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Water Use Strategies and Shoot and Root Traits of High-Yielding Winter Wheat Cultivars under Different Water Supply Conditions

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Abstract: Drought is the most important factor limiting winter wheat yield in the North China Plain (NCP). Choosing high-yielding cultivars is an important measure to minimize the negative effects of drought stress. Field studies were conducted with 10 cultivars in the 2020–2022 seasons under three irrigation treatments (I0, without irrigation; I1, irrigated at jointing stage; I2, irrigated at jointing and anthesis stages) in the NCP to examine the water use strategies and root and shoot traits of high-yielding cultivars under different water supply conditions. The results showed that yield variation among cultivars was 21.2–24.6%, 23.7–25.9% and 11.6–15.3% for the I0, I1 and I2 treatments, respectively. Under water deficit conditions (I0 and I1), high-yielding cultivars reduced water use during vegetative stages and increased soil water use during reproductive stages, especially water use from deeper soil layers. Those cultivars with higher root length density (RLD) in deep soil layers exhibited higher water uptake. Each additional millimeter of water used after anthesis from the 100–200 cm soil layers increased grain yield by 23.6–29.6 kg/ha and 16.4–28.5 kg/ha under I0 and I1, respectively. This water use strategy enhanced dry matter accumulation after anthesis, decreased canopy temperature (CT) and increased relative leaf water contents (RLWC), which ultimately improved grain yield. For winter wheat grown under I2, cultivars that decreased water use after anthesis had higher water productivity (WP). Root length (RL), root weight (RW) and root:shoot ratio were each negatively correlated with grain yield, while above-ground biomass was positively correlated with grain yield. Therefore, higher dry matter accumulation and smaller root systems are two important traits of high-yielding cultivars under sufficient water supply conditions (I2) in the NCP.

Keywords: winter wheat; grain yield; soil water use; root system; dry matter accumulation; canopy temperature

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1. Introduction

Winter wheat (*Triticum aestivum* L.) is the most widely grown wheat crop in the world, providing approximately 20% of the human daily calorie and protein demand [1]. Thus, this crop plays an important role in maintaining global food security [2]. However, increasing in temperature, decreasing in rainfall in the future make drought become the most important abiotic stress factors affecting winter wheat yield in worldwide [3–6]. Many studies have indicated that choosing better cultivars is a viable strategy for coping with drought stress [7–9].

Blum et al. [10] showed that the genetic gains in increased yields under water-limited conditions were related to soil water use. More-recent cultivars were able to absorb soil water from deeper soil layers after the jointing stage and contribute to high above-ground biomass [11,12]. Lu et al. [13] determined that under limited water supply conditions, cultivars that could reduce water use during the vegetative growth stage and increase water use during the reproductive growth stage were beneficial for increasing yield, while under well-irrigated conditions, high-yielding cultivars increased water use during the pre-anthesis as well as post-anthesis stages [14]. Figueroa-Bustos et al. [15] showed that under terminal drought conditions (drought stress occurring after anthesis), a high-yielding cultivar (Tincurrin) reduced water use in the early growth stage, while under an early-season drought condition (drought stress occurred 20–32 days after emergence), the same cultivar (Tincurrin) did not show high grain yield. Thus, the water consumption strategies of high-yielding cultivars depend on soil water conditions. Therefore, it is necessary to study the water use strategies of high-yielding cultivars under specific growing environments and conditions.

Plant-available soil water at sowing and seasonal rainfall can determine the grain yield of winter wheat under drought conditions [11,16]. The distribution of the root system along the soil profile plays an important role in soil water uptake [17]. In the North China Plain (NCP), the rooting depth of winter wheat can exceed 2.0 m at the anthesis stage [18]. Our previous studies have revealed high variation in the root system traits of modern wheat cultivars [19]. A smaller root length density (RLD) in the deep soil profile can restrict crop water use, resulting in more soil water being left unused at harvest [20]. Cultivars with greater root biomass and greater RLD in deeper soil layers exhibited enhanced soil water absorption after anthesis, contributing to high grain yield [21], while, a large root system in top soil layers can result in excessive water use during vegetative stages, having a negative influence on grain yield [22]. In addition, some studies indicated that roots are the major sink for assimilates, requiring more than 50% of the photosynthate to produce dry matter [23]. Cultivars with large root biomass would result in a yield penalty [24]. Thus, a comprehensive understanding of the relationships between root traits with soil water use and grain production is of great importance for choosing cultivars with higher grain yield under specific conditions.

Although root systems have important traits that are correlated with soil water uptake and grain yield, choosing cultivars based on root traits is difficult owing to a lack of direct and effective methods for studying root systems [25,26]. Root phenotyping has been mainly applied to plants growing in containers in the laboratory or greenhouses [27]. However, these controlled environments are quite different from field conditions [28]. Fortunately, there are strong correlations between root and shoot traits, and deep root traits can be indirectly estimated from above-ground traits. For example, it has been reported that a deep root system can increase soil water use after anthesis, thus delaying the senescence of the flag leaf, which can thereby maintain photosynthetic activity [29]. A higher leaf chlorophyll content (SPAD) at the late grain filling stage can reflect a stronger root water uptake ability and could accordingly be used as an indicator of deep-rooted and high-yielding cultivars [13]. Canopy temperature (CT) was found to be related to rooting depth and can be used as a powerful physiological selection tool [30]. Given the difficulty in the direct evaluation of root systems, it is also worth investigating the shoot traits of high-yielding cultivars under field conditions [31].

The NCP is one of the most important agricultural regions in China and provides more than half of China's wheat production [32]. Winter wheat and summer maize form the annual double cropping rotation system of the region. The NCP has a typical monsoon climate, with about 70–80% of the annual rainfall occurring in summer. The rainfall during the winter wheat growing season is typically about 60–180 mm, significantly less than the water requirements, which range from 430 to 500 mm [33,34]. Winter wheat is vulnerable to drought stress. Abundant rainfall during summer replenishes the soil moisture before winter wheat planting. Some studies have shown that stored soil water contributed 60–80% of crop water use under rainfed conditions, demonstrating that full use of stored soil water before sowing can help to meet crop water requirements and improve grain yield [34,35]. However, grain yield was not only affected by the total amount of stored soil water but also by its allocation during the growing period. Therefore, the objectives of this study were (1) to investigate the effects of water use strategies (i.e., pre- and post-anthesis water use) on grain yield and water productivity (WP) of winter wheat cultivars and (2) to assess the relationships of root and shoot traits with soil water use and grain yield under different water supply conditions. The study findings provided useful information for choosing high-yielding cultivars in arid and semi-arid areas.

