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DROUGHT STRESS

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Barley varieties in semi-controlled and natural conditions—Response to water shortage and changing environment

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Abstract
The yield potential of 60 spring barley varieties was examined under controlled drought and natural conditions in the years 2011–2013. The studied varieties were genotyped with the 1536-SNP barley oligonucleotide assay. In experiments with controlled drought conditions, the grain yield, 1,000-grain weight, number of productive tillers and length of the main stem were measured. Physicochemical properties such as the specific surface area, water adsorption energy, fractal dimension and nanopore radius of the plant leaves were determined and correlated with yield-forming traits. Field trials were conducted over 3 years at 14 locations, where along with the yield-related traits, monthly rainfall and average temperature were monitored. Five varieties of high yield and five varieties relatively stable under both semi-controlled and natural conditions were distinguished. The yield-related traits observed in various locations were related to environmental variables relevant to water availability. The sum of the rainfall in April and May was negatively correlated with the 1,000-grain weight and positively with the plant height. Positive relationships were found between plant height and temperatures in June and July. Five markers detected earlier as linked to the quantitative trait loci in the mapping populations were identified to have a coherent effect among varieties of various pedigree.

KEYWORDS
environmental variables, genotype-environment interaction, physicochemical parameters, response to drought, spring barley, stability

1 | INTRODUCTION

Barley is a cereal crop cultivated worldwide under a wide range of climatic conditions—from environments with sufficient rainfall to marginal environments with a frequent occurrence of limited water availability (Ceccarelli, 1994; Ceccarelli, Acevedo, & Grando, 1991). Drought is an extreme but often occurring phenomenon on all continents, including Europe, where the frequency of dry periods has increased in the recent years. For example, a deep water shortage occurred in 2003, 2006, 2007, 2008 and 2011, and caused severe economic losses in the agricultural sector (Spinoni, Naumann, Vogt, & Barbosa, 2015). Although barley adapts to different environmental conditions, a shortage of water causes many changes in the plant's morphological, physiological and biochemical levels, resulting in the limitation of growth and development and, finally, in the reduction of the grain yield. Drought at the pre-anthesis stages usually reduces the plant height, number of fertile tillers, spike length and seed set (Ferrante, Savin, & Slafer, 2008). Drought after anthesis mainly affects the final number of grains per spike, grain filling and final grain yield (Ugarte, Calderini, & Slafer, 2007). Therefore, the cultivation of spring barley varieties tolerant to a water deficit at different phenological stages is of special importance for farmers.

The size of the drought effects, and thus, the stress tolerance, is genetically controlled (Anjum et al., 2011; Bandurska et al., 2017; Blum, 1996; Chmielewska et al., 2016; Daszkowska-Golec & Szarejko, 2013; De Mezer et al., 2014; Filek et al., 2014; Forster et al., 2004; Jozefaciuk & Lukowska, 2013; Piasecka et al., 2017). Numerous genetic studies have been focused on the response of barley plants to water scarcity (Diab et al., 2004; Mansour et al., 2014; Mikolajczak et al., 2017; Mikołajczak et al., 2016; Ogrodowicz et al., 2017; Talamè et al., 2004; Teulat, Merah, Souyris, & This, 2001; Teulat et al., 1998, 2003; Tondelli et al., 2014; Wójcik-Jagła et al., 2013). Genetic maps well-saturated with molecular markers, used in these studies, have enabled the localization of quantitative trait loci (QTLs) with stable effects on the yield and the related traits under optimal and drought conditions, and the distinguishing of markers useful in the selection of genotypes more tolerant to drought.

One of the traits that may affect the response of barley plants to the water scarcity is their height. In barley, numerous genes control the plant height, the most important being the *sdw1/denso* incorporated into many modern, high-yielding cultivars. Plants possessing this gene are characterized by prostrate growth habitat at the juvenile stage, semi-dwarf stature as well as an increased number of tillers and increased grain yield but slightly decreased grain size (1,000-grain weight) (Jia et al., 2011; Kuczyńska, Mikołajczak, & Ćwiek, 2014; Kuczynska & Wyka, 2011; Kuczyńska et al., 2013; Thomas, Powell, & Swanston, 1991). Prostrate growth results in a dense ground cover around the plant, which reduces the soil evaporation (Baum et al., 2003; Ceccarelli et al., 1991).

Experiments evaluating varieties with respect to the grain yield and the tolerance to water stress can be conducted in a growth chamber, greenhouse or vegetation hall where the water application is controlled, or under field conditions in different locations and/or years, in which the availability of water during the vegetation period is difficult to predict (e.g. Mansour et al., 2014; Mikolajczak et al., 2017; Mikołajczak et al., 2016; Millet et al., 2016; Poorter et al., 2016; Wang, Vinocur, & Altman, 2003). The following question arises (Poorter et al., 2016; van Eeuwijk et al., 2018): to what extent can the results obtained under controlled or semi-controlled conditions be correlated with the results of the experiments conducted with the same varieties under natural conditions? The verification of this question would have been possible if the field experiments were conducted in a number of environments (locations and years), among which it would be possible to distinguish the environments of optimal and extreme water availability.

The purpose of the present study was to analyse the behaviour of barley varieties (registered in Poland, but of international origin) in experiments with a controlled application of drought conditions and in experiments conducted under natural conditions. In the latter, environmental variables related to water availability were observed and then used for an explanation of the observed phenotypic variation. The selection of the analysed phenotypic traits was targeted at distinguishing high-yielding varieties tolerant to a water shortage. The analysis of phenotypic variation with respect to SNP was performed and related to known QTL regions. Moreover, under controlled drought conditions, traits describing the fine structure and physicochemical properties of plant leaves were observed and correlated with the yield-forming traits. A few parameters that, according to us, reflect the effects of drought were analysed: specific surface area, a sensitive indicator of any structural and compositional changes in the fine surface; water adsorption energy, connected with the water binding forces of the surface; fractal dimension, a unique number related to the surface geometrical build-up; and nanopore radius, connected with the surface pore structure and describing the ability of the system to accumulate the capillary-condensed water.

2 | MATERIALS AND METHODS

Two types of experiments were conducted: (I) in 2013 with a controlled water application, at two locations: Institute of Plant Genetics, Polish Academy of Sciences, Poznań, Poland (E 16°55′, N 52°24′) (IGR), and Grabów Experimental Station, Grabów, Poland (E 21°31′, N 51°21′) of the Institute of Soil Science and Plant Cultivation—State Research Institute in Puławy (IUNG), and (II) in 2011–2013, under natural (field) conditions.

2.1 | Experiment I

Sixty two-rowed varieties of spring barley (*Hordeum vulgare* L.) registered in Poland (Supporting information Table S1) were used in the trials at IGR and IUNG conducted under semi-controlled greenhouse and vegetation hall conditions, respectively. The type of soil, fertilization and drought application were as described by Mikolajczak et al. (2017), the same in both locations. In brief, the plants were grown in double-walled Kick-Brauckman's pots of 10 dm^3 capacity filled with loamy soil mixed with sand in the weight ratio of 7:2. Soil moisture was established at 2.2–3.0 pF (easily available water) for the control and 3.4–3.6 pF (not easily available water) for the drought conditions. Three water regimes were studied: DI—10-day drought beginning at the three-leaf stage (phase 13 on the BBCH scale; Meier, 2001); DII—14-day drought stress beginning at the flag leaf stage (37 BBCH scale); and C—control (well-watered) conditions during the entire plant vegetation period. At each location, the experiment was performed in three replications (pots) in a completely randomized design. At IGR, the soil moisture was controlled gravimetrically every day by weighing and volumetrically (if necessary) by using the FOM/mts TDR soil moisture meter according to the reflectometry method (EasyTest, Institute of Agrophysics PAS, Poland); it was adjusted manually. At IUNG, the soil moisture in pots was controlled and regulated by an automatic irrigation system and additionally corrected using an electronic balance.

At maturity, the length of the main stem (LMS, in cm), number of productive tillers (NPT), 1,000-grain weight (TGW, in g) and grain weight per plant (GWP, in g) were observed.

The surface properties of leaves were measured at IUNG for plants harvested after completing the growth. The water vapour adsorption isotherms were measured by using the vacuum chamber method at a temperature T = 294 ± 0.2 K. To obtain different relative water vapour pressures, p/p_0, sulphuric acid of stepwise decreasing concentrations was used. The amount of adsorbed water, in (kg/kg), at a given p/p_0 value was measured after 48 hr of equilibration. The dry mass of the samples was estimated after drying the samples for 24 hr at 378 K. The adsorption data were used to derive the surface parameters as follows:

- Specific surface area S, (m^2/g), was calculated from the linear form of the Aranovich (1992) equation: $p/p_0/(a[1 - p/p_0]^{1/2}) = 1/(C_1S) + C_2\, p/p_0/S$, where C_1 and C_2 are constants.
- Average adsorption energy, E_{av} (given in the units of RT, where R is the universal gas constant and T is the temperature of the measurements), was estimated assuming that the water vapour adsorption energy at a given p/p_0 was equal to $E = -\log(p_0/p)$ and the amount of water vapour adsorbed in the monolayer a_m at a given E was equal to $a_m(E) = a(1 - p/p_o)^{1/2}$. The dependence of the first derivative of $a_m(E)$ on E gave the adsorption energy distribution function, f(E), from which the average adsorption energy was calculated as $\Sigma f(E_i)E_i$. The adsorption energy is usually presented as a negative value, but for the sake of convenience, we expressed it as an absolute value.
- Surface fractal dimension, D_s, was calculated from the slope A of the equation (Jarzebski, Lorenc, & Pajak, 1997) $\ln(a) = -A \ln(\ln[p_0/p]) + C$, where C is a constant and $D_s = 3 - A$.
- Average nanopore diameter, R_{av} (nm), was estimated assuming that the excess of adsorption over the monomolecular layer is due to the capillary condensation. The relative vapour pressure was translated into the nanopore diameter by using the Kelvin equation $R = C \ln(p_0/p)$, where C is a constant. The first derivative of the dependence of the amount of condensed water on R gave the pore size distribution function, f(R), from which the average nanopore radius was calculated as $\Sigma f(R_i)R_i$.

