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# Unveiling the Impact of Growth Traits on the Yield of Bread Wheat Germplasm Subjected to Waterlogging

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**Abstract:** Changes in the climate have led to the occurrence of extreme events that threaten the production of major crops, namely that of bread wheat (*Triticum aestivum* L.). Waterlogging imposed at the tillering stage can severely affect the yield, but several genotype features may counterbalance the negative impacts on yields. The aim of this work was to evaluate the effect of waterlogging on the number of fertile spikes, kernels per plant, and single kernel weight, as well as to assess the main culm and tiller participation in yields. We also investigated if the growth stages affected by stress would influence such traits. The study was conducted in climatized growth chambers using 23 genotypes from five distinct germplasm groups (Portuguese landraces, varieties with the introduced Italian germplasm, post-Green Revolution varieties with the introduced CIMMYT germplasm, advanced lines from the Portuguese wheat breeding program, Australian varieties). Variability was observed between and within the groups. Ten genotypes performed well under waterlogged conditions, showing promising results. Among these, GR-2 showed a rise in tiller yield, AdvL-3 in both the main culm and tiller yield, and the remaining ones displayed unaltered values in both the main culm and tillers. PL-1, PL-5, GR-1, GR-3, AdvL-2, Austrl-2, and Austrl-4 were able to compensate for the decreases observed for several traits, reaching harvest yield values that were unaffected in both the main culm and tillers. Rises in the tiller yield or in the tillers and main culm, GR-2 and AdvL-3 exhibited either stability or increases in all the studied parameters. Results also suggest a negative correlation between the growth stage reached during waterlogging and the effect of this stress on the number of spikes per plant, plant and tiller yield, kernel per spike (tillers), and single kernel weight (tillers). Our findings may contribute to a better understanding of wheat responses to waterlogging and to the development of solutions that mitigate the socio-economic impacts of 20–50% wheat yield reductions, thereby preserving the daily 20% supply of energy and protein required for human nutrition and global food security.

**Keywords:** *Triticum aestivum* L.; Portuguese landraces; Australian varieties; CIMMYT germplasm; advanced lines; tillers; main culm; yield; spikes; flooding

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## 1. Introduction

Wheat is one of the most extensively cultivated crops due to its high yields and superior nutritional and processing properties [1], which are tightly linked to global food security. Most of the wheat produced (79%) is used in wheat-based products and consumed by 2.5 billion people, providing vitamins, minerals, and 15–20% of daily protein and energy requirements [1–3].

Due to the severe consequences of global climate change, agriculture faces new challenges [4]. Extreme weather events, such as heavy rainfall, have increased over the past few decades and will predictably reach the majority of the world's crop-producing arable land [4–7]. Waterlogging is considered a severe abiotic stress causing soil water oversaturation around plant roots. It annually affects 15–20% of global wheat cropping regions [3], thereby resulting in substantial yield losses, which are similar to those caused by heat and drought [8]. The negative effects of waterlogging on wheat production have worsened over the past 50 years [5] as a result of the higher frequency and magnitude of extreme precipitation events [5,9].

Waterlogging hampers the gas exchanges between plant roots and the atmosphere [10], depriving plants of oxygen, impairing their ability to absorb nutrients and water, and decreasing their growth [2,7,11]. Under these circumstances, several vital metabolic processes like respiration, which is crucial for energy production, are inhibited, and plants use the available energy to survive, depicting a height decrease, lower biomass accumulation, and premature senescence [9,12,13]. The energy deficiency and disturbances in root hydraulic conductance also affect transpiration balance and photosynthetic activity. The reduction of stomatal conductance and the consequent limited carbon dioxide availability in tissues intensify the reduced carbohydrate production, thereby affecting the whole-plant metabolism [2,14–16]. Additionally, nutrient imbalance and/or toxicity as a result of changes in nutrient availability in waterlogged soils also contribute to the components of decreased yields (average kernel weight, number of kernels per spike, spike number per plant or unit surface) and yield losses [15,17–21].

A complex interaction of genetic and environmental factors determines the waterlogging tolerance of wheat. Several quantitative trait loci (QTL) associated with traits linked to waterlogging tolerance occurring at different growth stages have been identified. These QTL contribute to different aspects of tolerance, including those of the root traits, physiological responses, and overall plant performance under waterlogged conditions. Among them, one QTL located on chromosome 7A was found to account for the phenotypic variation in the germination rate [22]. Additionally, QTL associated with the survival and growth of seedlings under waterlogging were detected on chromosomes 2A, 2B, 3A, 3B, 4B, 5A, 6A, and 7S [23]. In wheat plants waterlogged at the vegetative stage, a single QTL (on chromosome 1BL) was associated with the variation in chlorophyll content [24]. However, other authors [25] reported the identification of three QTL on the same chromosome and one on chromosome 1D that account for the phenotypic variation in chlorophyll content. A gene linked to a QTL located on chromosome 2B and its involvement in the degradation of reactive oxygen species (ROS) was also identified during waterlogging [25]. Furthermore, within the same QTL, a gene involved in cell wall degradation revealed its role in aerenchyma formation in wheat seminal roots. This ultimately leads to the improved survival of the plants among the aboveground portion [26] due to increased oxygen supply and water uptake in such an environment. Three QTL related with the thousand kernel weight were identified on chromosomes 4AL, 5AS, and 7DL and were associated with waterlogging tolerance at the post-anthesis stage [27].

Depending on their growth stage, wheat plants respond differently to waterlogging. Reductions in the spike and kernel numbers were reported due to waterlogging imposed at the tillering stage, while stress imposed at the booting stage resulted in lighter kernels [28,29]. In wheat, several authors described the emergence, tillering, and maturity stages as less susceptible to the negative impacts of waterlogging [28]. However, yield reductions of up to 87% were reported due to 14 days of water stress initiated at the tillering stage for the germplasm from different genetic backgrounds [30]. In addition to the growth stage and genotype, the impacts of waterlogging were also influenced by the duration of the stress [9,31], temperature [32,33], the rhizosphere microbiome [34], soil texture, soil chemical composition [35], root architecture [36], and irradiation, among other factors. Waterlogging studies developed under environmentally controlled conditions can provide reliable data, thus allowing for the identification of the key traits underlying stress tolerance [3].

Wheat plants consist of one main culm and a variable number of tillers, the latter depending on the cultivar and environmental conditions. Thus, a large variability can be expected regarding the main culm or tiller's contribution to the yield either under optimal or adverse environments. In low-tillering varieties, the competition among the culm and tillers is minimized and uniform maturity is ensured [37–39]. On the other hand, high tillering may allow for yield maintenance by compensating for reductions in the average kernel weight and/or kernels per spike [40]. Additionally, tillers may aid weed competition [41] and can also be used to remobilize stored nutrients [42]. Tiller survival and development under waterlogging are essential as they are directly proportional to the number of spikes per plant [43]. Nonetheless, the preservation of fertile tillers does not guarantee the maintenance of yield, as their contribution to the final yield may be affected [43]. Yield reduction due to waterlogging is associated with low tiller survival [44,45], less fertile tillers, and reduced kernel size [16,46]. In addition, a decrease in the number of kernels per spike has been reported for both the main culm and tillers [18,47,48]. As yield components may be altered by environmental conditions, it is possible to select the most promising for yield gain [49,50] and to develop waterlogging-tolerant varieties as a key to maintain crop production in areas prone to such climate events. Additionally, the impact of this stress has been assessed when applied at a specific stage of growth. The evaluation did not consider whether variations in the growth cycle result in genotypes being exposed to one or more growth phases during the stress period. It also did not evaluate how this exposure may affect the yield and its different traits.

Waterlogging is one of the major constraints for agriculture. These events tend to occur with regularity throughout the key period for the development of kernels, thus impacting the features related to yields. The development of waterlogging-tolerant cultivars has consistently been a primary focus for plant breeders. Therefore, the evaluation of the existing germplasm under excess water conditions is crucial for the development and use of new or more adapted varieties that exhibit enhanced yield potential and consistent performance, thereby facilitating effective risk management. The quantification of losses resulting from waterlogging is essential in order to assess the importance of the traits considered as potential indicators of tolerance to this abiotic stress. Furthermore, the lack of waterlogging-tolerant cultivars that exhibit good performance in the particular soil and climate conditions of Portugal makes this study relevant.