2. Materials and Methods

2.1. Site Description

The experiments were conducted at Liujiazhuang (38.03° N, 114.53° E; elevation 50 m, Site 1) and Zhaozhuang (38.01° N, 114.41° E; elevation 50 m, Site 2) of Gaocheng City, Hebei Province, China, during the 2020–2021 and 2021–2022 winter wheat growing seasons, respectively. The two experimental stations are the research farms of Hebei Agricultural University, located in the northern part of the NCP at the base of Taihang Mountain. The meteorological characteristics of the two stations are similar, representing the typical monsoon climate of the NCP. Winter wheat (October to the beginning of the following June) and summer maize (June to September) form the annual double-cropping system. The annual rainfall is about 482 mm, with 70% of the rainfall falling in the summer maize season. The mean rainfall during the winter wheat season was 128.1 mm over the past 33 years. Water deficit usually occurs during the winter wheat growing season.

The soil is loamy and well-drained, with an average field capacity of 26.1% and 26.7% (determined gravimetrically) for the top 2 m soil profile of Site 1 and Site 2, respectively (Table 1). The nutrient contents in the topsoil tillage layer (0–20 cm) of the experimental field were measured as described by Li et al. [29] and are listed in Table 1. The soil bulk density was determined according to the method of Jabro et al. [36], and it was 1.33, 1.56, 1.55, 1.52, 1.58, 1.59, 1.45, 1.44, 1.44 and 1.44 g/cm^3 at Site 1 and 1.36, 1.47, 1.48, 1.45, 1.51, 1.55, 1.59, 1.55, 1.55 and 1.58 g/cm^3 at Site 2 for each 20 cm soil layer from 0 to 200 cm, respectively.

Table 1. Characteristics of soil at two experimental stations during the 2020–2022 seasons.

Sites	Bulk Density (g/cm^3)	Field Capacity (g/g)	Saturated Moisture (%)	Organic Matter (g/kg)	Ava. N (mg/kg)	Ava. P (mg/kg)	Ava. K (mg/kg)
Site 1	1.49	0.261	43.77	17.3	80.5	18.6	197.1
Site 2	1.51	0.267	43.02	18.3	86.1	18.0	189.3

2.2. Experimental Design and Field Management

During the 2020–2022 winter wheat growing seasons, 10 recently certified cultivars were used for the test, namely Liangxing66 (LX66), Shijiazhuang8 (SJZ8), Shimai22 (SM22), Heng4399 (H4399), Jimai585 (JM585), Jimai22 (JM22), Hengguan35 (HG35), Cangmai6002 (CM6002), Shiyou20 (SY20) and Kenong199 (KN199). The approximately 0.45 ha experimental area was divided into three main plots for three irrigation regimes. Between the two main plots, there was an unirrigated 2 m buffer zone to limit water movement. Each part was planted with 10 cultivars in a randomized plot design with three replicates, and each plot was 45 m^2 in area. The three irrigation regimes were as follows: I0 (no irrigation during the whole growing season, i.e., rainfed conditions); I1 (one period of irrigation at the jointing stage, i.e., limited water supply conditions); and I2 (two periods of irrigation at the jointing and anthesis stages, i.e., sufficient water supply conditions). The amount of irrigation was 80 and 70 mm/application in the 2020–2021 and 2021–2022 seasons, respectively, and the plots were not irrigated before seeding. Irrigation was conducted with a plastic hose connected to a low-pressure water transportation system that obtained water from a well. (The groundwater table was 50 m below the soil surface of the two study sites). A water flow meter was installed in the surface irrigation system to control the amount of water used for each plot. All other field management practices were the same for all treatments, except for the irrigation.

Winter wheat seed was sown by a hand-operated seeding machine on 6 October 2020 and 18 October 2021 and harvested on 6–10 June 2021 and 13–15 June 2022, respectively. Row spacing was 15 cm, and plant density was 345 plants/m^2 in the two seasons. In both years, fertilizers were applied based on local practices. Specifically, each plot was fertilized with a basal dose of 260.7 kg/ha of triple superphosphate (containing 46.0% P_2O_5) and 199.0 kg/ha of potassium chloride (containing 60.0% K_2O) before sowing. For the irrigation treatments, 260.8 kg/ha of urea (containing 46.0% N) was applied before sowing, with another 260.8 kg/ha of urea (containing 46.0% N) top-dressed during the jointing stage in early April during irrigation. For the no-irrigation treatment, all the urea (containing 46.0% N) was applied before sowing. Herbicides and pesticides were applied as necessary to ensure that the growth of winter wheat was free of weeds, diseases and insect problems.

2.3. Measurements

2.3.1. Weather Conditions

A standard meteorological station near the experimental site was used to collect daily weather data, including daily average temperature (T_{ave}, °C), sunshine hours (SHr, h), wind speed (u_2, m/s), relative humidity (%), rainfall (mm) and solar radiation (W/m^2). Daily reference evapotranspiration (ET_0, mm) was calculated with the crop-water program developed by FAO using the Penman–Monteith equation, which represented the definition of the hypothetical grass reference (albedo = 0.23, height = 0.12 m, surface resistance = 70 s/m) [37]. ET_0 was calculated based on the following equation:

$$ET_0\ (\mathrm{mm}) = \frac{0.408\Delta(R_n - G) + \gamma \frac{900}{T_{ave}+273}\, u_2(e_s - e_a)}{\Delta + \gamma\ (1 + 0.34\ u_2)} \tag{1}$$

where R_n and G are the net radiative flux density (W/m^2) and the soil heat flux density (W/m^2), respectively. γ is the psychrometric constant (Pa/°C), u_2 is the wind speed at 2 m height (m/s), T_{ave} is the average daily air temperature at 2 m height (°C), e_s is the saturated vapor pressure (kPa), e_a is the actual vapor pressure (kPa) and Δ is the slope of the vapor pressure curve (kPa/°C).