For more details on surface parameters estimation see Jozefaciuk and Lukowska (2013) and Jozefaciuk, Lukowska, and Szerement (2013).

2.2 | Experiment II

The data for 35 varieties (Supporting information Table S1) observed under field conditions were obtained from the trials conducted over 3 years (2011–2013) at 14 locations in Poland (Supporting information Table S2) by Research Center for Cultivar Testing, Słupia Wlk. (COBORU). Each trial was established in the randomized block design with two replications (15 m^2 plot, sowing rate: 300 or 350 seeds/m^2). The type of soil (according to the World Reference Base for Soil Resources 2014) is given in Supporting information Table S2. Fertilizers were used according to the soil test recommendations for the cultivation of barley.

Three traits observed in the trials were subjected to the analysis: 1,000-grain weight (TGW, g), grain yield (GY, dt/ha, standardized to 14% moisture) and plant height (PH, cm). In each trial (year and location), the environmental variables of monthly total rainfall R (mm) and monthly average temperature at 2 m height T (°C) were observed and are used here.

2.3 | Genotyping

Genomic DNA was extracted from young leaf tissue as described by Mikołajczak et al. (2016). Frozen DNA samples were submitted to the Illumina BeadLab at the University of California, Los Angeles (UCLA), and genotyped with the 1536-SNP barley oligonucleotide pool assay (BOPA1; Close et al., 2009). SNPs that were nonpolymorphic or produced ambiguous results were removed from the analysis.

2.4 | Statistical analysis

Relative drought effects were computed as the differences (value under drought - value under control) multiplied by 100 and divided by the values under the control conditions. Analysis of variance in Experiment I was performed separately for trials at IGR and IUNG on raw observations, with the fixed model including effects of drought treatments (D), varieties (V) and of D × V interaction. Analysis of variance in Experiment II was performed on varietal means with (a) the fixed model including effects of years (Y), locations (L), varieties (V) and of Y × L, Y × V, L × V interactions, and (b) with the fixed model including effects of soil complexes (S), varieties (V) and of S × V interaction. The explanation of the variety by environment interactions for yield was done by (a) the analysis according to the "additive main effects and multiplicative interaction" (AMMI) model of Gauch (1992) (see also Vargas, Crossa, van Eeuwijk, Ramires, & Sayre, 1999), with assessment of the instability of varieties by the coefficients proposed by Purchase, Hatting, and van Deventer (2000), and (b) by regressing the interaction effects (additive model residuals) for each variety on environmental main effects, as proposed by Caliński, Czajka, Kaczmarek, Krajewski, and Pilarczyk (2005), with regression coefficients representing the sensitivity of varieties to environmental conditions, sign of the coefficients representing the variety type (positive for intensive varieties, negative for extensive varieties), and determination coefficients representing the regression goodness of fit. The analysis of variety by environment interactions with respect to the influence of the environmental variables (amount of rainfall and temperature) was done by the factorial regression according to Vargas et al. (1999). Principal component biplots were obtained for the centred and normalized data. The significance of the Pearson correlation coefficients was assessed using the *t* test. The hierarchical grouping of the varieties based on the SNP data was performed using the simple matching similarity matrix and the average link algorithm. SNP effects were estimated in the linear mixed model containing fixed effects of environments and environment-specific allelic effect (coefficient of regression on the number of positive alleles in the diploid SNP genotype); the adjustment for the population structure was done by including in the model a random variety effect with covariance matrix of the form $2KV_g$, where K denotes the kinship matrix estimated from SNP data, and V_g the polygenic variance (Yu, Pressoir, & Briggs, 2006). All of the computations and the graphical visualizations of the results were performed using Genstat 18 (VSN Int., 2015).

The mean values of the traits observed for the varieties in Experiments I and II and the SNP marker data, stored in Supporting information Dataset1 and Dataset2, were annotated and formatted according to the recommendations of Ćwiek-Kupczyńska et al. (2016).

3 | RESULTS

3.1 | Yield-related traits under semi-controlled conditions (Experiment I)

The distributions of varietal means for the yield-related traits observed in IGR and IUNG (Supporting information Table S3a) are visualized in Figure 1a. Significant differences existed between the drought treatments and between the varieties in both the trials (at $p < 0.001$ in most of the cases, Supporting information Table S4a). The interaction of variety × drought treatment was significant in IGR for each trait and in IUNG for LMS and TGW ($p < 0.001$). We observed a significant reduction in TGW, GWP and LMS under drought DI and DII, whereas the NPT decreased slightly or increased, in comparison with the control, at IGR in DII. A better discrimination between the varieties cultivated under drought conditions and those cultivated under the control conditions was observed in IUNG (Figure 2), and both at IGR and at IUNG the effect of DII on the varieties was stronger than that of DI.

The correlations between the traits were similar in both experiments (Supporting information Table S5a). For TGW, GWP and LMS, positive correlation coefficients were recorded between the values of these traits for particular water treatments. Moreover, at both the locations, positive associations between GWP and TGW, and negative ones between NPT and LMS were observed. The correlations between the same traits observed in the IGR and IUNG trials were significant; some exceptions were noted in DII for TGW, NPT, and GWP, and in C, for LMS and GWP.

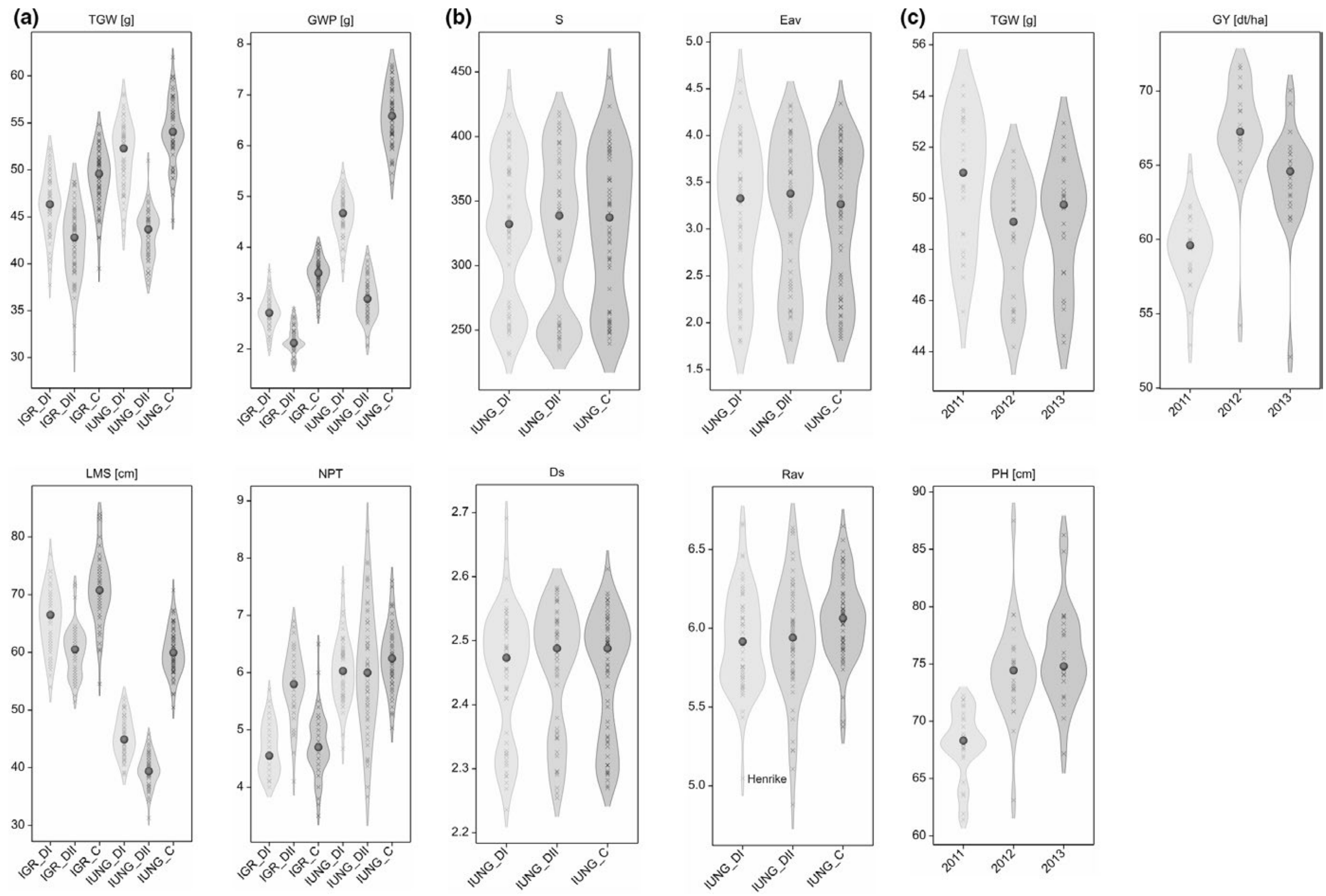

FIGURE 1 Distribution of mean values for varieties in various experiments. (a) Yield-related traits observed in Experiment I; (b) physicochemical traits observed in Experiment I; (c) yield-related observed in Experiment II. Crosses represent varieties, dots mark median values. Ds: surface fractal dimensions; Eav: average adsorption energy; GWP: grain weight per plant; GY: grain yield; LMS: length of the main stem; NPT: number of productive tillers; PH: plant height; Rav: average nanopore diameter; S: specific surface area; TGW: 1,000-grain weight. In B, Rav, IUNG_DI, the outlying value for Henrike removed from correlation analysis, Supporting information Table S5