The aim of this study was to evaluate, under controlled conditions, the impact of 14 days of waterlogging imposed at the tillering stage for the yield components and plant growth development of 23 bread wheat (*Triticum aestivum* L.) genotypes from distinct origins. The effects of stress on the final spike number per plant, kernel number per plant and per main culm, total of tillers, single kernel weight (from the main culm and tillers), changes in the main culm, and tiller contribution to the final yield were assessed. At the end of the water stress, changes in the phenotypic development due to waterlogging were also evaluated along with the correlation of these differences on the yield and its components.

## 2. Materials and Methods

### 2.1. Plant Material and Growth Conditions

Certified seeds of 23 bread wheat (*T. aestivum* L.) genotypes were initially multiplied in growth chambers (Fitoclima 10000 EHHF, ARALAB, Cascais, Portugal) under controlled conditions of temperature (22/15 °C, day/night), irradiance (ca. 500 µmol $m^{-2}$ $s^{-1}$), relative humidity (70/75%, day/night), photoperiod (14 h), and $CO_2$ (400 µL $L^{-1}$) in 5 L pots with field-collected loamy clay soil to ensure adequate seed vigor and uniform germination capacity (100%) as previously described [30].

The studied germplasm was selected from groups with distinct backgrounds (Table 1) and comprises Australian varieties and genotypes from different stages of wheat cultivation in Portugal, increasing genetic variability and thus the robustness of the study. Germplasm was supplied by the National Cereal Breeding Program taking place at the National Institute of Agricultural and Veterinary Research (INIAV, Portugal).

**Table 1.** Bread wheat (*T. aestivum* L.) germplasm supplied by the National Cereal Breeding Program (INIAV, Elvas, Portugal) and belonging to five groups according to genetic background and origins.

| Germplasm Group | | Genotype | |
|---|---|---|---|
| Portuguese landraces (Vasconcelos ancient collection) | PL | Alentejano | PL-1 |
| | | Ardito | PL-2 |
| | | Mocho Cabeçudo | PL-3 |
| | | Mocho de Espiga Quadrada | PL-4 |
| | | Mocho de Espiga Branca | PL-5 |
| Varieties with introduced Italian germplasm (developed by the Portuguese Cereal Breeding Program and released between 1950 and 1970) | IT | Restauração | IT-1 |
| | | Chaimite | IT-2 |
| | | Mara | IT-3 |
| | | Pirana | IT-4 |
| Post-Green Revolution cultivars with introduced CIMMYT germplasm (developed by the Portuguese Cereal Breeding Program and released between 1980 and 1989) | GR | Caia | GR-1 |
| | | Nabão | GR-2 |
| | | Roxo | GR-3 |
| | | Mondego | GR-4 |
| Advanced lines obtained through the Portuguese Cereal Breeding Program or CIMMYT | AdvL | Ducula/Gondo//Sokol [1] | AdvL-1 |
| | | Katunga × (Centauro/Vega) [2] | AdvL-2 |
| | | Kennedy × Roxo [3] | AdvL-3 |
| | | KLDR/Pewit1//Milan/Ducula [1] | AdvL-4 |
| | | GUS/3/Prl/Sara/Tsi/Vee#5/... [1] | AdvL-5 |
| Australian germplasm | Austrl | BT-Schomburgk | Austrl-1 |
| | | Excalibur | Austrl-2 |
| | | Sunvale | Austrl-3 |
| | | Sunlin | Austrl-4 |
| | | Trident | Austrl-5 |

[1] CIMMYT material; [2] Australian × Italian; [3] Australian × Portuguese.

Portuguese landraces (PL): the Vasconcellos collection, compiled in 1933, accurately reflects the genetic diversity of regional Portuguese wheat cultivars, with the current study selecting five varieties.

Varieties with the introduced Italian germplasm (IT): between the 1950s and 1970s, Portuguese breeders crossed landraces with Italian agronomic varieties, thus developing the first Portuguese cultivar (Pirana). Bread wheat varieties like Restauração and Chaimite were later cultivated along with highly improved Italian cultivars (Mara).

Post-Green Revolution cultivars with the introduced CIMMYT germplasm (GR): Cultivars containing dwarfism genes and that are linked to the Green Revolution marked the following period. With encouraging qualities in the bakery and agriculture industries, those cultivars (e.g., Caia and Mondego) demonstrated remarkable adaptability to Mediterranean climates and rust strains.

*Advanced Lines* (AdvL): Through collaboration with the Mexican program of CIMMYT, the exchange of resources, including advanced lines, is regularly incorporated into the national breeding program along with AdvL, which is obtained from the national program.

*Australian germplasm* (Austrl): In addition to the development of new or improved genotypes that are tolerant to major abiotic and biotic stresses, the selection of new germplasm (e.g., Australian) has also been a top priority. Australia has made significant progress in developing waterlogging-tolerant varieties. The underlaying interest in this fact increases due to the Mediterranean climate prevalent in certain regions with similarities with that of Portugal.

The newly obtained seeds were soaked in water, placed on moist filter paper, and kept at room temperature until the radicle and the first two lateral seminal roots emerged. The germinated seeds were then placed with the germ end facing down at a 2 cm depth in 5 L pots filled with sieved loamy clay soil (Table 2). The soil used in this study was collected from one of the regions that represents the national cereal culture system where poor and shallow soils prevail.

**Table 2.** Properties of the soil used in this study.

| Soil Properties | | |
|---|---|---|
| Texture | Sand (%) | 40 |
| | Clay (%) | 35 |
| | Silt (%) | 25 |
| Organic matter (%) | | 1.15 |
| Phosphorus (%) | | 0.05 |
| Potassium (%) | | 0.95 |
| Nitrogen (%) | | 0.03 |
| EC (μS $cm^{-1}$) | | 334.93 |
| $pH_{Ca}$ | | 6.68 |

### 2.2. Experimental Design and Waterlogging Implementation

Using the newly multiplied seeds, a total of 12 pots were prepared per genotype (7 seeds per pot). Plants were grown in a walk-in growth chamber, as described above. Out of these, 6 pots were assigned for control plants (WW) and the remaining 6 pots for waterlogged plants (WL), as shown in Figure 1. Thus, each genotype had a total of 6 pots (biological unit) and 42 plants (biological subunit) per treatment.

Treatments were established at the tillering stage (Zadoks growth scale, ZGS 22 to 25) [51]. WW plants were maintained at ca. 85% field capacity and WL plants were subjected to 14 days of waterlogging (WL). For that, pots were placed in plastic containers and filled with water until a water layer of ca. 0.5 cm was formed above the soil surface. When necessary, the water level was manually refilled with extreme caution to ensure minimal air intake. The water stress was suspended by removing the pots from the boxes. Subsequently, WW and WL plants were kept in the same conditions until harvest (Figure 1).

All plants were grown in the same walk-in growth chambers under a field capacity of ca. 85% and adjusted every 2 days, except during waterlogging. Plants were fertilized weekly with 250 mL of a 12% N, 4% P, and 6% K solution (Complesal, Bayer), except during the waterlogging period, during the two weeks immediately preceding and following stress and the final stages of maturation.

Due to space limitations, the study was conducted in three consecutive series. Series 1 was conducted with 10 genotypes (PL-2, PL-4, PL-5, IT-2; AdvL-1, AdvL-2; AdvL-3, AdvL-5, Austrl-4, and Aus-trl-5), Series 2 with 5 genotypes (IT-1, GR-2, Autrl-1, Austrl-2 and Austrl-3), and Series 3 with 8 genotypes (PL-1, PL-3, IT-3, IT-4, GR-1, GR-3, GR-4, and AdvL-4) (Figure 1), and they were carried out between June 2020 and July 2021.