Crop potential evapotranspiration (ET_p, mm), which can be regarded as the maximum value of seasonal evapotranspiration under ideal conditions, was calculated as follows:

$$ET_p\ (\mathrm{mm}) = ET_0 \times K_c \tag{2}$$

where K_c was 0.93 for the whole growth period of winter wheat according to Liu et al. [38].

2.3.2. Leaf Area Index

Phenological developments, including anthesis and maturity, were observed and recorded for the different cultivars based on the appearance date when 50% of plants reached that particular stage [39]. All plants within 1 m^2 were harvested by cutting at ground level at anthesis. Thereafter, 15–20 stems were representatively selected to determine the leaf area (LI-3000C, LI-COR Inc., Lincoln, NE, USA) for each plot. The crop density of each plot was monitored to calculate the leaf area index (LAI). The plant materials were then dried to a constant weight in a forced-draft oven at 80 °C to determine dry matter at anthesis.

2.3.3. Canopy Temperature, Chlorophyll Relative Content and Relative Leaf Water Content

Canopy temperature (CT, °C) was measured with a handheld infrared thermometer (THERMO SHOT F30, Tokyo, Japan) once a week from anthesis (Zadoks scale 64–65) to the late grain-filling stage (Zadoks scale 77) with emissivity set at 0.98. The thermal images were collected between 12:00–14:00 on cloudless and windless days with the view set to 45° relative to the canopy and shot vertically downward. Leaf chlorophyll content (SPAD) was measured using a SPAD-502 chlorophyll meter (Minolta, Tokyo, Japan) in the middle of the flag leaves of 30 stems during anthesis (Zadoks scale 64–65) and the middle grain-filling stage (Zadoks scale 75–76) for each plot. Each treatment had three replicates. The average value of each measurement was used as the CT and SPAD of the grain-filling stage for each cultivar.

At the middle grain-filling stage (Zadoks scale 75–76), the relative leaf water content (RLWC, %) of flag leaves was determined according to the method of Zegaoui et al. [40]. The fresh weight (FW, g) was weighted immediately after sampling 10 flag leaves for each plot. Leaves were then placed in distilled water for 12 h at 4 °C in the dark and turgid weight (TW, g) was measured after all leaves had been fully hydrated. Then, the leaves were dried in an oven for 30 min at 105 °C. Afterward, all plant samples were oven-dried at 80 °C to a constant weight to determine their dry weight (DW, g). RLWC was calculated based on the following equation:

$$\text{RLWC (\%)} = (\text{FW} - \text{DW})/(\text{TW} - \text{DW}) \times 100 \quad (3)$$

2.3.4. Root Sampling

Roots were measured during the grain-filling stage (223–229 and 211–215 days after sowing in 2020–2021 and 2021–2022, respectively) under I0 and I2 irrigation treatments. Three sites for each cultivar from the soil surface down to 200 cm were sampled using a 10 cm diameter soil corer [13]. The cores were taken to the laboratory and washed manually using a sieve with 0.25 mm apertures to obtain the live roots. Root length (RL, km/m^2) was measured based on the line-intersect method using a 1.27 cm grid after the roots were separated from other debris [41,42]. Subsequently, root samples were oven-dried to a constant weight at 80 °C to determine the dry weight (RW, g/m^2). The root length density (RLD, cm/cm^3) and root weight density (RWD, mg/cm^3) at different depths were calculated as the RL and RW divided by sampled soil volume, respectively.

2.3.5. Soil Water Depletion, Evapotranspiration and Water Productivity

Gravimetric soil water content (GSWC, %) was measured using the oven-drying method. During the winter wheat growing season, soil samples of each cultivar were collected at sowing, anthesis and maturity stages to a depth of 200 cm in 20 cm increments for GSWC determination. Each treatment had three replicates. Soil water storage (SWS, mm) for a given soil layer was calculated as follows [12]:

$$\text{SWS} = \text{GSWC} \times \text{BD} \times \text{SD} \quad (4)$$

where BD is the soil bulk density (g/cm^3) and SD is the soil depth (mm).

Soil water depletion (SWD, mm) is the change in SWS during a particular period for a given soil layer. In this study, changes in SWD were calculated as the difference in SWS from sowing to anthesis, anthesis to maturity and from sowing to maturity for the 0–100 cm (SWD1, mm), 100–200 cm (SWD2, mm) and 0–200 cm (SWD3, mm) soil layers.

Evapotranspiration (ET, mm) was calculated using the soil-water balance method as follows [43]:

$$\text{ET} = \text{P} + \text{I} + \text{SWD} + \text{CR} - \text{R} - \text{D} \quad (5)$$

where ET is the crop water use during a certain growing period (mm) and P is the rainfall (mm). I is irrigation amount (mm) and SWD is the change of SWS at the start of a period minus that at the end of a period for the 200 cm soil profile (mm). CR is capillary rise to the root zone (mm), R is runoff (mm) and D is drainage from the root zone (mm). CR was assumed to be negligible due to the groundwater table being below 50 m. Runoff was not observed due to the experimental plot being flat. D was taken as zero due to the low rainfall amount and limited irrigation conditions. Thus, ET = P + I + SWD was used in this experiment. Water productivity (WP, kg/m^3) was defined as the grain yield production per unit of water consumption, and was calculated as follows [44]:

$$WP = Y/ET/10 \tag{6}$$

where Y is the final grain yield (kg/ha) and ET is the actual crop water use during the whole growing season (mm). The factor of 10 is used to convert ET in mm into water volumes per land surface in m^3/ha.

2.3.6. Grain Yield and Above-Ground Biomass

At maturity, a 4 m^2 area in the middle of the experimental plot was harvested and all the plants were threshed by a thresher in order to obtain the grains. Grains were air-dried to a constant moisture content of 13%, then the grain yield was determined. Above-ground biomass at this stage was monitored using conventional methods.