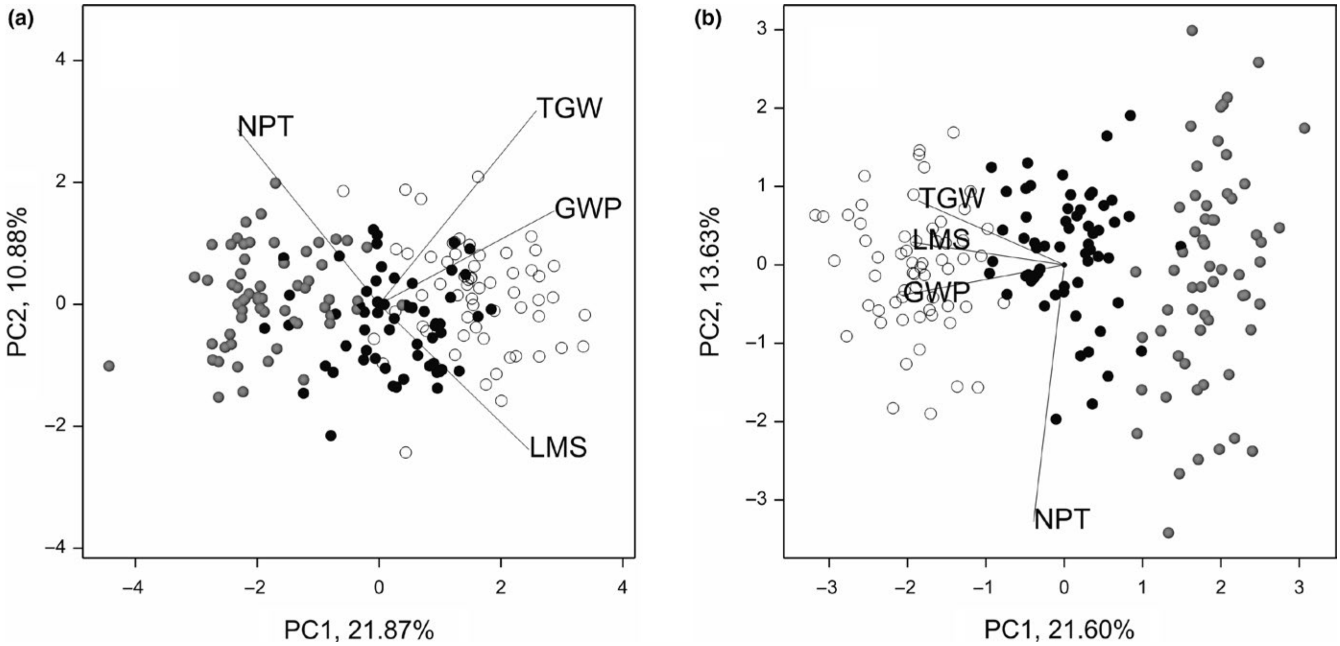

FIGURE 2 Principal component biplots constructed for traits observed for varieties under Drought I (black), Drought II (grey), and Control conditions (empty circles) in trials at IGR (a) and at IUNG (b) (Experiment I). GWP: grain weight per plant; LMS: length of the main stem; NPT: number of productive tillers; TGW: 1,000-grain weight

The effects of DI and DII (Supporting information Table S3b) were positively correlated for all of the traits within IGR and IUNG (except for NPT at IUNG) (Supporting information Table S5b), but not between the two locations. Considering the ranking of the varieties for GWP and their relative response to the drought for this trait, we could distinguish the varieties that had a high yield potential and were tolerant to a water deficit: Afrodite, Binal, Soldo and Tocada were ranked among top ten varieties for both the characteristics. The low relative drought effects for Binal and Afrodite resulted from a small reduction of TGW, whereas for Soldo and Tocada, they were attributed to an increase in the NPT and a relatively strong reduction of the LMS. The most tolerant to drought (rank 1) was Goodluck, but its yield potential was rather low (rank 35 for GWP). The highest relative effects of the drought (ranks 55–60) were found for the varieties Antek, Fariba, Mercada, Nadek, Prestige and Publican; these varieties (except Mercada and Publican) were also the low-yielding ones (Supporting information Table S3b).

The distributions of varietal means for the physicochemical parameters (Supporting information Table S3c) are visualized in Figure 1b. ANOVA (Supporting information Table S4a) showed a significant effect of the drought treatment on E_{av} and R_{av}, which were increasing and decreasing under the drought conditions, correspondingly, and significant differences between the varieties for all physicochemical parameters. The variety × treatment interaction was significant for all the traits except D_s.

The physicochemical parameters S, E_{av} and D_s were strongly correlated with one another (Supporting information Table S5c,d), whereas R_{av} was correlated negatively with the three other parameters in DII. The correlations between the physicochemical parameters and the yield-related traits were insignificant with the exception of S (and D_s, but not under the same conditions), which was positively correlated with LMS ($r = 0.30–0.38$, $p < 0.01$), and R_{av} in DII, which was positively correlated with NPT ($r = 0.38$, $p < 0.001$). The drought effects of S, E_{av} and D_s were correlated with each other and between the drought variants ($r = 0.38–0.95$); for R_{av}, only the drought effects of DI and DII were significantly correlated ($r = 0.49$, $p < 0.01$). The drought effects for R_{av} in DI were negatively correlated with the effects for NPT.

3.2 | Yield-related traits under natural conditions (Experiment II)

The distributions of varietal means for TGW, GY and PH (Supporting information Table S6) are visualized in Figure 1c. ANOVA (Supporting information Table S4b) revealed a strong significance ($p < 0.001$) of all of the sources of variation, except for the interaction year × variety for GY ($p = 0.055$) and the interaction location × variety for TGW ($p = 0.358$). The year 2011 was characterized by the highest TGW and the lowest GY, while 2012 was its opposite. The PH was the lowest in 2011. The top five varieties with respect to the average ranking according to GY (Supporting information Table S6) were Basic, Ella, KWS Olof, Natasia and Soldo; Basic, Ella and Soldo also had high rankings by TGW. The top yielding varieties were in the middle of the ranking for PH. The bottom five varieties for the average ranking by GY were Gawrosz, Marthe, Rubinek, Rufus and Xanadu; Gawrosz, Marthe, Rufus and Xanadu were also low ranking for TGW. Rufus and Gawrosz were among the tallest varieties.

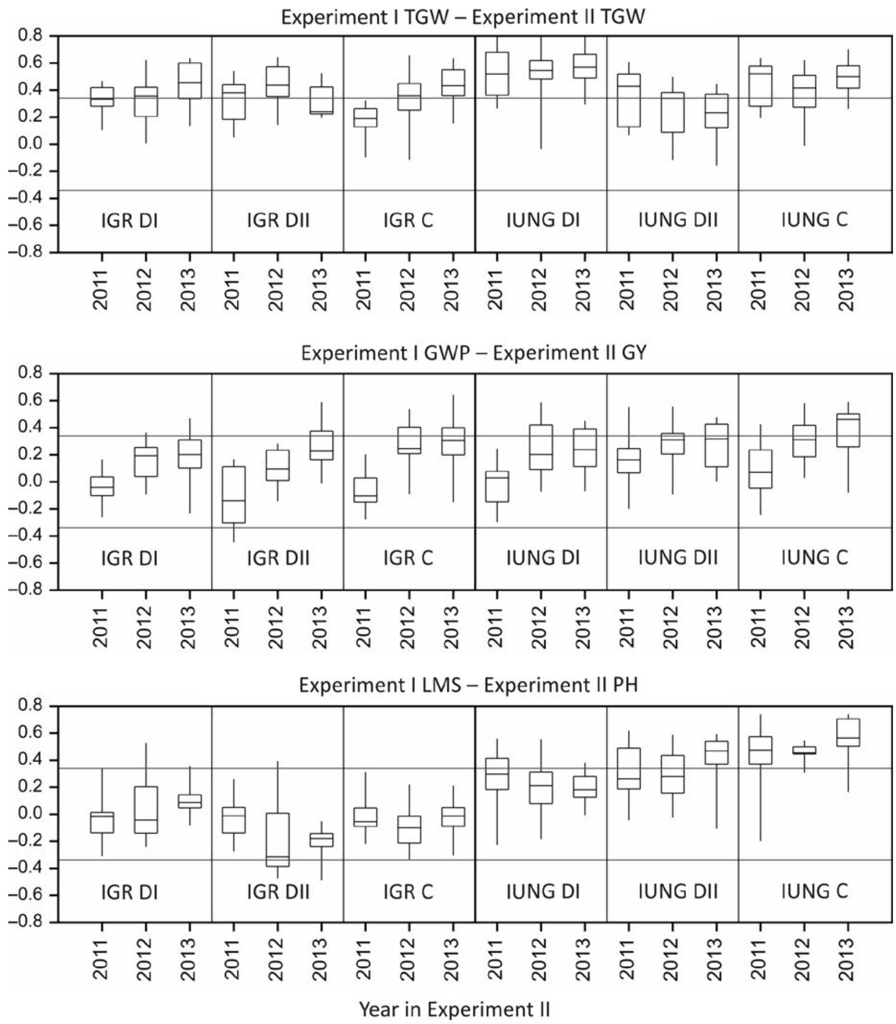

FIGURE 3 Correlations of traits observed in Experiments I and II. Each boxplot was constructed from 14 correlations computed between variety means observed in particular conditions in Experiment I and means observed in 14 locations, in particular year, in Experiment II. Horizontal lines mark thresholds of significance at $p < 0.05$. GWP: grain weight per plant; GY: grain yield; LMS: length of the main stem; PH: plant height; TGW: 1,000-grain weight