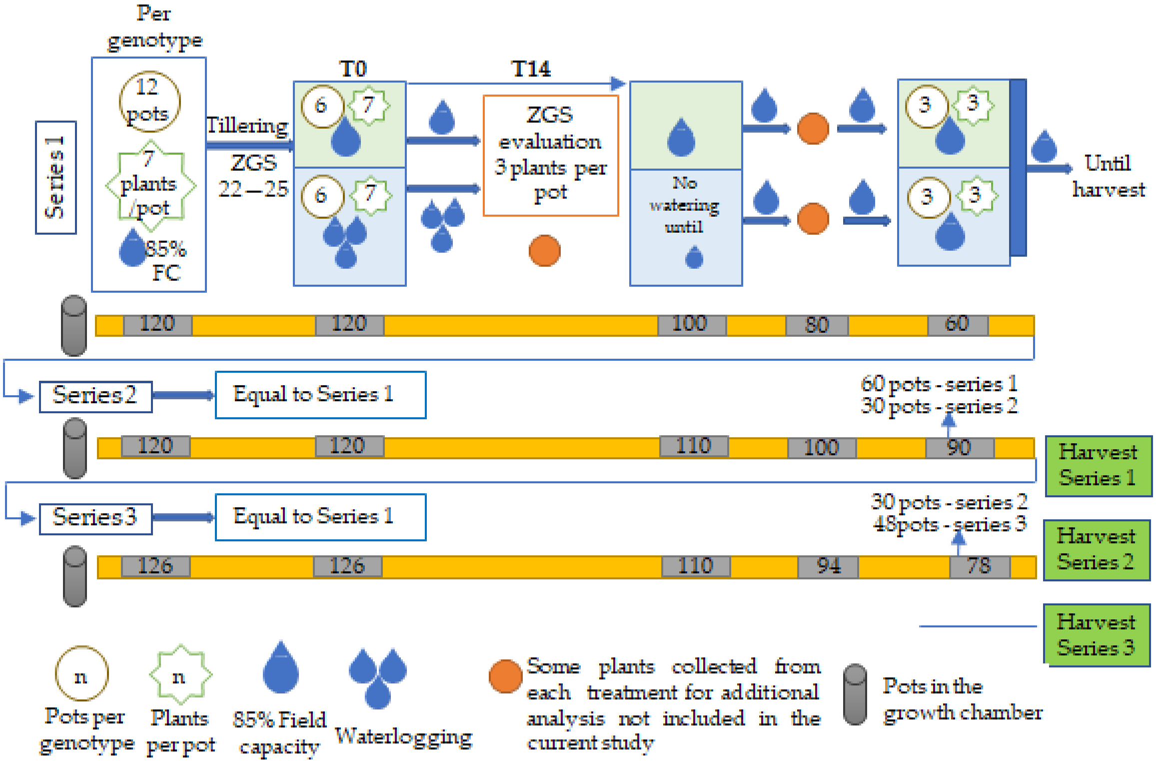

**Figure 1.** Flowchart of the study illustrating the key events by genotype and along the three implemented series (Series 1: 10 genotypes; Series 2: 5 genotypes; Series 3: 8 genotypes).

### *2.3. Plant Evaluation and Measurements*

For each genotype, the phenotypic development of the three plants per pot was recorded at the beginning (T0) and end (T14) of waterlogging in all pots, for a total of 6 pots and 18 plants per treatment.

For additional analysis, which was not included in the current study, four out of the seven plants from each pot (WW and WL) were collected at the end of the stress period. Additionally, more plants from each genotype were harvested for each treatment after a seven-day recovery period (T7R) and after a 14-day recovery period. Three pots with 3 plants each, both per treatment and per genotype, were allowed to grow until they reached full maturity (Figure 1). These pots were the basis for the results presented in this study (except for that of phenotypic development, as explained above).

At the end of the growth cycle, 3 pots (9 plants) per treatment and per genotype were harvested and oven-dried for 72 h at 35 °C to eliminate excess humidity. Spikes were detached from the main culm and fertile tillers, counted, individually weighed, and manually threshed. The number of kernels per spike and the kernel weight were also recorded.

### *2.4. Statistical Analysis*

Data were analyzed using a two-way ANOVA to evaluate the differences between water treatments (WW or WL) and/or tissue (main culm or tillers) and their interaction, followed by a Tukey's test for mean comparisons. A 95% confidence level was adopted for all tests, which were performed independently for each genotype using the software PAST (Paleontological Statistics software, version 3, University of Oslo, Norway). Biological replicates were used in this study, with $n$ = 6 pots for the assessment of phenotypic development and $n$ = 3 pots for the remaining evaluations.

PCA analysis were performed in PAST software, and the data from the two main principal components was plotted.

## 3. Results

### 3.1. Number of Spikes per Plant

Regarding the number of spikes per plant, a wide range of results was observed, with the WW plants reaching harvest with values of between 1.5 and 7.8 grain-producing spikes and the WL plants maintaining the maximum value and decreasing the minimum to that of 1.0 (Figure 2). This variability was observed not only between the 23 genotypes but also within each group of germplasm. The minimum value did not differ between groups, ranging from 1.5 to 2.4 for WW plants and from 1.0 to 1.9 for WL plants. In contrast, the maximum value for WW plants ranged from 3.6 to 7.8 in WW plants and from 1.8 to 7.7 in WL plants (Figure 2).

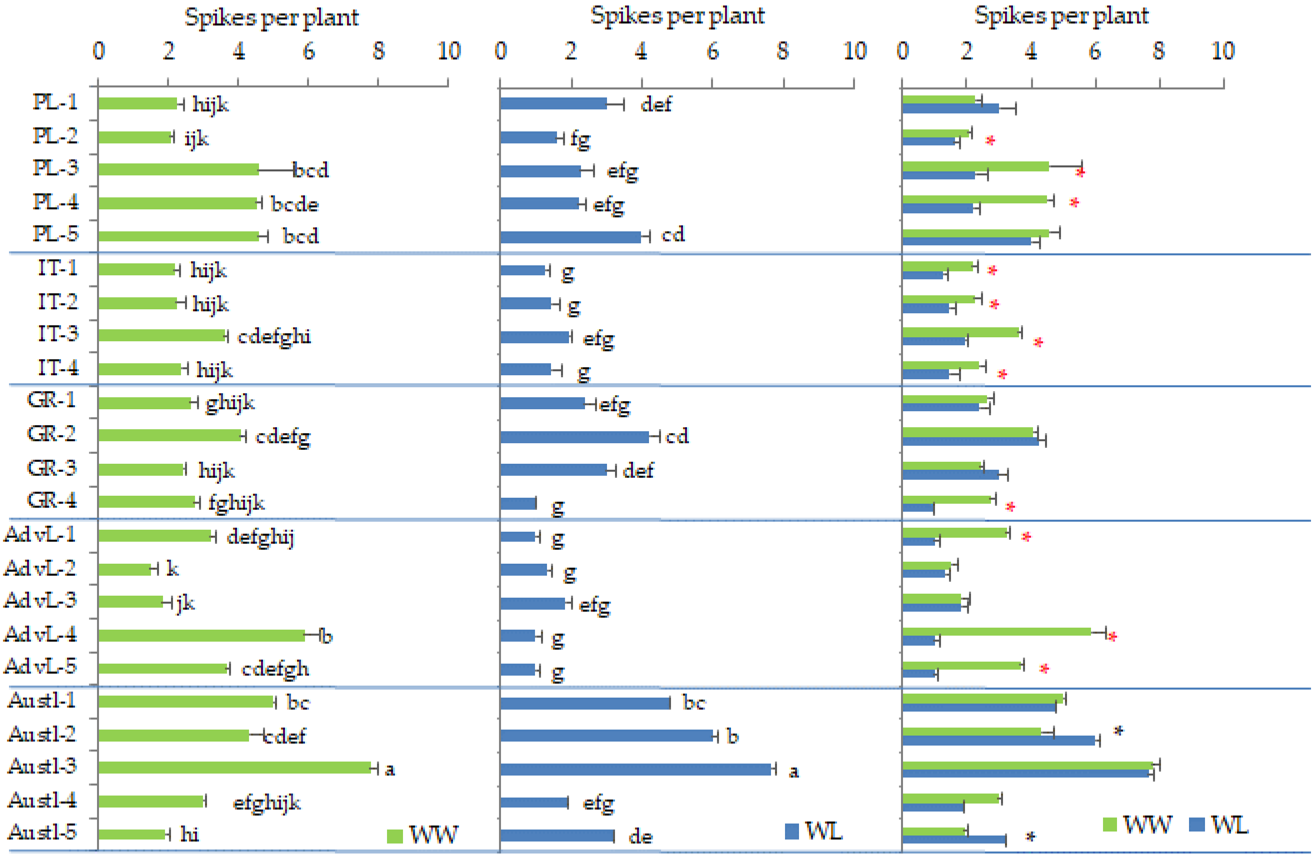

**Figure 2.** Number of spikes per plan (mean ± SE) in the control (WW) and waterlogged (WL) plants of 23 bread wheat genotypes (*T. aestivum* L.) belonging to 5 distinct germplasm groups as follows: (PL) Portuguese landraces, (IT) varieties with the introduced Italian germplasm, (GR) post-Green Revolution varieties with the introduced CIMMYT germplasm, (AdvL) advanced lines from the National Cereal Breeding Program (INIAV), and (Austrl) Australian varieties. Significant differences ($n = 3$ pots; $p < 0.05$) between genotypes in the same water treatment (WW or WL) are indicated through a, b, c, d, e, f, g, h, i, j, k, with the letter a used for the highest value. Differences between WW and WL plants are indicated through * for each genotype (in red for decreases and in black for increases).

