tiller significantly decreased, but simultaneously the total grain yield produced by the tillers showed a tendency to increase. It confirms the increase of their number. Simultaneously, tolerant genotypes which were well-watered in the control treatment showed a higher productivity of a single tiller than the sensitive ones. It resulted from higher weight of 1000 grains. However, obtaining a smaller total grain yield from the tillers indicated that their number was lower. In response to the stress, sensitive genotypes decreased the grain yield of both the main stem and the tillers due to the reduced number of grains per spike and the weight of 1000 grains.

### Stress at flag leaf stage (S2)

Among yield components, weight of 1000 grains seems to be the one that decides upon the tolerance of spring barley genotypes to drought stress at flag leaf stage.

In the response to the stress at flag leaf stage, tolerant genotypes increased their grain yield per plant and per spike, and harvest index following the increase of weight of 1000 grains (Table 3). However, under optimal moisture conditions of the control treatment, these genotypes showed smaller grain yield and harvest index than the sensitive ones. They produced also a smaller number of fertile tillers per plant. Smaller productivity of singular spike resulted from smaller weight of 1000 grains, despite a higher number of grains.

The sensitive genotypes responded to the stress with reducing the productivity per plant due to the diminished number of fertile tillers and the diminished productivity of a singular spike. This decrease in the grain yield of a spike

Table 3. Effect of drought stress at flag leaf stage (S2) on grain yield per plant and its components of barley genotypes.

| Treatment | Grain yield per plant [g] | | Number of fertile tillers per plant | | Grain yield per spike [g] | | Number of grains per spike | | WTG [g] | | Harvest index | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Genotypes tolerant to S2 stress | | | | | | | | | | | | |
| Control | 4.11 b | B | 5.1 a | B | 0.82 b | A | 20.8 a | A | 39.5 b | B | 0.47 b | B |
| S2 stress | 4.68 a | A | 5.0 a | A | 0.95 a | A | 19.6 a | A | 48.5 a | A | 0.50 a | A |
| LSD (α = 0.05) | 0.479 | | 0.534 | | 0.090 | | 1.67 | | 3.56 | | 0.020 | |
| Genotypes sensitive to S2 stress | | | | | | | | | | | | |
| Control | 5.56 a | A | 5.7 a | A | 0.99 a | A | 19.3 a | B | 51.3 a | A | 0.52 a | A |
| S2 stress | 3.80 b | B | 5.1 b | A | 0.76 b | B | 15.6 b | B | 48.9 b | A | 0.45 b | A |
| LSD (α = 0.05) | 0.187 | | 0.21 | | 0.046 | | 0.78 | | 1.03 | | 0.012 | |
| LSD (α = 0.05) for the difference between genotypes tolerant and sensitive to S2 stress | | | | | | | | | | | | |
| Control | 0.447 | | 0.23 | | 0.043 | | 0.83 | | 1.37 | | 0.010 | |
| S2 stress | 0.213 | | 0.29 | | 0.064 | | 1.02 | | 1.97 | | 0.16 | |

Control – control treatment (no drought stress); S2 – stress at flag leaf stage; WTG – weight of 1000 grains; LSD – Least Significant Difference; smaller letters for comparisons of the treatments inside the genotype groups; uppercase for comparisons of the genotype groups inside the treatments

Table 4. Effect of drought stress at flag leaf stage on spike yield components of barley genotypes.