3.3 | Correlations between traits observed under semi-controlled and natural conditions

For TGW, the correlations between the varietal means in Experiments I and II were in general positive and frequently significant (Figure 3), particularly for IUNG DI and IUNG C. GY measured in Experiment II was in general not significantly correlated with GWP measured in Experiment I. The PH frequently showed a negative correlation with the LMS measured at IGR (DI, DII and C), and a positive correlation with the LMS measured at IUNG, particularly with IUNG C.

3.4 | Stability of yielding under semi-controlled and natural conditions

The AMMI analysis was conducted for GWP measured in Experiment I at IGR and IUNG in three drought regimes (six combined environments) and for GY measured in Experiment II at 14 locations over 3 years (42 combined environments). The characteristic of the interaction caused by the conditions at IGR was rather different from that at IUNG (Figure 4a), with IUNG DII and IUNG C contributing more to the total interaction than IGR DI, DII and C. In Experiment II (Figure 4b), Mercada and Stratus exhibited particularly large interactions, and also Nowa Wieś and Pawłowice (as we checked, removing these two locations from ANOVA for GY in Supporting information Table S4B resulted in the p value for Y × V changing from 0.055 to 0.004, making this interaction significant). The varieties Ella, Iron, Natasia, Soldo and Suweren had GWP in Experiment I and GY in Experiment II of more than 100% of the standard varieties (Supporting information Table S7). The varieties Blask, Ella, Olympic, Skald and Xanadu were relatively stable in both Experiment I and Experiment II (were among the 10 varieties with the smallest instability coefficient). Mercada was particularly unstable in both Experiments.

In Experiment I, among the unstable varieties (not top ten according to stability), three varieties showed a significant regression on the environmental means (sensitivity) and a relatively large determination (>50%) (Supporting information Table S7); two of them were intensive (Garner and Skarb) and one was extensive (Prestige). In Experiment II, five unstable varieties exhibited a significant regression and a relatively large determination (>14%); two of them were intensive (Mercada and Tocada) and three extensive (Gawrosz, Kormoran, and Rubinek).

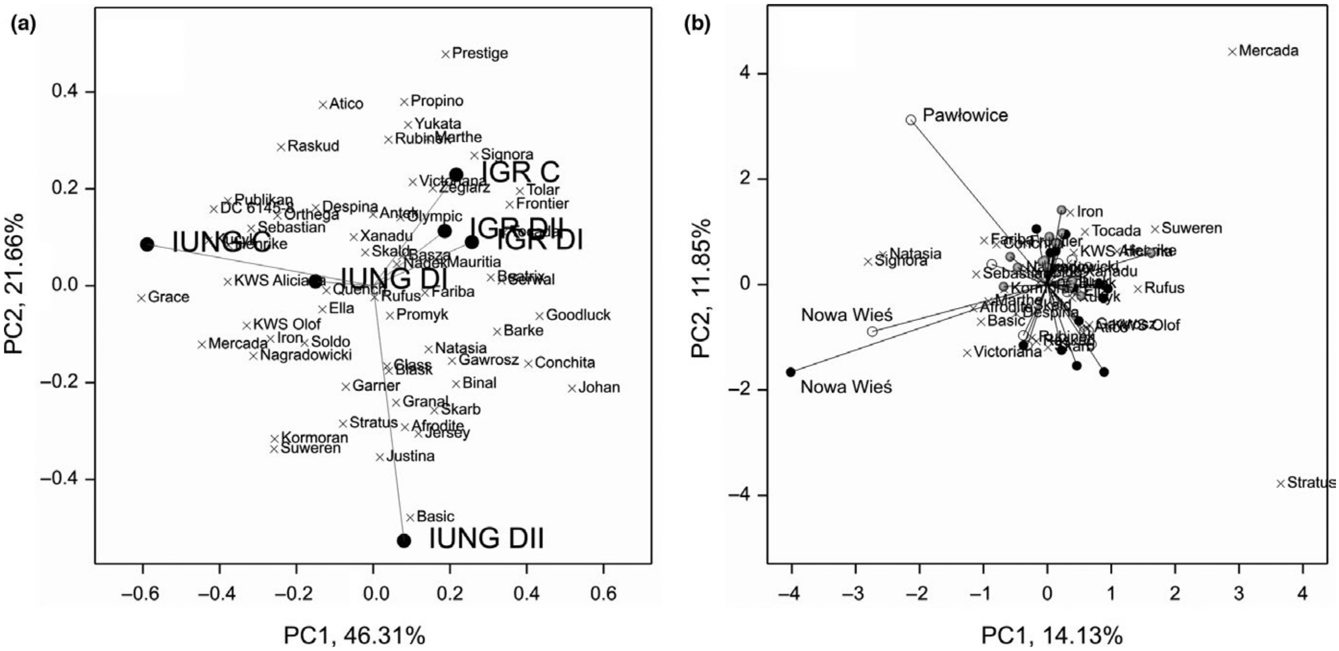

FIGURE 4 Additive main effects and multiplicative interaction biplots for yield traits. (a) Experiment I, grain weight per plant observed in six environments; (b) Experiment II, yield per plot observed in 42 trials in 2011, 2012 and 2013 represented by, correspondingly, black, grey and empty circles

3.5 | Analysis of environmental conditions and their influence on trial means

Using the amounts of rainfall and the temperature levels observed at the locations of Experiment II (Figure 5a,b), we computed the environmental variables aligned with the developmental stages of barley and representing the total rainfall (R) and the average temperature (T) over the months: I–III (pre-sowing period), IV–V (germination, leaf development, tillering and stem elongation), VI–VII (booting, heading, development of seeds and grain filling) and VIII (ripening and senescence). The year 2011 was characterized by lower rainfall RI–III and RIV–V and higher temperatures TI–III and TIV–V than the year 2013 (Figure 5c). The year 2012 was intermediate between 2011 and 2013 with respect to these parameters. The environmental variables for months VI–VII and VIII were more stable over the years.

The trial means in Experiment II for TGW were negatively correlated with RIV–V (Table 1a); the means for GY were negatively correlated with RVIII and positively with TVIII; and the means for PH were positively correlated with RIV–V, TVI–VII and TVIII. We detected significant differences between the trial means for the experiments conducted on different soils for TGW, GY and PH; the interaction of varieties with soil complexes was not significant (Table 1b, Supporting information Table S4c).

3.6 | Explanation of variety × environment interaction for GY by environmental variables

For eleven varieties, the sensitivity to at least one environmental variable was significant (Table 2a). Among the varieties declared earlier as unstable, Atico, KWS Olof, Raskud and Tocada showed a negative response to the amount of rainfall RI-III; and Frontier, Natasia, Raskud and Victoriana, a negative response to rainfall RVIII. Raskud expressed a positive response to the temperatures TIV–V, TVI–VII and TVIII, Tocada—to temperatures TVIII, and Victoriana—to temperatures TVI-VII and TVIII. Kormoran, declared earlier as unstable and extensive, showed large negative deviations in trials on rich soils (of wheat type, Table 2b), while Tocada, declared as unstable and intensive, exhibited a large negative deviation in the trials on poor soils.

3.7 | Genetic similarity of varieties

SNP of the 60 varieties genotyped in this study and of the 5 varieties, Cam/B1/CI, Georgie, Harmal, Lubuski and Maresi, genotyped by Mikołajczak et al. (2016), was analysed. The hierarchical clustering (Figure 6) showed no special grouping of the varieties with respect to the marker genotypes; Cam/B1/CI and Harmal (accessions of Asian origin) were clearly distant from the rest of varieties. The most similar pairs of varieties were DC 6145-8 and Iron (99.85% identical loci; the same breeder), Olympic and Quench (99.63%), and Skarb and Stratus (99.05%; the same breeder); however, we did not find a general correspondence between the grouping of the varieties based on the marker data and on information on their ownership or type.