2.4. Statistical Analysis

Significant differences in the mean values were determined by a Duncan test at $p < 0.05$. The relationships between grain yield, WP and root:shoot ratio, and the relationships between grain yield, RL, RW and soil water consumption as well as the relationships between CT and RL were analyzed by linear correlation analysis. The relationships between root traits, shoot traits, grain yield and WP were analyzed by a Pearson's correlation using RStudio software (Version 4.2.3, RStudio Inc., Boston, MA, USA). Data analysis was carried out using Microsoft Excel 2019 (Microsoft, Redmond, CA, USA) and IBM SPSS Statistics 23 (IBM, Stanford, CA, USA), and figures were created in SigmaPlot (Version 14.0, Systat Software Inc., San Jose, CA, USA) and Origin 9.0 (Origin Lab Corporation, Northampton, MA, USA).

3. Results

3.1. Weather Conditions during the 2020–2022 Winter Wheat Growing Seasons

Figure 1 shows the daily reference evapotranspiration (ET_0), daily average temperature (T_{ave}), accumulated rainfall and sunshine hours (SHr) during the winter wheat growing seasons. The seasonal ET_0 was 576.8 mm in 2020–2021 and 588.1 mm in 2021–2022 (Figure 1A). The T_{ave} was 9.1 °C during the 2020–2021 season and 9.3 °C during the 2020–2022 season (Figure 1B). The ET_0 and T_{ave} values fluctuated greatly from jointing to the grain-filling stage in the second season, which had a negative influence on seed formation. Most of the annual rainfall fell in the summer seasons, and the average soil water content was greater than 80% of the field capacity in the 0–200 cm soil layer before sowing (Figure 2). However, the mean rainfall during winter wheat seasons was only 74.5–75.6 mm, which was much lower than the 33-year average of 128.1 mm, especially after the jointing stage (Figures 1C and 2). The rainfall during anthesis to maturity was only 9.6 and 24.4 mm for 2020–2021 and 2021–2022, respectively; while, from recovery to jointing, the rainfall in 2020–2021 was 25.2 mm, higher than that in 2021–2022, which was 2.5 mm. The seasonal SHr in the two seasons were 1564.7 and 1641.8 h, respectively (Figure 1D). The results indicated that there were large variations in weather factors during the winter wheat growing season and the winter wheat crop was vulnerable to water stress due to the low rainfall and high ET_0 after anthesis in both seasons.

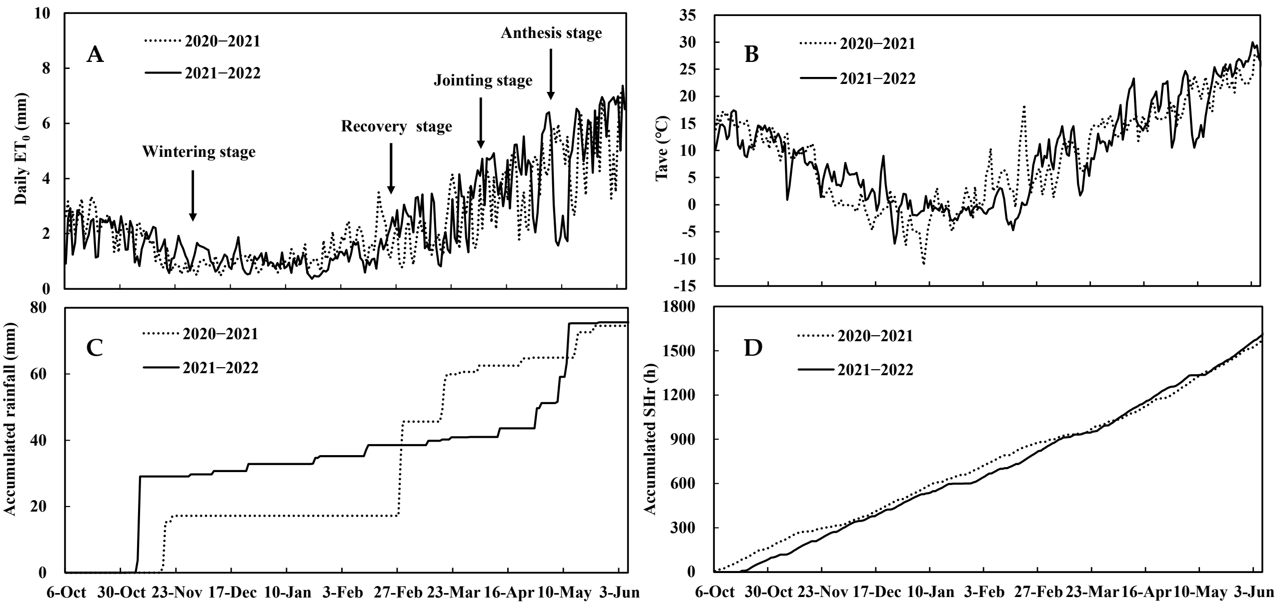

Figure 1. Site meteorological parameters daily reference evapotranspiration (ET_0) (**A**), daily average temperature (T_{ave}) (**B**), accumulated rainfall (**C**) and accumulated sunshine hours (SHr) (**D**) during the 2020–2022 seasons.

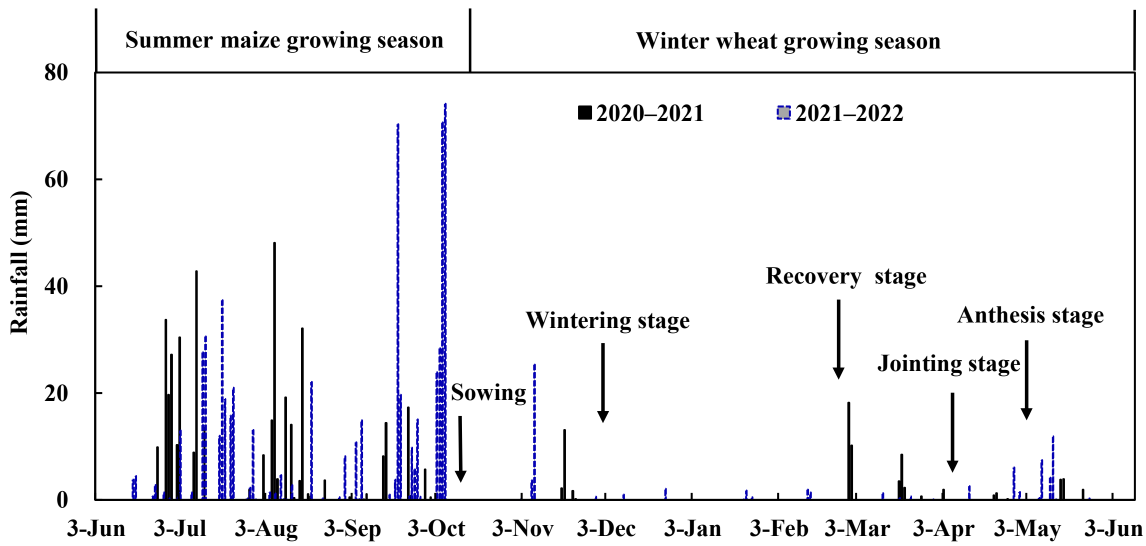

Figure 2. Annual daily rainfall during the 2020–2022 seasons.