| Treatment | Grain yield per spike [g] | | | | | | No. of grains per spike | | | | WTG [g] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | main stem | | a tiller | | total tillers | | main stem | | a tiller | | main stem | | a tiller | |
| Genotypes tolerant to S2 stress | | | | | | | | | | | | | | |
| Control | 1.06 b | B | 0.74 b | B | 3.04 a | B | 24.5 a | A | 20.1 a | A | 43.4 b | B | 36.9 b | B |
| S2 stress | 1.31 a | A | 0.85 a | A | 3.39 a | A | 25.0 a | A | 18.7 b | A | 52.4 a | B | 45.3 a | A |
| LSD (α = 0.05) | 0.113 | | 0.084 | | 0.598 | | 1.67 | | 1.27 | | 3.40 | | 3.61 | |
| Genotypes sensitive to S2 stress | | | | | | | | | | | | | | |
| Control | 1.23 a | A | 0.93 a | A | 4.37 a | A | 23.2 a | B | 19.8 a | A | 53.4 a | A | 47.0 a | A |
| S2 stress | 1.15 b | B | 0.65 b | B | 2.65 b | B | 21.4 b | B | 16.3 b | B | 53.7 a | A | 39.7 b | B |
| LSD (α = 0.05) | 0.048 | | 0.041 | | 0.269 | | 0.76 | | 0.61 | | 0.86 | | 1.22 | |
| LSD (α = 0.05) for the difference between genotypes tolerant and sensitive to S2 stress | | | | | | | | | | | | | | |
| Control | 0.050 | | 0.042 | | 0.324 | | 0.82 | | 0.69 | | 1.27 | | 1.41 | |
| S2 stress | 0.066 | | 0.054 | | 0.323 | | 0.99 | | 0.77 | | 1.02 | | 1.63 | |

Control – control treatment (no drought stress); S2 – stress at flag leaf stage; WTG – weight of 1000 grains; LSD – Least Significant Difference; smaller letters for comparisons of the treatments inside the genotype groups; uppercase for comparisons of the genotype groups inside the treatments resulted from the reduction of both the weight of 1000 grains, and the number of grains per spike. The sensitive genotypes reduced also harvest index.

The performance of barley genotypes depended on both main stems, and the tillers (Table 4). Stress at flag leaf stage of tolerant genotypes increased grain yield, and the weight of 1000 grains of both main stems, and the tillers. Despite the reduced number of fertile tillers per plant, the stress increased total grain yield produced by tillers. However, the increase was not statistically proven. Under conditions of control treatment, genotypes tolerant to drought stress at flag leaf stage showed smaller grain yield and weight of 1000 grains of both main stem and a tiller than did the sensitive ones.

The response of sensitive genotypes to the stress at flag leaf stage depended on the decrease of productivity of both types of shoots: the main stem because of the reduced number of grains per spike and a tiller also due to diminished weight of 1000 grains. In combination with decreased productive tillering, it caused a significant reduction of grain yield per whole plant.

## DISCUSSION

In the present study, the population of 206 spring barley genotypes, including 142 breeding lines, their parental forms characterized by different climatic habits, and 60 cultivars registered and cultivated in Poland showed differentiated behaviors in terms of their response with grain yield and yield components to temporary drought stresses under climate conditions of Poland. The stresses were applied for 11 days at tillering stage or for 14 days at flag leaf stage.

The results of the study allowed to segregate tested genotypes into clusters of tolerant and sensitive ones separately to each stress. Genotypes were recognized as sensitive when they reduced their grain yield, while the tolerant ones showed a similar or increased productivity under stress conditions. The congenial approach for selection of barley drought tolerant and sensitive genotypes by cluster analysis was successfully used before by Ajalli et al. (2012), Eivazi et al. (2013) and Kiflu Tarekegn (2009).

In our study most of the tested genotypes were identified as sensitive to both drought stresses, however more genotypes tolerated an early stress than they did the late ones. It is in agreement with other studies on the effects of drought stresses at different growth stages of barley. According to Samarah (2005), barley was the most sensitive to later drought stress just before and during spike emergence, as well as during and post-anthesis stages of grain filling.