3.8 | QTL effects

From all of the QTLs described by Mikołajczak et al. (2016); Mikolajczak et al. (2017) and Ogrodowicz et al. (2017), 74 were

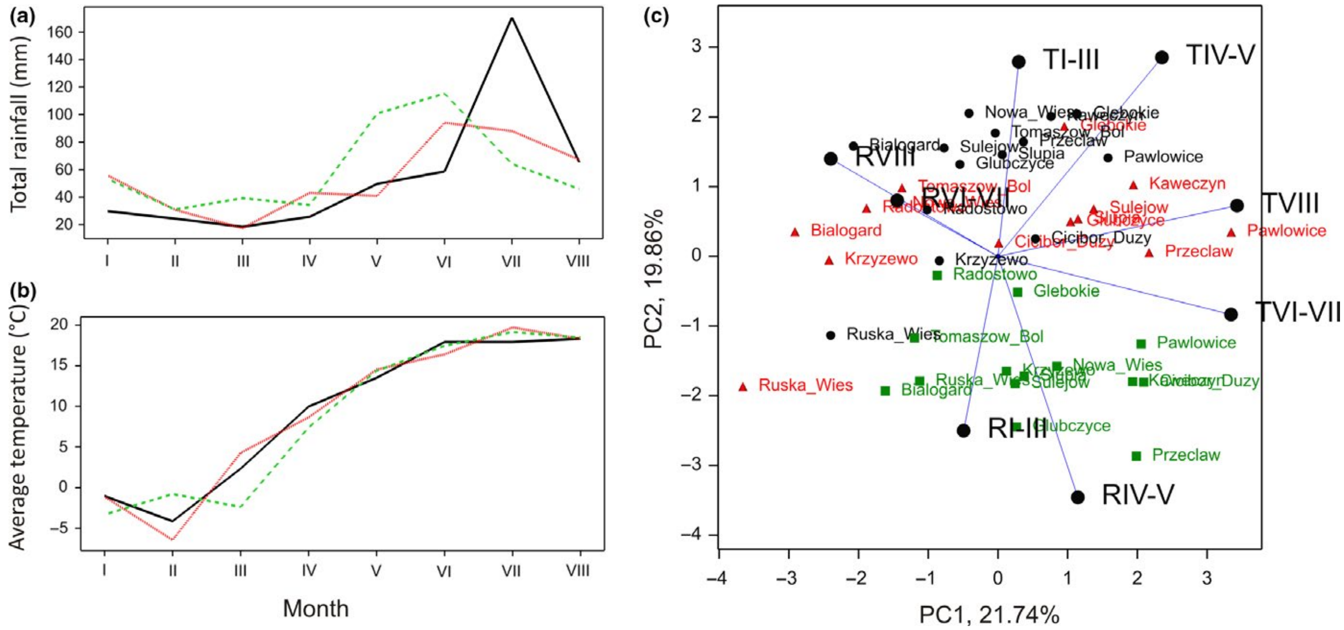

FIGURE 5 Characterization of weather conditions in trials of Experiment II. (a) Profiles of total monthly rainfall. (b) Profiles of average monthly temperature. (c) Principal component biplot obtained from standardized environmental variables describing rainfall (R) and temperature (T) aggregated over months (I–III, IV–V, VI–VII, VIII). In a and b continuous, dotted and dashed lines represent correspondingly, years 2011, 2012, 2013; in (c) years 2011, 2012 and 2013 are represented by, correspondingly, spheres, cones and cubes

selected for the traits that could be associated with the traits observed in Experiment I or Experiment II (Supporting information Table S8; 1,000-grain weight—TGW; grain weight per square metre, grain weight per plant—GWP, GY; length of the main stem—LMS, PH; number of productive tillers per plant—NPT). Alleles increasing values of the traits (positive alleles) and the markers closest to the QTLs were defined. Using the regression of the trait means on the number of positive marker alleles in the varieties (with the adjustment for the population structure), we computed the effects of the positive alleles in the 6 environments considered in Experiment I and in the 42 trials considered in Experiment II, averaged them, and selected the QTLs for which the mean effect was significantly greater than zero; this gave us a list of 7 and 23 marker loci that exhibited the expected (positive) effect in the set of varieties observed in Experiments I and II, respectively (Supporting information Table S9).

Five of these loci, marked in Supporting information Table S9, were repeated in Experiments I and II (three for TGW and two for LMS-PH). The genotypes in these marker loci for the 60 varieties are given in Supporting information Table S10. For TGW, the rank of the variety Mercada having a combination of positive (favourable) alleles at markers 2822–739, SNP ABC09432-1-1-160 and 4679–1549 (AA/GG/CC) was in Experiment I equal to 16, and in Experiment II—to 4; the average ranks of the 8 varieties with a combination of negative (unfavourable) alleles (GG/AA/AA) were, correspondingly, 43 and 18. For the PH, LMS-PH, there were two varieties with a combination of positive (unfavourable for this trait) alleles at markers 10207–1024 and 1066–2110 (GG/CC): Gawrosz ranked seventh in terms of the PH in Experiment I and first in Experiment II, and Jersey ranked first in Experiment I; the combination of negative alleles (favourable, AA/GG) was exhibited by 39 varieties with the average rank for LMS in Experiment I equal to 31 and average rank for PH in Experiment II equal to 14 (however, note the high ranking of Afrodite and Atico, i.e. ranks 1 and 2, respectively, having the AA/GG genotypes, in Experiment II). The variety Mercada had favourable genotypes for TGW (increasing, AA/GG/CC) and LMS-PH (decreasing this trait, AA/GG).

4 | DISCUSSION

In the present study, a holistic approach to the analysis of data collected in the experiments conducted under semi-controlled and natural conditions was applied with the aim of comparing the behaviour of spring barley varieties in various environments and to identify varieties with a good yield potential under extreme conditions, particularly under drought. The analysed data provided information which is not obtainable from routine recommendation or post-registration trials.

4.1 | Semi-controlled conditions

In the greenhouse trials, the grain yield per plant was considered to be the indicator of the yield potential, and in addition, the 1,000-grain weight, number of productive tillers and length of the main stem were examined. The negative effects of drought at the flag leaf stage were stronger than, but correlated with, the effects of an earlier drought at the three-leaf stage. Similarly, Samarah, Alqudah,

TABLE 1 Trial means versus environmental variables

	Months	1,000-grain weight (TGW)	Grain yield (GY)	Plant height (PH)
(a)				
Rainfall	I–III	−0.24	−0.20	0.05
	IV–V	−0.27*	0.10	0.38**
	VI–VII	−0.16	−0.04	−0.20
	VIII	0.17	−0.27*	−0.23
Temperature	I–III	−0.05	−0.15	−0.11
	IV–V	−0.01	−0.01	0.03
	VI–VII	−0.20	0.14	0.38**
	VIII	−0.21	0.32*	0.36*

	1,000-grain weight (TGW)		Grain yield (GY)		Plant height (PH)	
Soil complex	Mean	*SEM*	Mean	*SEM*	Mean	*SEM*
(b)						
Very good wheat	52.09	1.305	76.58	4.218	73.77	2.013
Good wheat	48.94	1.085	70.83	2.264	75.09	2.314
Very good rye	49.57	0.791	51.59	3.528	71.25	2.649
Good rye	45.86	3.842	46.05	6.724	63.12	6.401
p-value for differences between soil complexes (ANOVA *F* test)	<0.001		<0.001		<0.001	

(a) Correlations of trial means for traits observed in Experiment II and environmental variables; (b) Mean values for groups of trials performed on different soils and corresponding ANOVA test. *SEM*: standard error of the mean.
*, **Correlations significant at $p < 0.05$, 0.01.

Amayreh, and McAndrews (2009) reported that barley was the most sensitive to the later drought stress just before and during the spike emergence, as well as during and post the anthesis stages of grain development. We selected four varieties (Afrodite, Binal, Soldo and Tocada), which were characterized by both a good yield potential and a low relative yield reduction under the considered drought conditions in Experiment I.

In the part of the experiment performed at IUNG, based on the assumption that the drought-induced biochemical processes may alter the plant surface characteristics, the physicochemical parameters were measured on the barley plant leaves; to the best of our knowledge, such a measurement was performed for the first time in a large set of cereal varieties. The four measured parameters were used earlier to describe the effects of aluminium stress on plants roots collected from hydroponic studies (Jozefaciuk & Szatanik-Kloc, 2001, 2003; Szatanik-Kloc & Jozefaciuk, 2007). In the present study, attempts to extract the roots grown in soils revealed the material contaminated by the soil components and/or depleted from the fine roots, which adhered to the soil granules. Therefore, we decided to study plant leaves, hoping that their properties could be altered by a drought, as well. The mean effect of a drought was significant for adsorption energy, which increased under drought conditions. This may reflect a biochemical mechanism induced by the plant to protect the water lost by the leaves. Further, the nanopore radius decreased under the drought conditions, which supports the prevention of the water loss, as well. Therefore, the changes in two of the measured parameters occurred in the direction favourable for a better defence against a water deficit. In the case of the two mentioned parameters and the specific surface area, the reaction to drought was different for varieties; this could indicate a genetic source of variability. The changes in the surface area, adsorption energy and fractal dimension caused by a drought were, in general, positively correlated, and (for the late drought period) negatively correlated with the changes in the nanopore diameter, which implied that a coordinated change in the direction of the surface better adjusted to the drought. As the above phenomena have been not studied till date, more studies are necessary to better understand the presented results.