Waterlogging reduced the number of spikes per plant in 11 genotypes by up to 83% (AdvL-4). In contrast, WL plants of Austrl-2 and Austrl-5 produced more 38 and 67% fertile spikes, respectively, at harvest when compared with WW plants.

All the groups that were subjected to waterlogging had at least two genotypes with an unaltered number of spikes except the IT group where all the varieties were negatively affected. As all the genotypes ended the growing cycle with a fertile spike on the main culm, the observed differences resulted from the loss in tillers due to waterlogging.

### 3.2. Kernel Number per Plant

Waterlogging led to significant decreases (from 16.4% to 61.1%) in the kernel number per plant of 13 genotypes across all the studied groups (Figure 3—plant). The highest impact was observed for the IT group, with decreases in the kernel number per plant in all the varieties. On the contrary, an increase in the kernel number per plant in WL plants was found in PL-3 (21.9%), GR-2 (29.0%), and AdvL-3 (18.1%), whereas PL-1, PL-5, GR-1, GR-3, Austrl-2, Austrl-3, and Autrl-5 were unaffected. These results may reflect changes in the kernel number of the main culm, in the total number of tillers, or in both.

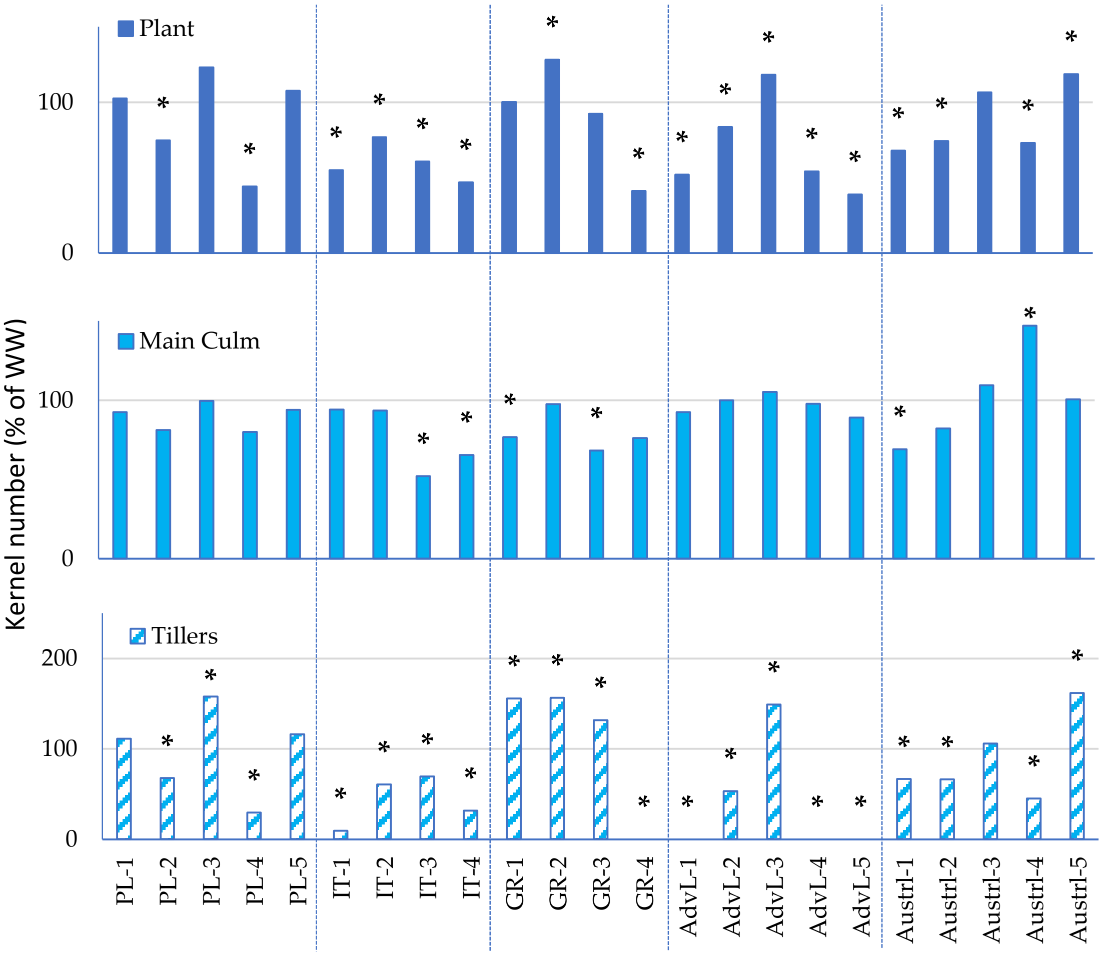

**Figure 3.** Impact (%) on waterlogged plants (WL) when compared with control plants (WW) of 14 days of waterlogging on the final kernel number (plant, main culm, and total of tillers) in *T. aestivum* L. genotypes from five germplasm groups with different origins. (PL) Portuguese landraces, (IT) varieties with the introduced Italian germplasm, (GR) post-Green Revolution varieties with the introduced CIMMYT germplasm, (AdvL) advanced lines from the National Cereal Breeding Program (INIAV), and (Austrl) Australian varieties. For each genotype, significant differences ($n = 3$; $p < 0.05$) between WW and WL plants are indicated through *.

Waterlogging tended to reduce the kernel number of the main culm and tillers (Figure 3). However, these decreases were only significant in the main culm of 5 genotypes (23.4–47.9%) and in tillers of 14 genotypes (31.0% to 100% reduction). Among the latter, eight genotypes showed declines of over 50% in the kernel number produced by tillers. In three genotypes (IT-3, IT-4, and Austrl-1), the observed plant declines were the result of a concurrent reduction in the main culm and tiller kernel number. On the other hand, decreases in nine genotypes (PL-2, PL-4, IT-1, IT-2, GR-4, AdvL-1, AdvL-2; AdvL-4, and AdvL-5) were due to a lower value in tillers as the number of main culm kernels was unaffected by waterlogging. Among these genotypes, GR-4, AdvL-1, AdvL-4, and AdvL-5 showed a 100% reduction, with no kernels being produced by tillers (Figure 3—Tillers). A higher kernel number produced by the main culm of Austrl-4 (46.8%) was insufficient in compensating for the loss in tillers, thus resulting in a decrease in plant kernel number (Figure 3).

Among the genotypes whose numbers of kernels per plant were unaffected, this apparent stability was only the result of an unchanged grain number of both the main culm and tillers in PL-1, PL-5, and Austrl-3. An increased kernel number of the total tillers of GR-1 (55.4%) and GR-3 (29.9%) has compensated for the losses found in the main culm (23.5 and 31.4%, respectively).

Regarding the increase in the kernel number per plant, three genotypes (GR-2, AdvL-3, and Austrl-5) stood out, with rises of 29.0%, 18.1%, and 18.7%, respectively. In these plants, the total number of kernels produced by tillers increased by 58.0% (GR-2), 48.8% (AdvL-3), and 61.6% (Austrl-5) (Figure 3).

### *3.3. Kernel Number per Spike*

Within the studied germplasm, the number of kernels per spike on WW plants ranged from 24 to 61 on the main culm and from 6 to 59 on tillers. In 16 genotypes, the main culm produced more kernels per spike than the tillers did. In PL-1, PL-2, PL-4, IT-2, IT-4, and AdvL-2, the main culm and tillers produced an equal number of kernels per spike. In Austrl-4, a higher number of kernels per spike of tillers in relation to the main culm (43 and 33, respectively) was also observed. Overall, PL genotypes displayed lower values than those of the other groups (Figure 4).

The number of kernels per spike on the main culm of six genotypes (IT-3, IT-4, GR-1, GR-3, Austrl-1, and Austrl-2) decreased between 18.1% and 47.0% due to waterlogging. In the tillers of the WL plants of GR-4, AdvL-1, AdvL-4, and AdvL-5, no grains were produced, while decreases of 29.6, 62.0, and 56.0% were observed for PL-1, IT-1, and Austrl-2, respectively (Figure 4). However, water stress also increased the number of kernels per spike in the main culm of Austrl-4 (46.8%) as well as in the tillers of PL-3 (332.0%), IT-2 (66.6%), IT-3 (89.5%), GR-1 (82.8%), and AdvL-3 (48.8%). In IT-3 and GR-1, these increases coincided with the aforementioned decreases in the main culm (Figure 4).