3.2. Grain Yield and Water Productivity of Different Cultivars

The environmental conditions combined with irrigation treatments and cultivars resulted in a wide range of grain yields (Figure 3). Averaged across the 10 cultivars, the mean grain yield was increased by 20.2% from I0 to I1 and by 4.0% from I1 to I2 in 2020–2021. The values were 16.0% and 4.5% in 2021–2022, respectively. The results indicated that one irrigation at the jointing stage significantly improved grain yield. In contrast, the increase in grain yield became smaller with further irrigation application. There was a significant variation in grain yields among contemporary cultivars. The yield variations among cultivars were 21.2–24.6%, 23.7–25.9% and 11.6–15.3% for I0, I1 and I2, respectively. The largest yield differences between cultivars were 1484.3, 2077.2 and 1041.3 kg/ha under I0, I1 and I2 in 2020–2021, and the values were 1698.9, 1892.3 and 1293.6 kg/ha in 2021–2022, respectively. Results indicated that choosing better cultivars was necessary to mitigate the adverse effects of climate and water deficit.

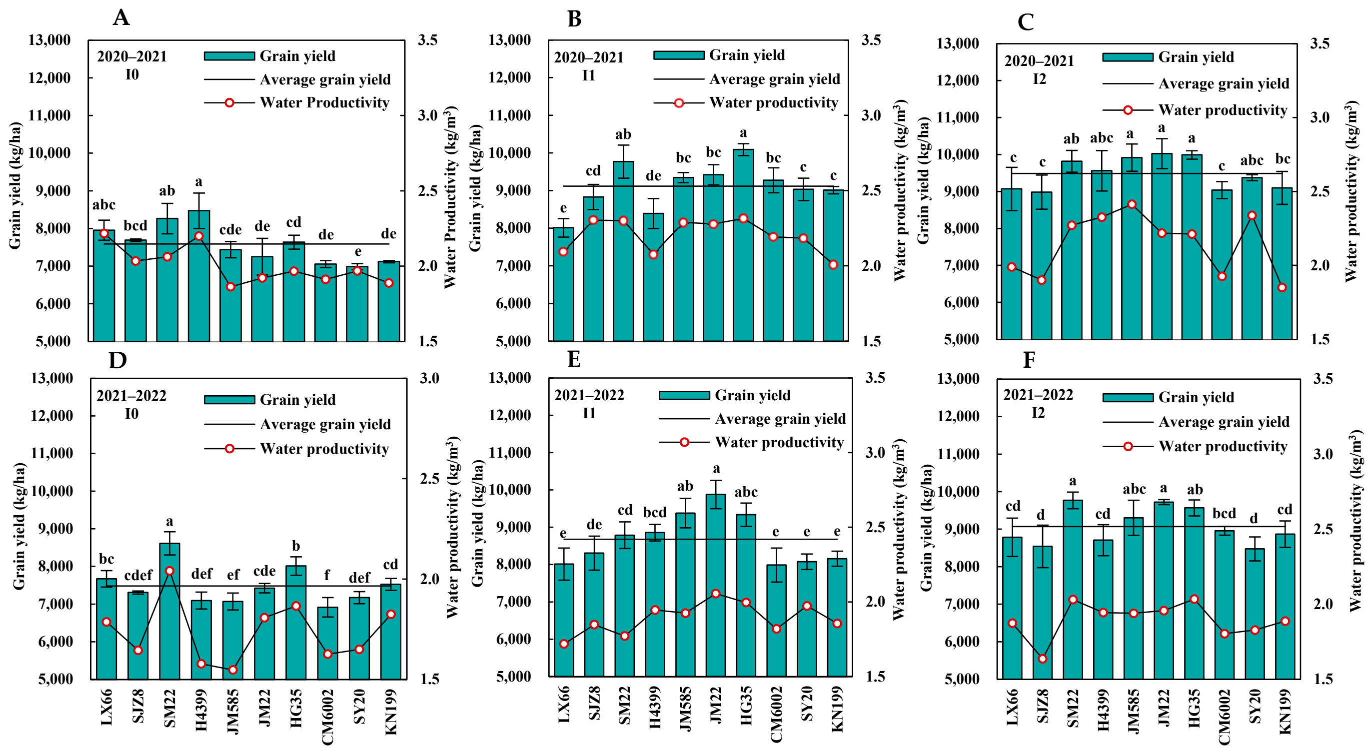

Figure 3. Grain yield, average grain yield of the 10 cultivars and water productivity (WP) of the 10 cultivars under no irrigation (**A**,**D**), one irrigation (**B**,**E**) and two irrigations (**C**,**F**) during the 2020–2022 seasons (Bars represent the standard deviation of three replicates. The different lowercase letters for the 10 cultivars in the same irrigation treatment indicates a significant difference at $p < 0.05$).

The performance and ranking of cultivars were influenced by both environmental factors and genotypes. In general, among the cultivars, SM22 and HG35 always had the greater grain yields, while CM6002 and SY20 always had the lower grain yields under the three irrigation treatments in both seasons. On average, the grain yield of high-yielding cultivars was 13.2%, 8.5% and 7.6% higher than that of the low-yielding cultivars for I0, I1 and I2 in 2020–2021; the corresponding values were 18.0%, 12.8% and 10.9% in 2021–2022, respectively. In addition, LX66 achieved higher grain yield under I0, but had relatively lower grain yield under the irrigation treatments, indicating this cultivar was more suitable for rainfed conditions. On the contrary, JM585 and JM22 achieved relatively higher grain yields under irrigation treatments, while obtaining relatively lower grain yields under rainfed conditions. This indicates that these two cultivars were more suitable for sufficient water supply conditions. The response of the remaining cultivars (SJZ8, H4399 and KN199) varied among irrigation levels and growing seasons, indicating those cultivars were more sensitive to environmental factors. Figure 4 reveals significant positive correlations between water producitivity (WP) and grain yield during the two seasons, indicating that cultivars with high grain production generally have high WP.