4.2 | Natural conditions

In 2011, deep drought and high temperatures occurred in the spring, whereas in the next 2 years, the weather conditions were more conducive for the development of the barley plant. The pre-anthesis drought in 2011 negatively influenced the plant growth. Many plants dried out before flowering, developing plants had poor tillering capacity, leading to fewer spikes per unit area and, finally, to the reduction of the grain yield (see also AL-Ajlouni et al., 2016; Mikołajczak et al., 2016). On the other hand, in spikes, only a few seeds developed, and the rainfall that occurred in late June and July during grain filling positively affected the TGW.

TABLE 2 Explanation of interaction of varieties by environmental variables

Variety	Number of trials	Ranking by stability (characteristics from Supporting information Table S7)	Rainfall				Temperature			
			RI-III	RIV-V	RVI-VII	RVIII	TI-III	TIV-V	TVI-VII	TVIII
(a)										
Atico	42	17	−0.14							
Frontier	14	13				−0.20				
KWS Aliciana	42	10				−0.15				
KWS Olof	42	23	−0.15							
Natasia	42	32				−0.15				
Olympic	14	4	−0.17							
Raskud	28	16	−0.14			−0.15		4.97	8.49	6.09
Skald	42	6				−0.20				
Soldo	14	2	−0.17							
Tocada	42	21	−0.15							4.93
Victoriana	42	30				−0.14			7.09	4.95

Variety	Ranking by stability (characteristics from Supporting information Table S7)	Soil complex				*p*-value for differences between soil complexes
		Very good wheat	Good wheat	Very good rye	Good rye	
(b)						
Goodluck	1	−1.84	−0.84	1.86	1.22	0.037
Kormoran	12 (extensive)	−2.52	−1.24	3.11	−0.27	0.026
Tocada	21 (intensive)	4.50	−0.09	−1.78	−1.67	0.005

(a) Factorial regression on environmental variables. Listed are only varieties for which at least one regression coefficient (sensitivity to environmental variable) was significant at $p < 0.05$.
(b) Mean interaction deviations in trials on different soil complexes. Listed are only varieties for which the means were significantly different at $p < 0.05$.

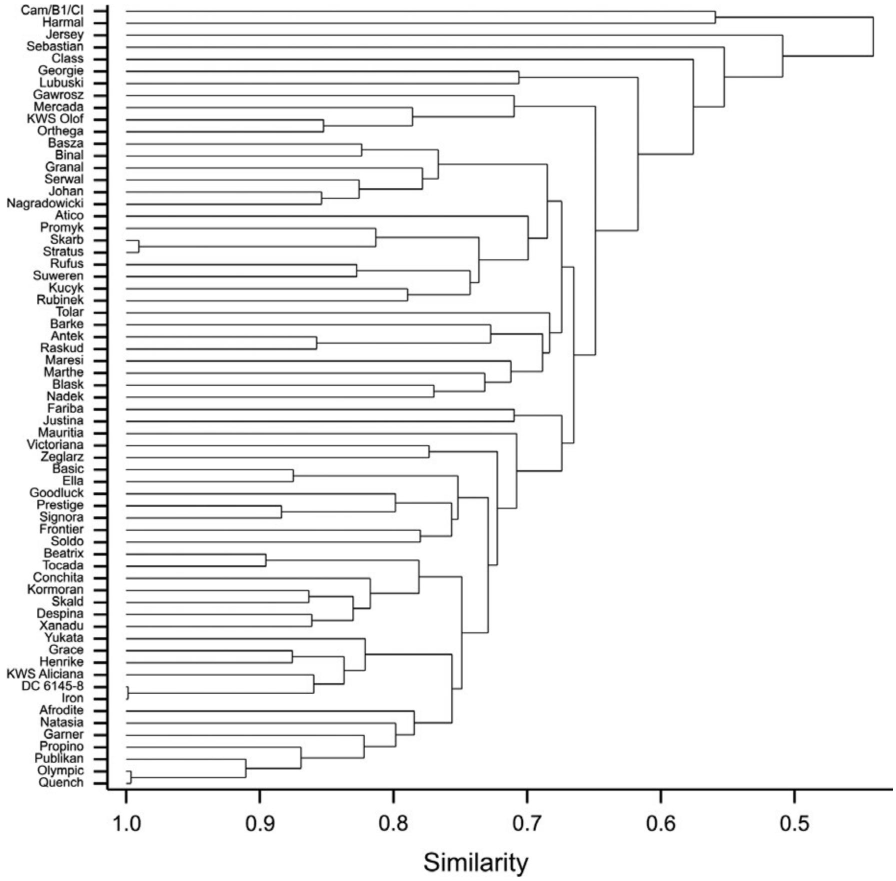

FIGURE 6 Hierarchical clustering of 60 varieties studied in this report and 5 varieties studied in Mikołajczak et al. (2016) (Cam/B1/CI, Georgie, Harmal, Lubuski, Maresi), based on SNP BOPA1 marker data, using simple matching similarity matrix and average link algorithm

Correlations between the traits observed in Experiments I and II were not always strict, indicating that the trials performed under controlled conditions could be used to assess the TGW under natural conditions, but not to predict the plot yield from the yield per plant. In Mikołajczak et al. (2016); Mikolajczak et al. (2017), no QTL for the grain yield per plant identified in the greenhouse (with controlled drought) was found for the grain yield per plot in experiments conducted under field conditions. PH also appeared to be a trait that could not be predicted by observing the stem length in the greenhouse experiments. More reliable for such predictions appeared to be the observations obtained in a vegetation hall (IUNG), where the insolation and temperature during the day were close to those under natural conditions.

The analysis for GWP in Experiment I and GY in Experiment II allowed distinguishing the five varieties (Ella, Iron, Natasia, Soldo and Suweren), which were superior to the others and the standards in both parts of the study. Moreover, the relative stability over the environments for five varieties was observed under both semi-controlled and natural conditions.

The observed negative correlation between TGW and RIV–V (sum of rain in April and May) was attributed to the development of the tillers during this period, as more precipitation is conducive to tillering. In contrast, the larger is the number of tillers (spikes) per plant, the larger is the number of grains on the plant but of a smaller TGW. This negative correlation between TGW and NPT was also observed in Experiment I (IUNG). The negative correlation between GY and RVIII may be attributed to the fact that the abundant rainfall during ripening may result in plant lodging, leading to yield reduction. In turn, GY was positively correlated with TVIII because the higher temperature in the considered month was favourable to grain ripening. The positive correlation of PH with RIV–V seemed to be obvious, because during this period stems elongated, and the precipitation at this time was conducive to the corresponding stage of plant development. Similarly, positive relationships between PH and temperatures TVI–VII and TVIII confirmed that a higher temperature positively affected the final stem elongation, particularly the elongation of the peduncle and, consequently, the final PH. Low determination coefficients for all of the above relationships (details not shown) indicated that the associations between the studied traits and the measured climatic variables were not strong—temperature and precipitation were the admittedly important parameters of the environment, but their effects on the yield were dependent on their interaction with the other environmental factors. As expected, ANOVA revealed that the soil quality (i.e. its physical characteristics such as the level of clay and sand content, water field capacity and productive complex) was the important factor determining the level of TGW, GY and PH. The dependence of the yield level on the soil characteristics was also reported by Rodriguez, Rau, Papa, and Attene (2008). However, unlike us, these authors did not reveal the correlation between the monthly and the cumulative rainfall and the environmental means of the grain yield.

The environmental weather variables (rainfall and temperature) successfully explained the interaction of some of the varieties defined earlier as "unstable" but not defined as "intensive" or "extensive" by using only the trial means. Among the weather variables, RI-III and RVIII played the most important role in this explanation (for six varieties).

4.3 | Genotype–phenotype integration

Despite extensive genotyping by a set of well-defined SNP BOPA1 markers, our investigation, because of the restricted pool of the barley varieties considered, did not have the power of the contemporary large-scale association studies. However, to our knowledge, the SNP data are novel information for most of the varieties. They revealed no structure within the studied group of varieties related, for example, to ownership or usage type; nevertheless, some pairs of varieties, genotypically very similar, were originated from the same breeder. Accessions of Asian origin (as expected) and some European varieties were very distant from the other accessions.

Out of the 74 QTLs reported by Mikołajczak et al. (2016) and Ogrodowicz et al. (2017) in the RIL populations, only five QTLs exhibiting the same additive effect as that in the mapping study were found in both Experiment I and Experiment II. This was not unexpected, as the fine positioning and estimated QTL effects are known to depend on the population. Three of these QTLs, for TGW, were linked to the markers 2822–739, ABC09432-1-1-160 and 4679–1594, and two for LMS-PH to the markers 10207–1024, 1066–2110. All these markers were found to have stable effects in natural and controlled environments in the mapping populations (Mikolajczak et al., 2017; Mikołajczak et al., 2016; Ogrodowicz et al., 2017). Two varieties with positive alleles in both markers linked to LMS (Gawrosz and Jersey) were very high, whereas varieties having alleles decreasing height were numerous (which reflects the breeding selection process) and were located in the middle of the ranking. Similar studies were performed by Wang et al. (2014) who detected a new QTL for PH on the 7H chromosome with the closest SSR marker bPb–9269, which showed a sufficient allelic effect and was consistently expressed in various environments; therefore, it can be successfully used in breeding programs. Mikołajczak et al. (2016) identified in the Georgie × Harmal population, in the linkage group 7H.2 at SNP 6353–524, a QTL for PH (QLSt.GH–7H.2) with the Harmal allele A reducing the stem length; in the present study, the effect of allele A at this SNP was not consistent with that in the mapping study (negative but not significant in Experiment I, and positive in Experiment II). However, this could be attributed to the very low frequency (0.06) of this allele in the studied population. It was in the homozygous state only in three varieties (Antek, Barke and Raskud), which were rather low under semi-controlled conditions, but two of them (Antek and Barke) were not studied in Experiment II, and the one that was studied, Raskud, was tall. Therefore, although our results are not conclusive on the usefulness of this marker for breeding, they indicate a potential of genetic information that might be obtained in larger association studies.