### *3.4. Single Kernel Weight (SKW)*

Regarding the average single kernel weight (SKW), variability was observed among genotypes and within groups (Figure 5).

For the control plants, the SKW ranged from 32.3 to 53.4 mg in the main culm and 21.8 to 62.4 mg in the tillers. There were no differences between the SKW values of the main culm and the tillers in 16 genotypes, but a heavier kernel in the main culm was observed for two Portuguese landraces (PL-1, PL-2), three IT genotypes (IT-2, IT-3, and IT-4), one from the GR group (GR-4), and one advanced line (AdvL-5) (Figure 5).

In WL plants, the SKW fluctuated between 11.0 and 64.5 mg in the main culm and from 16.7 to 56.9 mg in the tillers (Figure 5), while the tillers produced no kernels in GR-4, AdvL-1, AdvL-4, and AdvL-5. In addition, waterlogging did not induce changes in the SKW trend in 12 genotypes, with 3 genotypes maintaining heavier main culm kernels (PL-1, PL-2, and IT-3) and 9 preserving no differences between the main culm and tiller SKW values (PL-3, PL-4, PL-5, GR-2, GR-3, AdvL-2, AdvL-3, Austrl-1, Austrl-2, Austrl-3, Austrl-4, and Austrl-5) (Figure 5). For IT-4, the lower SKW value that were observed for the tillers of the control plants changed in response to stress, with WL plants exhibiting identical main culm and tiller values. This change was due to a decrease in the main culm SKW together with the unchanged value in the tiller SKW. In contrast, the balance between the SKW of the main culm and that of the tillers in GR-1 was altered as a result of decreased tiller SKW. Despite IT-1 WL plants maintaining lighter kernels in tillers, stress induced decreases in the SKW for both the main culm and tillers (49.5 and 53.5%, respectively). For

GR-4 and Advl-4, the absence of kernels in tillers was concomitant with SKW decreases in the main culm (73.3 and 58.3%, respectively).

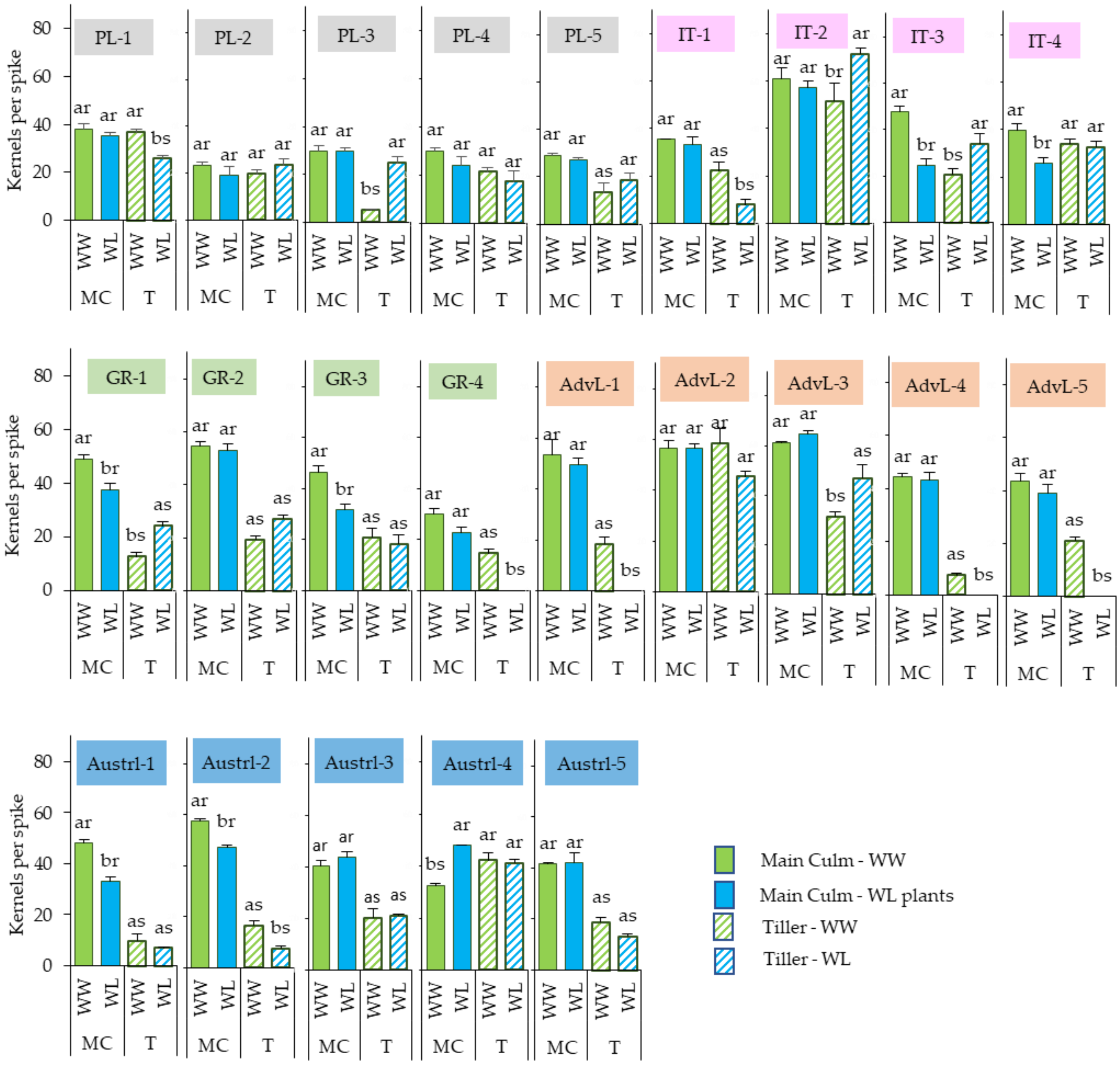

**Figure 4.** Kernels per spike at harvest (mean ± SE) in the main culm (MC) and per tiller (T) in control plants (WW) and waterlogged ones for 14 days at the tillering stage for *T. aestivum* L. genotypes from five germplasm groups with different origins. (PL) Portuguese landraces, (IT) varieties with the introduced Italian germplasm, (GR) post-Green Revolution varieties with the introduced CIMMYT germplasm, (AdvL) advanced lines from the National Cereal Breeding Program (INIAV), and (Austrl) Australian varieties. Significant differences ($n = 3$; $p < 0.05$) between WW and WL plants for the MC or T are indicated through letters (a, b) for each genotype. Letters (r, s) expressed significant differences between the MC and T for the same water regime (WW or WL) and for each genotype. The letters a and r represent the highest values.