3.3. Crop Water Use and Soil Water Depletion of Different Cultivars

Figure 5 shows the seasonal crop water use (ET), soil water depletion (SWD) and contribution of SWD to the seasonal ET of the 10 cultivars under I0, I1 and I2 during the 2020–2022 seasons. In both seasons, seasonal ET increased with the increase in irrigation application, and for I2, it was 82.9–84.1% of the ET_p, which can be considered the optimal water condition for the highest yield (Figure 5C,F) [43]. In both seasons, the contribution of SWD to the seasonal ET decreased with the increase in water supply. On average, SWD contributed 80.3% and 82.5% of the seasonal ET for I0, 62.6% and 68.2% for I1 and 47.1%

and 55.0% for I2 in 2020–2021 and 2021–2022, respectively. The results indicated that the stored soil water before winter wheat sowing plays an essential role in crop water use, especially under rainfed and limited water supply conditions.

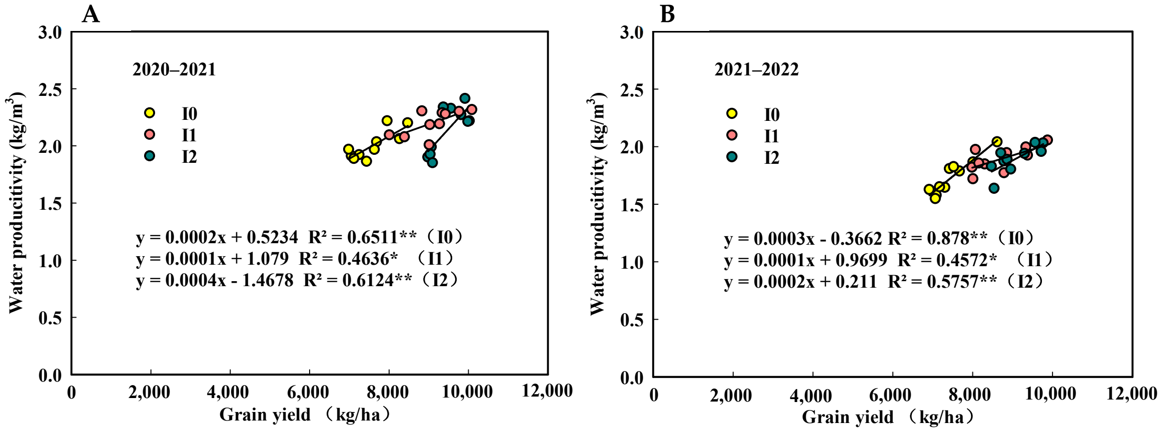

Figure 4. Relationships between water productivity (WP) and grain yield under no irrigation (I0), one irrigation (I1) and two irrigations (I2) during the 2020–2021 (**A**) and 2021–2022 (**B**) seasons (* significant at $p < 0.05$; ** significant at $p < 0.01$).

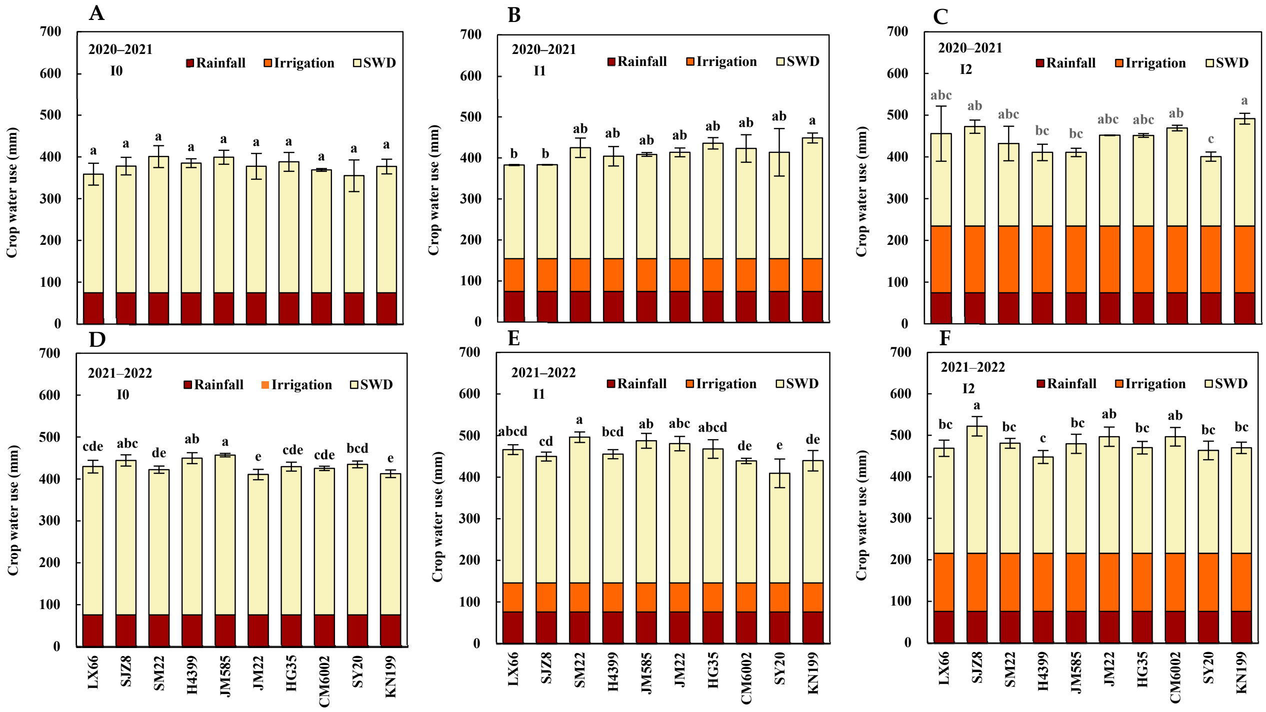

Figure 5. Crop water use during sowing to maturity under no irrigation (I0) (**A**,**D**), one irrigation (I1) (**B**,**E**) and two irrigations (I2) (**C**,**F**) during the 2020–2022 seasons (Bars represent the standard deviation of three replicates. The different lowercase letters for the 10 cultivars in the same irrigation treatment indicates a significant difference at $p < 0.05$).