The phenomenon is well explained in the literature (Ajalli, Salehi, 2012; Beigzadeh et al., 2013; Bertholdsson, 1999; Francia et al., 2013; Garcia del Moral et al., 1991; Khaiti, 2012; Khokhar et al., 2012; Przulj, Momcilovic, 2001, Samarah, 2005; Samarah et al., 2009). Soil water regime and the pattern of precipitation during the vegetation period affect grain yield through modifications in processes of yield components forming (Farooq et al., 2009). Water deficit at tillering stage usually causes yield losses due to reductions in number of fertile tillers and spikes. If the plants develop under unfavorable conditions for a longer time, the maintenance of higher yield potential at earlier growth stages can result in its higher reduction at later stages. However, under propitious moisture conditions, and after the stress removal, plants get the possibility to create new tillers and continue their growth and development (Dhanagond et al., 2014; Křen et al., 2014; Svobodová, Míša, 2004). According to Self and Pederson (1978) grain yield is positively correlated with rainfall during stem elongation, which is the most active growing period of the crops. This creates good possibility of re-growth after the stress, which occurred at earlier development stages. Brestič (1996) explained that water deficits affecting plants at earlier stages of ontogenesis can be compensated for by an activity of the root system and adaptation and rehydratation support functions of self-regulating systems. If the stress is present at early growth stages only, its implications are smaller than those at later growth stages because re-growth processes at later stages are more difficult (Jamieson et al., 1995).

Drought stress at the growth period from double ridge to anthesis, and around anthesis, reduces potential grain number per unit area (Cossani et al., 2009; Fisher, 1985; Savin, Slafer, 1991;) due to lower fertilization caused by pollen sterility and/or ovule abortion (Hossain et al., 2012) and the sink strength soon after anthesis, which might have been a major factor affecting post-anthesis growth, as reported by other authors (Calderini et al., 1997; Acreche, Slafer, 2009). The stress, which is usually accompanied by high temperatures during grain filling period decreases mean grain weight (Acevedo et al., 2002; Wardlaw et al., 1980). It results from the reductions in the time of translocation of carbohydrate reserves to the grain (Przulj, Momcilovic, 2001), in the duration and rate of grain filling (Haddadin, 2015; Hossain et al., 2012; Samarah, 2005), and in activities of sucrose- and starch-synthesizing enzymes (Farooq et al., 2009). Water shortage at grain filling stage, which reduces photosynthesis rate, forces the plant to utilize the reserves of storage materials from vegetative organs (Méndez et al., 2011). However, higher contribution in final grain yield of dry matter stored before anthesis usually decreases barley grain yield (Bidinger et al., 1977).

Plant behaviors to cope with drought normally involve a mixture of stress avoidance and tolerance strategies, which are specific for each genotype (Chaves et al., 2002; Farooq et al., 2009; Zare et al., 2011). According to Méndez et al. (2011) tolerant genotypes accumulate in the stem higher contents of fructants than more sensitive ones, which affects not only grain size but also grain number. Different types of the response to drought stress were partly explained by ability to re-grow under conditions of subsequent watering (Acevedo et al, 2002; Brestič, 1996; Cabezza et al. 1993; Dhanagond et al., 2014; Svobodová, Míša, 2004). Perlikowski et al. (2013) showed ability of *Festuca arundinacea* genotype to repair damaged cell membranes following watering after short drought treatment. The trait, completed by reduced transpiration during the stress, could be crucial to survival during longer drought periods.

In our study barley genotypes tolerant to the stresses showed good ability to re-grow. Those tolerant to the stress at tillering stage did not reduce or even increased their grain yield due to the increased number of fertile tillers per plant and despite the reduced productivity of both main stem and a tiller. It indicates that tolerant genotypes showed ability to re-grow after subsequent watering by production of additional tillers and explains the reason for their tolerance to drought stress at early development stage. Tillering has great agronomic importance in cereals since it may partially or totally compensate the differences in plant number after crop establishment and may allow crop recovery from early stress (Acevedo et al., 2002). According to Baker and Gallagher (1983) bud differentiation into tillers and tiller appearance generally ends just before stem elongation starts. However, Longnecker et al. (1993) suggests, that tillering does not end at specific wheat development stage, but rather it is controlled by a number of genetic and environmental factors. In the study of Svobodová and Míša (2004), spring barley plants compensated for stress implications by productive tillers that developed after the stress at the beginning of stem elongation stage.