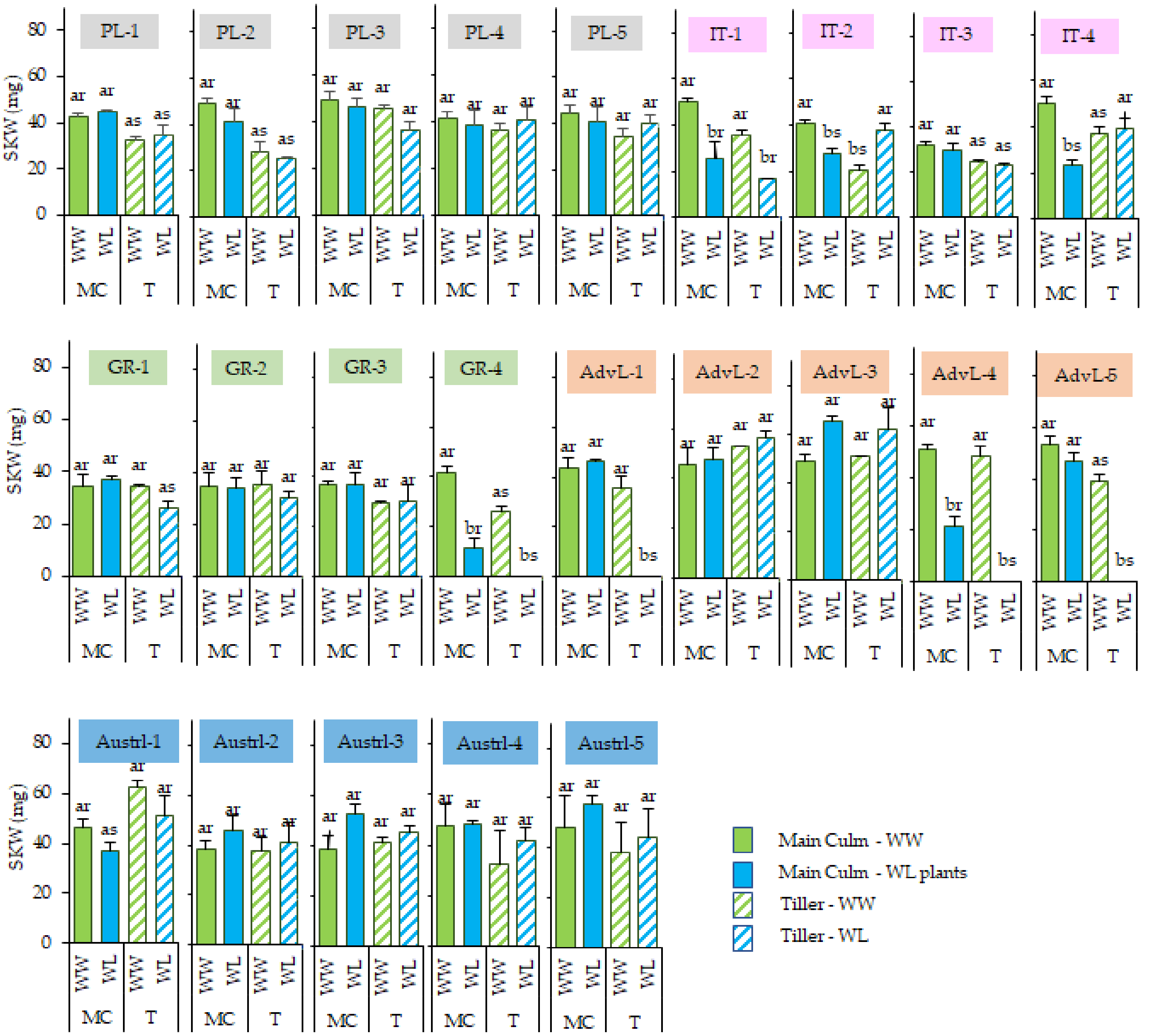

**Figure 5.** Single kernel weight (SKW, mg, mean ± SE) of 23 *T. aestivum* L. genotypes from five germplasm groups with different genetic backgrounds as follows: Portuguese landraces (PL), varieties with the introduction of the Italian germplasm (IT), post-Green Revolution varieties with the introduction of the CIMMYT germplasm (GR), advanced lines (AdvL) from the National Cereal Breeding Program (INIAV), and Australian varieties (Austrl). Comparisons of the mean SKW (mg) for each genotype are as follows: control (WW) or waterlogged (WL) plants in the main culm (MC) and tillers (T). For each genotype, different letters (a, b) indicate significant differences between WW and WL plants for the MC or T, and (r, s) indicate significant differences between the MC and T in the same water regime (WW or WL). (ANOVA, $n = 9$, $p < 0.05$).

### *3.5. Main Culm and Tiller Contribution to the Final Yield*

Regarding the contribution of the main culm and tillers to the final yield (g plant$^{-1}$), a high variability was observed for all the germplasm groups in control and waterlogged plants (Figure 6).

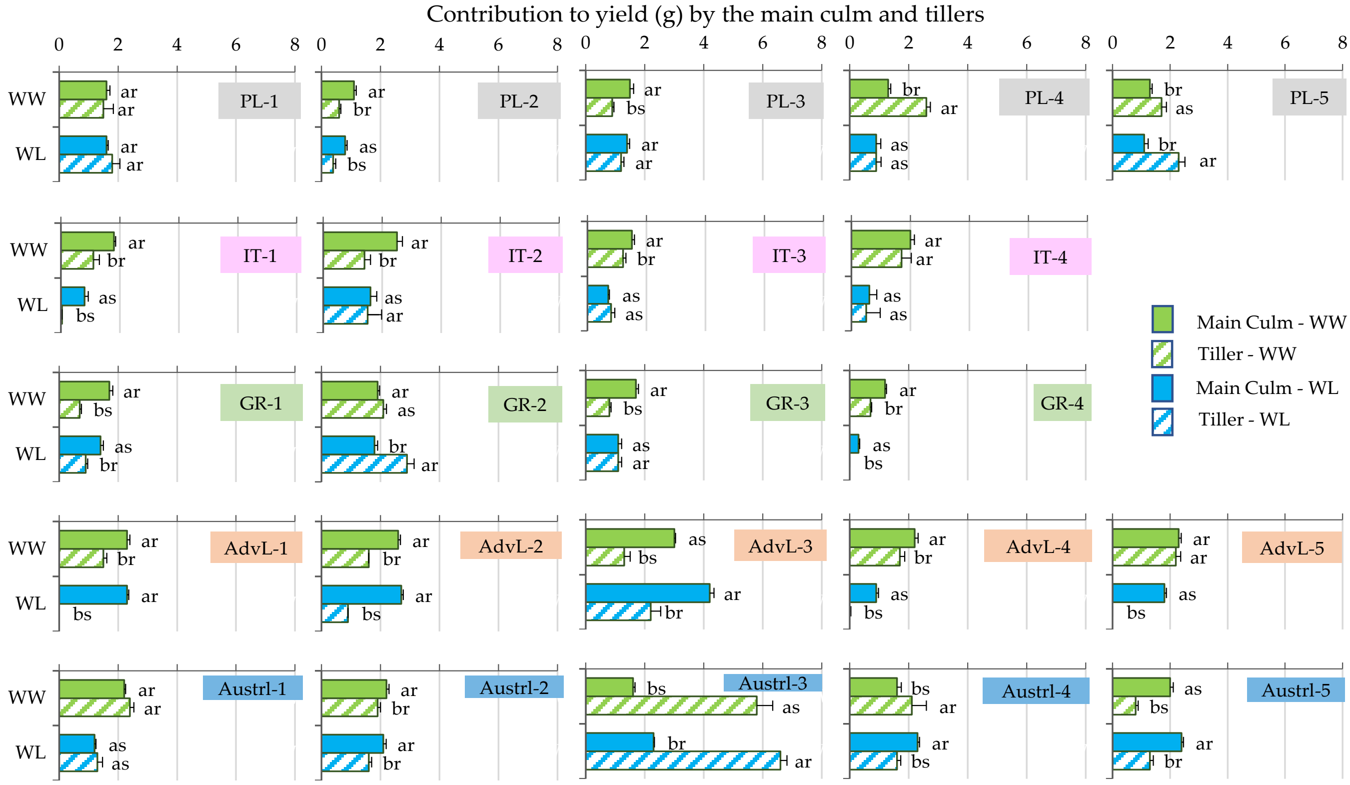

**Figure 6.** Contribution (mean ± SE) to the yield (g plant$^{-1}$) of the main culm (MC) and the total of tillers (T) in 23 *T. aestivum* L. genotypes from five germplasm groups with a different genetic background as follows: Portuguese landraces (PL), varieties with the introduction of the Italian germplasm (IT), post-Green Revolution varieties with the introduction of the CIMMYT germplasm (GR), advanced lines (AdvL) from the Portuguese Cereal Breeding Program (INIAV, I.P.), and Australian varieties (Austrl). For each genotype, comparisons were performed on the main culm (MC) and tillers (T) under control conditions (WW) or waterlogged (WL) ones. For each genotype, different letters (a, b) indicate significant differences between the MC and T in the same water regime (WW or WL) and (r, s) differences between WW and WL plants for the same tissue (MC or T); (ANOVA, $n = 3$, $p < 0.05$).

Tillers tended to give a lower input to the yield than the main culms of both WW and WL plants (46.4–74.6% less and 43.6–100% less, respectively). Despite a similar number of genotypes that this trend under WW or WL (8 genotypes) conditions showed, the final contribution of the main culm and tillers in the stressed plants incorporated several changes.

Certain genotypes were able to maintain the yield of both the main culm and tillers in WL plants (PL-1, PL-3, PL-5, IT-2, IT-3, IT-4, GR-2, Austrl-1, Austrl-2, and Austrl-4). With stable values in the main culm, the tiller yield increased by 50.1%) in GR-2, while in PL-4 and AdvL-1 it decreased (71.9–100%) with stressed plants. Similarly to AdvL-1, GR-4, AdvL-4, and AdvL-5 were severely affected with no input to the yield by the WL tillers at harvest. In addition, this was concomitant with declines in the main culm's yield of GR-4 (69.6%) and AdvL-4 (75.0%). IT-1, IT-3, and IT-4 suffered simultaneous reductions in the main culm (53.2–75.0%) and in tiller (43.8–96.4%) yields (Figure 6). With opposed the behavior of AdvL-3, the main culm (40%) and tiller (69.2%) yields were increased in WL plants.