As shown in Figure 5A, there was no significant difference in SWD or seasonal ET during the whole growth stage among the 10 cultivars under I0 during the 2020–2021 season. However, the allocation of SWD and ET during pre- and post-anthesis significantly differed among the cultivars, which can influence yield formation. As shown in Figure 6, the crop water use at sowing to anthesis was higher than that at anthesis to maturity of winter wheat cultivars, especially under I0 during the two seasons (Figure 6A,B). Irrigation at the jointing stage promoted the absorption of soil water during the reproductive stages (Figure 6C,D). In general, 21.9–51.8% and 20.4–39.3% of SWD was used after anthesis under I0, 61.1–73.5% and 44.8–61.2% under I1 and 44.9–72.0% and 32.5–56.3% under I2 in 2020–2021 and 2021–2022, respectively. The rainfall was only 9.6 and 24.4 mm during anthesis to maturity in 2020–2021 and 2021–2022, respectively, substantially lower than the crop water requirements. Under rainfed conditions, cultivars with more soil water consumption before anthesis would lead to less water available after anthesis, which had a negative influence on yield formation.

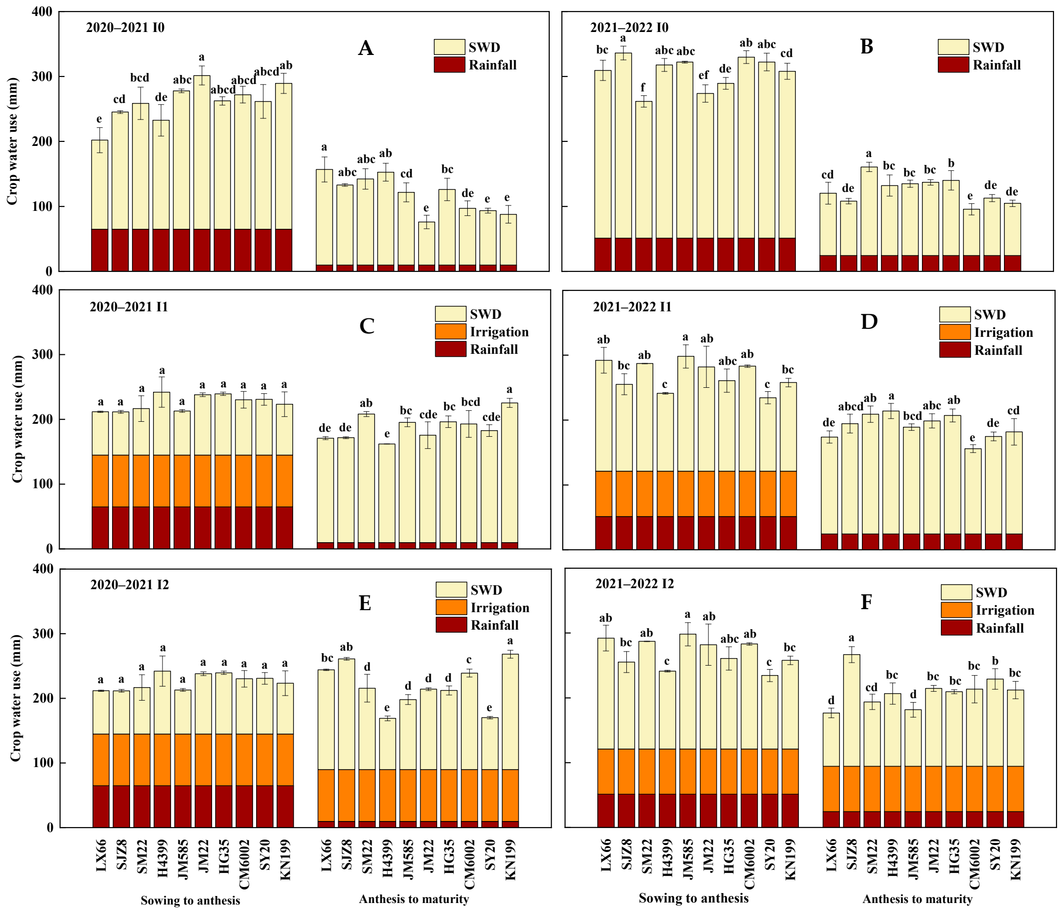

Figure 6. Crop water use during sowing to anthesis and anthesis to maturity under no irrigation (I0) (**A**,**B**), one irrigation (I1) (**C**,**D**) and two irrigations (I2) (**E**,**F**) during the 2020–2022 seasons (Bars represent the standard deviation of three replicates. The different lowercase letters for the 10 cultivars in the same stage indicates a significant difference at $p < 0.05$).

3.4. Influences of Pre- and Post-Anthesis Water Consumption on Grain Yield and Water Productivity

Regulating the proportion of soil water consumption between pre- and post-anthesis was necessary to obtain high grain yield under rainfed conditions. In the 2021–2022 season, for example, the soil water consumption was 238.2 and 278.6 mm at sowing to anthesis for HG35 (high-yielding cultivar) and CM6002 (low-yielding cultivar) under I0, respectively. However, at anthesis to maturity, the soil water consumption was 115.7 and 71.2 mm for HG35 and CM6002, respectively (Figure 6B). Thus, HG35 used 40.4 mm less soil water during its vegetative stage, while it extracted 44.5 mm more soil water during its reproductive stage compared with CM6002. Overall, the low soil water consumption before anthesis led to more water being available after anthesis, resulting in increased grain production. Specifically, the grain yield and WP of HG35 were 15.9% and 14.8% higher than those of CM6002 (Figure 3D). Even so, the stored soil water in the subsoil layers was not fully utilized by the high-yielding cultivar.