In the case of the response to drought stress at flag leaf stage, the tolerant genotypes mitigated the stress results due to increased productivity of both main stems and tillers as a result of a higher weight of 1000 grains. Simultaneously, they reduced the number of grains per spike of a tiller. Therefore, the re-grow ability of genotypes tolerant to drought stress at flag leaf stage resulted from the possibility to increase singular grain weight on both types of shoots, which was related to compensation between the yield components.

The phenomena of mutual compensation, competition, and other complicated relations between yield components, and plants in the canopy were described by many authors (Albrizio et al., 2010; Cossani et al., 2009; Janfrozzadh, Niazi Fard, 2014; Křen et al., 2014; Svobodová, Míša, 2004). Reduced number of grains per spike was usually compensated by higher weight of 1000 grains and adversely, bigger grains were possible to obtain only under conditions of place availability from diminished grain set and kernel growth.

In our study, genotypes sensitive to drought S1 and S2 stresses showed poor ability to re-grow after the stresses removal. Those sensitive to the drought stress at tillering stage reduced grain yield by decreasing productivity per single spike. It could be concluded, that water deficit restricted initiation of generative organ primordia. Additionally, the genotypes did not show ability to produce new tillers after the stress removal. Both main stems and tillers reduced number of grains per spike and the tillers reduced weight of a singular grain. Similar results were presented earlier by Jamieson et al. (1995) and Svobodová, Míša (2004).

Genotypes sensitive to the stress at flag leaf stage decreased plant productivity by reduction of the number of fertile tillers, and the productivity of singular spike of the main stem due to a decreased number of grains per spike and a tiller also as a result of decreased weight of 1000 grains. Eivazi et al., (2013) observed similar effects for drought stress at grain filling stage. However, in studies of Samarah (2005) the late stress was detrimental to grain yield mainly due to reduction in the number of tillers bearing fertile spikes and grains. Simultaneously, late formed tillers significantly contributed to a higher number of fertile spikes and total grain yield under optimal water conditions compared with terminal drought stress treatment. Under Mediterranean conditions of the study by Cossani et al. (2009), the differences between the tested genotypes generated by water shortage in post-flowering growth stages were explained mainly by differences in grain number per unit area, which could be the result of both grain number per spike or number of fertile tillers per area unit. According to Křen et al. (2014) and García del Moral et al. (2003) a cultivar with high plasticity, in years unfourable for achieving a high spike number, should provide sufficient compensation by increasing the spike productivity associated with high number of grains per spike ensuring the achievement of high number of grains per unit area.

In this paper, the general morphological constrains in productivity of spring barley genotypes as a result of drought stress imposed separately at early and late growth stage were highlighted. It made possible to cathegorize the 206 genotypes into groups of tolerant and sensitive to the drought stresses. It was found that genotypes tolerant to temporary drought stress are suitable for the cultivation in poor moisture conditions rather than in optimal ones. The conditions enable the compensation of yield losses by late tillering in the case of the stress at tillering stage or by the increased WTG in the case of the stress at flag leaf stage. A more detailed analysis of individual genotypes should include the physiological characteristics. That is the subject of a separate investigation within the same research project.

## CONCLUSIONS

1. Spring barley shows higher tolerance to drought stress at tillering stage than at flag leaf stage.
2. Spring barley genotypes differ in their response to temporary drought stress due to differentiated ability to regrow under conditions of subsequent watering.
3. The tolerance of barley genotypes to drought stress at tillering stage results from the ability to create additional fertile tillers after the stress removal.
4. The tolerance of barley genotypes to drought stress at flag leaf stage results from ability to compensate for reduced grain number per spike by increasing the weight of 1000 grains.

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