### 3.6. Changes in Phenotypic Development during Waterlogging

Regarding plant development, all plants from all genotypes were in an identical stage at the beginning of water treatment (T0), with no observable differences between WW and WL plants (Figure 7). Throughout the 14-day period of waterlogging, all genotypes displayed progress in their growth in both well-watered (WW) and waterlogged (WL) plants. At the end of the water treatment, no developmental delays were perceived for any of the genotypes between the plants exposed to stress and those that were kept in a comfortable water environment. On the contrary, AdvL-4, Austrl-2, Austrl-4, and Austrl-5 showed acceleration in their development in WL plants (Figure 7). In the Austral-2 and Austrl-4 varieties, the main culms of WW plants were at the booting stage (Zadoks growth scale, ZGS 40–49), whereas they had already reached the stage of spike emergence (ZGS 50–59)in WL plants (Figure 7). In Austrl-5, although the WL plants exhibited a higher growth rate, their developmental stage was equivalent to that of WW plants. In the AdvL-4, the ZGS of WW plants corresponded with the spike emergence stage, progressing to the anthesis stage (ZGS 60–69) in WL plants. Despite all the genotypes facing the same 14-day period of waterlogging, which started at the same developmental growth stage (Tillering, ZGS 22–25), their growth rate was not uniform. This resulted in nine genotypes being waterlogged during tillering and stem elongation (PL-1, PL-3, PL-5, IT-3, GR-1, GR-2, GR-3, AdvL-2, and AdvL-3), while others also experienced stress during the booting stage (PL-4 and Austrl-5). In addition, genotypes with faster development rates faced waterlogging events at later growth stages, thereby also suffering stress during the period of spike emergence (PL-2, IT-2, IT-4, AdvL-1, AdvL-5, Austrl-1, Austrl-2, Austrl-3, and Austrl-4) or even during anthesis (IT-1, GR-4, AdvL-4) (Figure 7).

### *3.7. Principal Component Analysis of the Studied Parameters*

A principal component analysis (PCA) was performed on the waterlogged plants to evaluate the similarity between the groups and the correlation among the studied parameters (Figure 8). PC1 accounted for 38.3% of the total variation, while PC2 contributed 19.4%, thus resulting in a combined proportion of 57.7% (Figure 8). The main determinant of the variance in PC1 among genotypes was the plant yield, including the main culm and tillers as well as the number of spikes and the total number of kernels produced by the tillers. Additionally, the single kernel weight (SKW) on tillers and the number of plant kernels also played a role. On the other hand, the development stage reached at the end of waterlogging (ZGS), the main culm SKW, and the kernel number per spike were the key factors associated with the observed variation in PC2.

PCA analysis indicates that the Australian germplasm is distinct from the others, as shown in Figure 8. This analysis also suggests some similarity between the remaining groups (Figure 8). PCA vectors showed several positive correlations between the different parameters. These included the number of spikes per plant and the number of kernels per spike in tillers; plant yield, with tiller yield and SKW (T); number of kernels per plant, both in tillers and in the main culm; and main culm yield, with its number of kernels per spike and SKW. Conversely, the Zadoks growth stage that was achieved at the end of the waterlogging treatment (ZGS) displayed a negative correlation with all the traits related to tillers (except kernel number), with the number of spikes per plant (depending on the number of productive tillers as all the plants presented a yield-contributing main culm), and, finally, with the planet yield (Figure 8).

**Figure 7.** Changes in plant growth development (mean ± SE) evaluated using the Zadoks Growth Scale (ZGS) in the main culm of 23 *T. aestivum* L. genotypes from five germplasm groups with different genetic backgrounds as follows: Portuguese landraces (PL), varieties with the introduction of the Italian germplasm (IT), post-Green Revolution varieties with the introduction of the CIMMYT germplasm (GR), advanced lines (AdvL) from the Portuguese Cereal Breeding Program (INIAV, I.P.), and Australian varieties (Austrl). For each genotype, comparisons were performed on the main culm (MC) under control conditions (WW) or waterlogged (WL) in the beginning (T0) and after 14 days of stress (T14). For each genotype, different letters (a, b) indicate significant differences between WW and WL plants at T0 or T14 and (r, s) differences between T0 and T14 for the same water regime (WW or WL). (ANOVA, $n = 6$, $p < 0.05$).

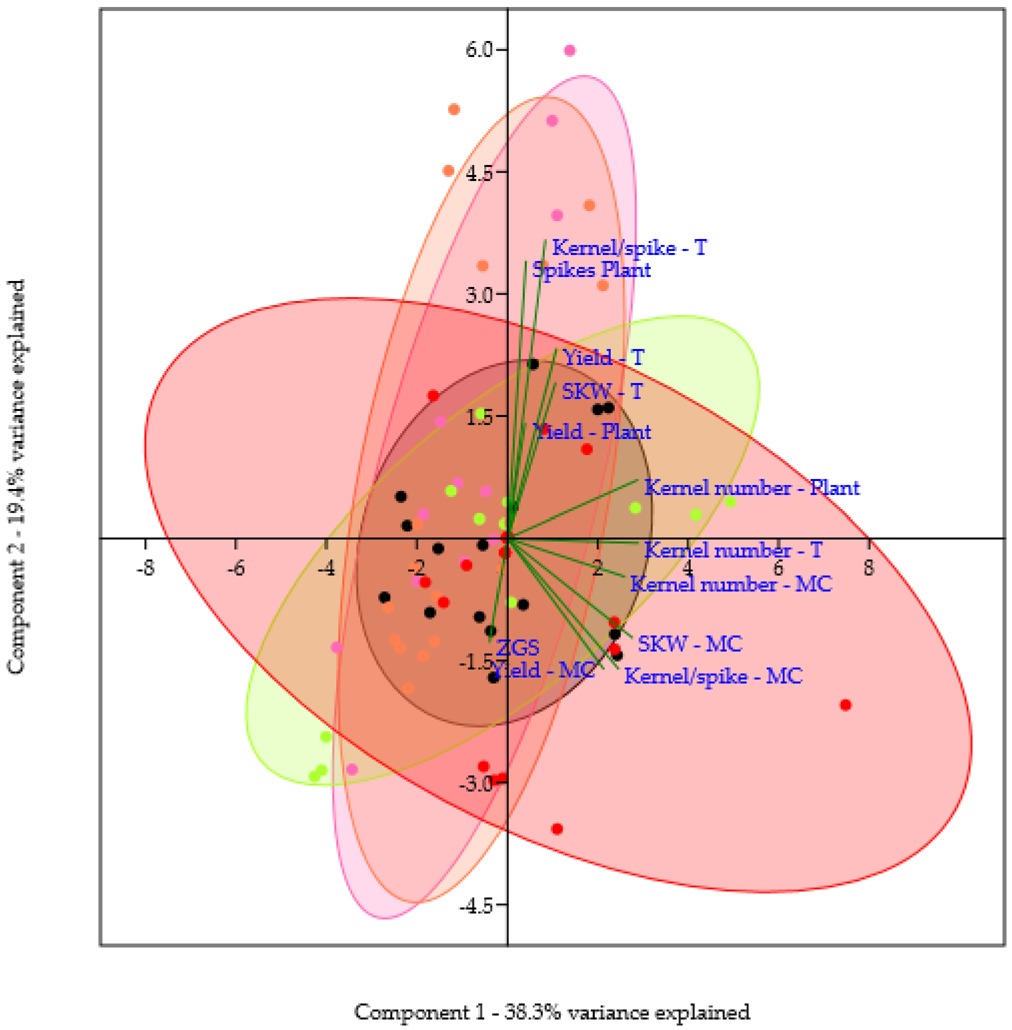

**Figure 8.** Principal component analysis (PCA) for PC1 and PC2 using the biological replicates for each studied parameter in the waterlogged plants. Matrix correlation between groups. ● Portuguese landraces, ● varieties with the introduction of the Italian germplasm (IT), ● post-Green Revolution varieties with the introduction of the CIMMYT germplasm (GR), ● advanced lines (AdvL) from the Portuguese Cereal Breeding Program (INIAV, I.P.), and ● Australian varieties (Austrl). For each genotype, normalized data of the yield (plant, main culm—M, and tillers—T), kernel number (plant, MC, and T), kernels per spike (MC and T), spikes per plant, and single kernel weight (MC and T). collected at harvest, and the development stage achieved at the end of waterlogging (ZGS) were used. ($n = 3$ to 6). Regarding the vectors, if they are in close proximity, thereby forming a small angle, the two variables they represent exhibit a positive correlation. If they intersect at 90°, it is unlikely that they are correlated. When they diverge and form a large angle (nearly 180°), they exhibit a negative correlation.