In conclusion, our studies confirmed that the results of the experiments conducted under semi-controlled conditions (greenhouse and vegetation hall) do not always repeat under natural (field) conditions (for similar results, see, e.g. Malhi & Nyborg, 1993; Bartzas, Zaharaki, & Komnitsas, 2015; Millet et al., 2016; Poorter et al., 2016). However, we were able to distinguish varieties of high yield evaluated both as the grain weight per plant and the grain yield per plot (Ella, Iron, Natasia, Soldo, and Suweren) as well as the varieties of relatively stable yielding under both semi-controlled and natural conditions (Blask, Ella, Olympic, Skald, and Xanadu). We could relate the mean level of the yield-related traits observed in diverse testing locations to the level of the basic environmental parameters relevant to the water availability. Moreover, the same parameters explained the instability of certain varieties, underlining the need for environmental variables tracking in plant studies. Only a few markers associated with the QTLs detected earlier in the mapping populations were identified as having a coherent effect in varieties of various pedigrees—three associated with the 1,000-grain weight and two associated with the stem length/plant height. These markers seem to be promising for the selection of barley plants, and we indicated the sources of advantageous alleles in the studied pool of varieties. We found the signs of a low usefulness of the yield assessment in a greenhouse for predicting the yield under field conditions. We inferred a possibility of extending the lists of traits observed in abiotic stress-related investigations with the physicochemical parameters describing plant leaf surfaces; in our opinion, they could provide particularly interesting results when used in connection with molecular phenotyping with respect to the (increasingly known) agents responsible for the stress signalling and the stress response in plants.

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REFERENCES

AL-Ajlouni, Z. I., Al-Abdallat, A. M., Al-Ghzawi, A. L. A., Ayad, J. Y., Elenein, J. M. A., Al-Quraan, N. A., & Baenziger, P. S. (2016). Impact of pre-anthesis water deficit on yield and yield components in barley (*Hordeum vulgare* L.) plants grown under controlled conditions. *Agronomy*, *6*, 33. https://doi.org/10.3390/agronomy6020033

Anjum, S. A., Xie, X., Wang, L., Saleem, M. F., Man, C., & Lei, W. (2011). Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research*, *6*, 2026–2032. https://doi.org/10.5897/AJAR10.027

Aranovich, G. L. (1992). The theory of polymolecular adsorption. *Longmuir*, *3*, 736–739. https://doi.org/10.1021/la00038a071

Bandurska, H., Niedziela, J., Pietrowska-Borek, M., Nuc, K., Chadzinikolau, T., & Radzikowska, D. (2017). Regulation of proline biosynthesis and resistance to drought stress in two barley (Hordeum vulgare L.) genotypes of different origin. *Plant Physiology and Biochemistry*, *118*, 427–437. https://doi.org/10.1016/j.plaphy.2017.07.006

Bartzas, G., Zaharaki, D., & Komnitsas, K. (2015). Life cycle assessment of open field and greenhouse cultivation of lettuce and barley. *Information Processing in Agriculture*, *2*, 191–200. https://doi.org/10.1016/j.inpa.2015.10.001

Baum, M., Grando, S., Backes, G., Jahoor, A., Sabbagh, A., & Ceccarelli, S. (2003). QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross 'Arta'×H–spontaneum. *Theoretical and Applied Genetics*, *107*, 1215–1225. https://doi.org/10.1007/s00122-003-1357-2

Blum, A. (1996). Crop responses of drought and the interpretation of adaptation. *Plant Growth Regulation*, *20*, 135–148. https://doi.org/10.1007/978-94-017-1299-6_8

Caliński, T., Czajka, S., Kaczmarek, Z., Krajewski, P., & Pilarczyk, W. (2005). Analyzing multi-environment variety trials using randomization-derived mixed models. *Biometrics*, *61*, 448–455. https://doi.org/10.1111/j.1541-0420.2005.00334.x

Ceccarelli, S. (1994). Specific adaptation and breeding for marginal conditions. *Euphytica*, *77*, 205–219. https://doi.org/10.1007/BF02262633

Ceccarelli, S., Acevedo, E., & Grando, S. (1991). Breeding for yield stability in unpredictable environments: Single traits, interaction between traits, and architecture of genotypes. *Euphytica*, *56*, 169–185. https://doi.org/10.1007/BF00042061

Chmielewska, K., Rodziewicz, P., Swarcewicz, B., Sawikowska, A., Krajewski, P., Marczak, Ł., … Stobiecki, M. (2016). Analysis of drought-induced proteomic and metabolomic changes in barley(*Hordeum vulgare* L.) leaves and roots unravels some aspects of biochemical mechanisms involved in drought tolerance. *Frontiers in Plant Science*, *7*, 1108. https://doi.org/10.3389/fpls.2016.01108

Close, T. J., Bhat, P. R., Lonardi, S., Wu, Y., Rostoks, N., Ramsay, L., … Waugh, R. (2009). Development and implementation of high-throughput SNP genotyping in barley. *BMC Genomics*, *2010*, 582. https://doi.org/10.1186/1471-2164-10-582

Ćwiek-Kupczyńska, H., Altmann, T., Arend, D., Arnaud, E., Chen, D., Cornut, G., … Krajewski, P. (2016). Measures for interoperability of phenotypic data: Minimum information requirements and formatting. *Plant Methods*, *12*, 44. https://doi.org/10.1186/s13007-016-0144-4

Daszkowska-Golec, A., & Szarejko, I. (2013). Open or close the gate – stomata action under the control of phytohormones in drought stress conditions. *Frontiers in Plant Science*, *4*, 138. https://doi.org/10.3389/fpls.2013.0013

De Mezer, M., Turska-Taraska, A., Kaczmarek, Z., Głowacka, K., Swarcewicz, B., & Rorat, T. (2014). Differential physiological and molecular response of barley genotypes to water deficit. *Plant Physiology and Biochemistry*, *80*, 234–248. https://doi.org/10.1016/j.plaphy.2014.03.025

Diab, A. A., Teulat-Merah, B., This, D., Ozturk, N. Z., Benscher, D., & Sorrells, M. E. (2004). Identification of drought-inducible genes and differentially expressed sequence tags in barley. *Theoretical and Applied Genetics*, *109*, 1417–1425. https://doi.org/10.1007/s00122-004-1755-0

Ferrante, A., Savin, A., & Slafer, G. A. (2008). Wheat and barley floret development in response to nitrogen and water availability. *The Italian Journal of Agronomy*, *3*, 205–206.

Filek, M., Łabanowska, M., Kościelniak, J., Biesaga-Kościelniak, J., Kurdziel, M., Szarejko, I., & Hartikainen, H. (2014). Characterization of barley leaf tolerance to drought stress by chlorophyll fluorescence and electron paramagnetic resonance studies. *Journal of Agronomy and Crop Science*, *2014*, 228–240. https://doi.org/10.1111/jac.12063

Forster, B. P., Ellis, R. P., Moir, J., Talame, V., Sanguinet, M. C., Tuberosa, R., … Salem, M. B. (2004). Genotype and phenotype associations with drought tolerance in barley tested in North Africa. *Annals of Applied Biology*, *144*, 157–168. https://doi.org/10.1111/j.1744-7348.2004.tb00329.x

Gauch, H. G. (1992). *Statistical analysis of regional yield trials - AMMI analysis of factorial designs*. Amsterdam, the Netherlands: Elsevier.

Jarzebski, A. B., Lorenc, J., & Pajak, L. (1997). Surface fractal characteristics of silica aerogels. *Langmuir*, *13*, 1280–1285. https://doi.org/10.1021/la960011z

Jia, Q., Zhang, X. Q., Westcott, S., Broughton, S., Cakir, M., Yang, J., … Li, C. (2011). Expression level of a gibberellin 20–oxidase gene is associated with multiple agronomic and quality traits in barley. *Theoretical and Applied Genetics*, *122*, 1451–1460. https://doi.org/10.1007/s00122-011-1544-5

Jozefaciuk, G., & Lukowska, M. (2013). New method for measurement of plant roots specific surface. *American Journal of Plant Sciences*, *4*, 1088–1094. https://doi.org/10.4236/ajps.2013.45135

Jozefaciuk, G., Lukowska, M., & Szerement, J. (2013). Determination of energetic and geometric properties of plant roots specific surface from adsorption/desorption ishoterm. *American Journal of Plant Sciences*, *4*, 1554–1561. https://doi.org/10.4236/ajps.2013.48187

Jozefaciuk, G., & Szatanik-Kloc, A. (2001). Aluminium-induced changes in the surface and micropore properties of wheat roots: A study using the water vapor adsorption-desorption technique. *Plant and Soil*, *233*, 95–108. https://doi.org/10.1023/A:1010373116199

Jozefaciuk, G., & Szatanik-Kloc, A. (2003). Changes in specific area and energy of root surface of cereal plants in Al-solution cultures. Water vapor adsorption studies. *Plant and Soil*, *250*, 129–140. https://doi.org/10.1023/A:1022813018940

Kuczyńska, A., Mikołajczak, K., & Ćwiek, H. (2014). Pleiotropic effects of the sdw1 locus in barley populations representing different rounds of recombination. *Electronic Journal of Biotechnology*, *17*(5), 217–223. https://doi.org/10.1016/j.ejbt.2014.07.005

Kuczyńska, A., Surma, M., Adamski, T., Mikołajczak, K., Krystkowiak, K., & Ogrodowicz, P. (2013). Effects of the semi–dwarfing sdw1/denso gene in barley. *Journal of Applied Genetics*, *54*, 381–390. https://doi.org/10.1007/s13353-013-0165-x

Kuczynska, A., & Wyka, T. (2011). The effect of the denso dwarfing gene on morpho-anatomical characters in barley recombinant inbred lines. *Breeding Science*, *61*, 275–280. https://doi.org/10.1270/jsbbs.61.275

Malhi, S. S., & Nyborg, M. (1993). Compaction of soils: Yield of barley in greenhouse and field. *Communications in Soil Science and Plant Analysis*, *24*, 13–14. https://doi.org/10.1080/00103629309368891

Mansour, E., Casas, A. M., Gracia, A. P., Molina-Cano, J. L., Moralejo, M., Cattivelli, L., … Igartua, E. (2014). Quantitative trait loci for agronomic traits in an elite barley population for Mediterranean conditions. *Molecular Breeding*, *33*, 249–265. https://doi.org/10.1007/s11032-013-9946-5

Meier, U. (2001). Growth stages of mono-and dicotyledonous plants – BBCH Monograph. Retrieved from https://www.julius-kuehn.de/publikationsreihen-des-jki/bbch-skala/

Mikolajczak, K., Kuczynska, A., Krajewski, P., Sawikowska, A., Surma, M., Ogrodowicz, P., … Gudyś, K. (2017). Quantitative trait loci for plant height in Maresi x CamB barley population and their associations with yield-related traits under different water regimes. *Journal of Applied Genetics*, *58*, 23–35. https://doi.org/10.1007/s13353-016-0358-1

Mikołajczak, K., Ogrodowicz, P., Gudyś, K., Krystkowiak, K., Sawikowska, A., Frohmberg, W., … Kuczyńska, A. (2016). Quantitative trait loci for yield and yield–related traits in spring barley populations derived from crosses between European and Syrian cultivars. *PLoS ONE*, *11*(5), e0155938. https://doi.org/10.1371/journal.pone.0155938

Millet, E. J., Welcker, C., Kruijer, W., Negro, S., Coupel-Ledru, A., Nicolas, S. D., … Tardieu, F. (2016). Genome-wide analysis of yield in Europe: Allelic effects vary with drought and heat scenarios. *Plant Physiology*, *172*(2), 749–764. https://doi.org/10.1104/pp.16.00621

Ogrodowicz, P., Adamski, T., Mikołajczak, K., Kuczyńska, A., Surma, M., Krajewski, P., … Krystkowiak, K. (2017). QTLs for earliness and yield-forming traits in the Lubuski × CamB barley RIL population under various water regimes. *Journal of Applied Genetics*, *58*, 49–65. https://doi.org/10.1007/s13353-016-0363-4

Piasecka, A., Sawikowska, A., Kuczyńska, A., Ogrodowicz, P., Mikołajczak, K., Krystkowiak, K., … Kachlicki, P. (2017). Drought related secondary metabolites of barley (Hordeum vulgare L.) leaves and their mQTLs. *The Plant Journal*, *89*(5), 898–913. https://doi.org/10.1111/tpj.13430

Poorter, H., Fiorani, F., Pieruschka, R., Wojciechowski, T., van der Putten, W. H., Kleyer, M., … Postma, J. (2016). Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist*, *212*, 838–855. https://doi.org/10.1111/nph.14243

Purchase, J. L., Hatting, H., & van Deventer, C. S. (2000). Genotype × environment interaction of winter wheat (*Triticum aestivum* L.) in South Africa: II Stability analysis of yield performance. *South African Journal of Plant and Soil*, *17*, 101–107. https://doi.org/10.1080/02571862.2000.10634878

Rodriguez, M., Rau, D., Papa, R., & Attene, G. (2008). Genotype by environment interactions in barley (Hordeum vulgare L.): Different response of landraces, recombinant inbred lines and varieties to Mediterranean environment. *Euphytica*, *163*, 231–241. https://doi.org/10.1007/s10681-007-9635-8

Samarah, N. H., Alqudah, A. M., Amayreh, J. A., & McAndrews, G. M. (2009). The effect of late-terminal drought stress on yield components of four barley cultivars. *Journal of Agronomy and Crop Science*, *195*(6), 427–441. https://doi.org/10.1111/j.1439-037X.2009.00387.x

Spinoni, J., Naumann, G., Vogt, J. V., & Barbosa, P. (2015). The biggest drought events in Europe from 1950 to 2012. *Journal of Hydrology: Regional Studies*, *3*, 509–524. https://doi.org/10.1016/j.ejrh.2015.01.001

Szatanik-Kloc, A., & Jozefaciuk, G. (2007). Changes in micropore system of roots of wheat and triticale seedlings under aluminum stress as determined using water vapor adsorption- desorption. *Acta Physiologiae Plantarum*, *29*, 425–430. https://doi.org/10.1007/s11738-007-0051-4

Talamè, V., Sanguineti, M. C., Chiapparino, E., Bahri, H., Ben Salem, A., Forster, B. P., … Tuberosa, R. (2004). Identification of Hordeum spontaneum QTL alleles improving field performance of barley grown under rainfed conditions. *Annals of Applied Biology*, *144*, 309–319. https://doi.org/10.1111/j.1744-7348.2004.tb00346.x

Teulat, B., Merah, O., Souyris, I., & This, D. (2001). QTLs for agronomic traits from a Mediterranean barley progeny grown in several environments. *Theoretical and Applied Genetics*, *103*, 774–787. https://doi.org/10.1007/s001220100619

Teulat, B., This, D., Khairallah, M., Borries, C., Ragot, C., Sourdille, P., … Charrier, A. (1998). Several QTLs involved in osmotic-adjustment trait variation in barley (Hordeum vulgare L.). *Theoretical and Applied Genetics*, *96*, 688–698. https://doi.org/10.1007/s001220050790

Teulat, B., Zoumarou-Wallis, N., Rotter, B., Salem, M. B., Bahri, H., & This, D. (2003). QTL for relative water content in field-grown barley and their stability across Mediterranean environments. *Theoretical and Applied Genetics*, *108*, 181–188. https://doi.org/10.1007/s00122-003-1417-7

Thomas, W. T. B., Powell, W., & Swanston, J. S. (1991). The effects of major genes on quantitatively varying characters in barley. 4. The GPert and denso loci and quality characters. *Heredity*, *66*, 381–389. https://doi.org/10.1038/hdy.1991.48

Tondelli, A., Francia, E., Visioni, A., Comadran, J., Mastrangelo, A. M., Akar, T., … Pecchioni, N. (2014). QTLs for barley yield adaptation to Mediterranean environments in the 'Nure' × 'Tremois' biparental population. *Euphytica*, *197*, 73–86. https://doi.org/10.1007/s10681-013-1053-5

Ugarte, C., Calderini, D. F., & Slafer, G. A. (2007). Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. *Field Crop Research*, *100*, 240–248. https://doi.org/10.1016/j.fcr.2006.07.010

van Eeuwijk, F. A., Bustos-Korts, D., Millet, E. J., Boer, M. P., Kruijer, W., Thompson, A., … Chapman, S. C. (2018). Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. *Plant Science*. https://doi.org/10.1016/j.plantsci.2018.06.018

Vargas, M., Crossa, J., van Eeuwijk, F. A., Ramires, M., & Sayre, K. (1999). Using partial least squares regression, factorial regression, and AMMI models for interpreting genotype × environment interaction. *Crop Science*, *39*, 955–967. https://doi.org/10.2135/cropsci1999.0011183X003900040002x

VSN International (2015). *Genstat for windows*, 18th ed. Hemel Hempstead, UK: VSN International. Web page: Genstat.co.uk

Wang, W., Vinocur, B., & Altman, A. (2003). Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. *Planta*, *218*, 1–14. https://doi.org/10.1007/s00425-003-1105-5

Wang, J., Yang, J., Jia, Q., Zhu, J., Shang, Y., Hua, W., & Zhou, M. (2014). A new QTL for plant height in barley (Hordeum vulgare L.) showing no negative effects on grain yield. *PLoS ONE*, *9*(2), e90144. https://doi.org/10.1371/journal.pone.0090144

Wójcik-Jagła, M., Rapacz, M., Tyrka, M., Kościelniak, J., Crissy, K., & Zmuda, K. (2013). Comparative QTL analysis of early short-time drought tolerance in Polish fodder and malting spring barleys. *Theoretical and Applied Genetics*, *126*(12), 3021–3034. https://doi.org/10.1007/s00122-013-2190

Yu, J., Pressoir, G., & Briggs, W. H. (2006). A unified mixed-model method for association mapping that accounts for multiple level of relatedness. *Nature Genetics*, *38*, 203–208. https://doi.org/10.1038/ng1702

SUPPORTING INFORMATION

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