## 4. Discussion

Wheat yield is influenced by two key factors as follows: the kernel number per plant or unit area and the average size of individual kernels, which are measured by their dry mass or weight [3]. The total number of plant kernels is related to the number of spikes per plant and kernels per spike. In turn, the spike number strongly depends on the fertile tiller amount. Among the genotypes under study, a large variability was observed regarding the number of fertile spikes both in WW and WL plants. This can potentially be attributed to the inclusion of very different germplasm groups, namely landraces, Australian varieties, as well as genotypes obtained by the National Cereal Breeding Program over the past decades. The Portuguese landraces studied are part of a collection (Vasconcelos wheat collection) [52] that resulted from a re-selection of the Portuguese wheat germplasm and is representative of the genetic variability of regional varieties that had been cultivated in the country for centuries [53]. With the launch of the breeding program in 1942, foreign germplasm was introduced, such as the Italian germplasm and the Mexican germplasm (International Wheat and Maize Improvement Center, CIMMYT), thus expanding germplasm variability. While certain varieties were well adapted to the Mediterranean climate (PL and Southern Australian varieties), others were developed to have a high potential under near-optimal environmental conditions (introduction of the CIMMYT semi-dwarf germplasm) [54]. The strong adaptability to uncertain climate conditions of the Mediterranean region may include high-tillering capacity (resulting in an increased number of spikes per plant) alleviating the adverse consequences of suboptimal crop establishment that is caused by delayed drought or premature frost events [40]. On the other hand, the inclusion of semi-dwarfing genes and the release of elite cultivars with a high yield potential led to fewer productive tillers per plant [37] in many of the newly produced cultivars. Furthermore, the recently developed advanced lines may contribute to this extensive range of variation as they incorporate the germplasm from different origins, including from Australia, Italy, Mexico, and Portugal.

In this study, the high variability observed for control plants was also evident under waterlogging. Additionally, stress decreased the number of final fertile spikes in 11 genotypes and increased them in 2 genotypes. The declines are in accordance with several studies where reductions were found due to waterlogging at the tillering stage [14,29,30,46,55]. A reduced spike number was linked to fewer fertile tillers [14,20,21,46,55], which may be attributed to reduced tiller initiation, growth, or/and an increased abortion. Slafer et al. (2014) [50] found that tiller number is the yield component that exhibits the highest degree of plasticity, and environmental constraints can affect its emergence, development, and senescence [56]. In addition, cereals often compensate for yield component [57], and the observed rise in spikes per plant might be attributed to enhanced tillering acting as a compensatory mechanism for adverse climatic conditions, similar to the traits exhibited by some cultivars that are highly acclimated to the Mediterranean climate [40,58].

Waterlogging led in substantial reductions in kernel number per plant in 14 genotypes across all the examined groups. In 10 of these genotypes, these declines were consistent with the drop in the number of spikes, which can be attributed to a fall in tiller number. Our findings align with those demonstrating reported decreases in the number of kernels per plant, with this particular yield attribute being the most affected one [12,21,46,59]. Despite an increase in the spike number of Austrl-2 and the stability in Austrl-1, waterlogging led to reductions in the number of kernels per plant in these genotypes, thereby suggesting a decrease in spikelet and/or floret fertility. Conversely, an increased kernel number per plant in the WL plants of GR-2, AdvL-3, and Austrl-5 did not always result from increased spikes per plant as a stable number of the first two genotypes, as well as an increased number of the latter, were found at the end of the growing cycle. While tillering reduction is a major factor limiting yield, other factors may also affect the yield of waterlogged plants [12,46]. In our study, certain genotypes showed reduced, increased, or unaffected kernel number per spike. These findings support several authors' results that waterlogging decreases the kernel number per spike [15,55,59–61] or that wheat plants' compensation capacity increases it [50]. Certain genotypes can cope with waterlogging, displaying no changes in this trait in stressed plants [17,60]. Our findings in waterlogging tolerance may also be linked to genotype differences in the growth cycle duration. Even though all the genotypes were at the same phenological stage at the beginning of the treatment (Tillering, between ZGS 22 and ZGS 25), plant development may affect the number of days subjected to waterlogging during the period in which the number of kernels per spike is established (20–30 days prior and 10 days after anthesis) [62,63]. During this time, floret primordia differentiate, some degenerate and die, and the number of surviving florets determines the kernels per spike [15,63]. Previous research found that waterlogging during stem elongation (ZGS 30–39) reduced spike growth before anthesis (ZGS 60–69) with a concurrent reduction in the number of fertile florets [21,61]. In our study, changes in kernel number per spike were observed for both the main culm and/or tillers, with the strongest impacts found in the latter (reductions of 29.6–100% and/or increases of 48.8–332.0%).

Despite several authors reporting that in wheat single kernel weight has a lesser influence on yield [12,28] and that changes due to waterlogging were less severe than those observed for the remaining yield traits [12], our findings suggested that 14 days of waterlogging beginning at the tillering stage significantly influenced the single kernel weight of certain genotypes, with decreases and/or increases in the single kernel weight of the main culm's spikes as well as of tillers. Declines of this trait due to waterlogging were previously reported [15,21,48,64], although the effects were not distinguished between the tillers and main culm. As waterlogging can lead to nutrient deficiency [2,19], sensitive genotypes may lack the resources for the spike growth and kernel filling [61,65], thereby lowering the SKW.

In this study, changes in the main culm and tiller yield were caused by variations in one or more yield traits. This is consistent with previous findings that lower tillering or increased tiller mortality reduced the spike number per plant [6,12,14,16,29,44,55,60] and increased floret abortion and/or that infertility reduced kernels per spike [12,18,28,48,55,59,60]. In addition, lighter kernels were also found [48], which were mostly due to the reduced size or/and the inadequate filling related to the reduced assimilates that were stored and poor culm-to-kernel carbohydrate remobilization [12,17,48,64]. Our results point to decreases in the main culm yield of seven genotypes due to a reduction in the kernel number per spike (IT-3, GR-1, GR-3, and Austrl-2), or in the SKW (IT-1, T-2, and AdvL-4), or in both (IT-4). In the dynamics of total tiller participation in the yield, the number of fertile ones significantly affects the final tiller yield. Seven of the nine genotypes with a declining tiller yield had fewer spikes per plant, thereby denoting a reduction in tiller number. However, decreases found in tiller yield were also due to a conjugation of less spikes per plant with lower kernels per spike (PL-4) or a conjugation with a lighter SKW (IT-1).

Among genotypes with an incremented tiller yield under waterlogging (GR-2 and Advl-3), they had an enhanced kernel number per spike, which is consistent with wheat's capacity to increase the kernel number per spike [28] since spikes can differentiate up to 9–10 floret primordia per spikelet [66]. The main culm yield increased in AdvL-3 was due to the single kernel weight.

Our findings pointed to ten genotypes that showed high potential. Among them, eight did not show any changes in the yield of the main culm and tillers (PL-1, PL-5, GR-1, GR-3, AdvL-2, Austrl-2, Austrl-4, and Austrl-5). GR-2 exhibited a rise in tiller yield, and AdvL-3 showed an increase in both the main culm and tiller yield. Overall, the results also suggested that a lower growth rate seems to have a beneficial effect as all of the promising genotypes reached stem elongation or booting by the end of waterlogging period. Moreover, the most significant negative impacts were observed for genotypes with a faster rate of development, with some cases achieving anthesis at the end of stress.

## 5. Conclusions

Bread wheat genotypes exhibited a range of yield-related responses when subjected to 14 days of waterlogging during the tillering stage. Impacts were observed on the number of spikes and kernel number per plant as well as on the main culm, tiller kernels per spike, and weight of individual kernels. Due to tillering decreases or increases, the number of spikes per plant changed significantly. Trait variability was observed within germplasm groups and also between them, with the Italian group being the most affected one. Among the remaining ones, different responses were found, with certain genotypes exhibiting either negative or positive effects, while others were unaffected. Despite the stress that was imposed at the same growth stage, variability in development rates led to different effects, thereby suggesting that the less stages there are that are affected the less frequent and significant the observed impacts will resultantly be. Our study found that six of the eight genotypes that reached stem elongation and 4 of the 6 that reached the booting stage constituted the promising genotypes.

Results may contribute to breeding efforts to enhance wheat yield potential and stability in view of non-optimal growth conditions and increasing climate instability.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

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