Correlation analysis between soil water consumption in different soil layers during pre- and post-anthesis with both grain yield and WP among the 10 cultivars was conducted for the 2020–2022 seasons. As shown in Table 2, from sowing to anthesis, there were significant and negative relationships between soil water consumption in the 0–100 cm (SWD1) and 0–200 cm (SWD3) soil layers with either grain yield or WP under I0 in 2020–2021. In addition, significant and negative relationships were also found between soil water consumption in the 100–200 cm (SWD2) and 0–200 cm (SWD3) soil layers with either grain yield or WP under I0 in 2021–2022. However, from anthesis to maturity, the soil water consumption in the 100–200 cm (SWD2) soil layers was significantly positively correlated with grain yield under I0 and I1 in both seasons. Each additional millimeter of water extracted from the 100–200 cm soil layers after anthesis generated an extra grain yield of 23.6–29.6 kg/ha and 16.4–28.5 kg/ha under I0 and I1, respectively (Figure 7). Furthermore, across all whole growth stages, positive relationships between soil water consumption in the 0–200 cm (SWD3) soil layers and grain yield were also observed under I1 in both seasons. Table 2 also indicates grain yield and WP were positively correlated with the ratio of post-anthesis water consumption to seasonal ET (ET-post/ET), but negatively correlated with the ratio of pre-anthesis water consumption to seasonal ET (ET-pre/ET) under I0 in both seasons. Under the I2 treatment, from anthesis to maturity, there were significant negative relationships between soil water consumption in the 0–100 cm (SWD1) and 0–200 cm (SWD3) soil layers with WP in both seasons. A significantly negative relationship was also found between ET-post/ET and WP in 2020–2021. These findings indicated that some cultivars used less soil water during vegetative stages and extracted more soil water during reproductive stages, especially from deep soil layers, which benefited the increase in grain production under water deficit conditions (I0 and I1). While cultivars with lower soil water use after anthesis were conducive to increasing WP under sufficient water supply conditions.

3.5. Relationships between Root and Shoot Traits and Soil Water Use and Grain Yield

3.5.1. Root Traits

The spatial distribution of root system determines the ability of crop to absorb soil water. As shown in Figure 8, the mean root length density (RLD) of winter wheat among cultivars declined with increasing soil depth in the 0–200 cm soil layers. Most of the root systems were concentrated in the 0–40 cm soil layers. Drought stress conditions generally promote the growth of the root systems in deeper soil layers. In both seasons, I0 produced higher RLD than I2 in the 100–200 cm soil layers. Regardless, the RLD in deep (100–200 cm) soil layers was always lower than 0.8 cm/cm3, which restricted the full use of the soil water by winter wheat [45].

Table 2. Correlations between soil water consumption in the 0–100 cm (SWD1), 100–200 cm (SWD2) and 0–200 cm (SWD3) soil layers during pre- and post-anthesis, and the ratio of pre-anthesis (ET-pre) and post-anthesis (ET-post) water consumption over the seasonal crop water use (ET) with both grain yield and water productivity (WP) of winter wheat under no irrigation (I0), one irrigation (I1) and two irrigations (I2) during the 2020–2022 seasons.

Seasons			**From Sowing to Anthesis**			**From Anthesis to Maturity**			**From Sowing to Maturity**			**ET-Pre/ET**	**ET-Post/ET**
			SWD1	**SWD2**	**SWD3**	**SWD1**	**SWD2**	**SWD3**	**SWD1**	**SWD2**	**SWD3**		
2020–2021	I0	Grain yield	– **	NS	– *	*	**	**	NS	*	NS	– **	**
		WP	– **	– *	– **	*	*	**	– *	NS	NS	– **	**
	I1	Grain yield	NS	– *	NS	NS	*	NS	NS	NS	*	NS	NS
		WP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	I2	Grain yield	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		WP	NS	NS	NS	– *	– **	– **	NS	– *	– **	**	– **

Table 2. *Cont.*

Seasons			From Sowing to Anthesis			From Anthesis to Maturity			From Sowing to Maturity			ET-Pre/ET	ET-Post/ET
			SWD1	SWD2	SWD3	SWD1	SWD2	SWD3	SWD1	SWD2	SWD3		
2021–2022	I0	Grain yield	NS	– **	– **	NS	*	*	NS	NS	NS	– *	*
		WP	NS	– **	– **	NS	NS	NS	– *	NS	– *	– *	*
	I1	Grain yield	NS	NS	NS	NS	*	*	NS	*	*	NS	NS
		WP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	I2	Grain yield	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS
		WP	NS	NS	NS	– *	NS	– *	NS	NS	NS	NS	NS

NS: not significant; * significant at $p < 0.05$; ** significant at $p < 0.01$; '–' meaning negative correlation.

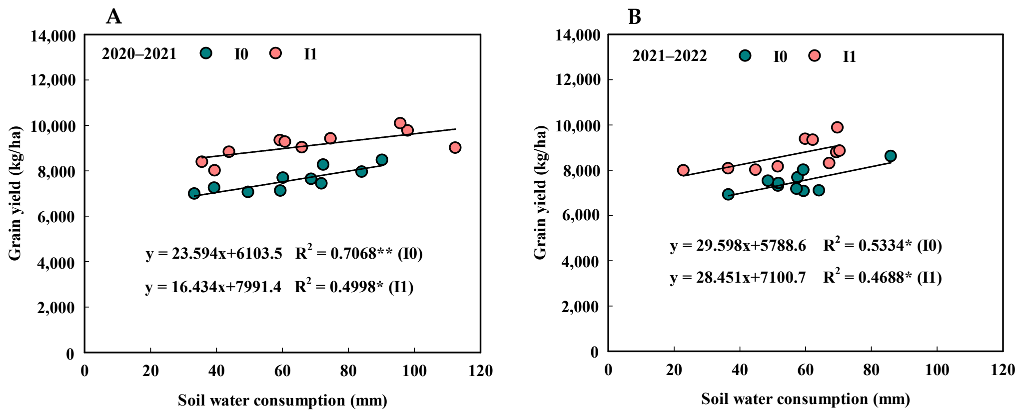

Figure 7. Relationships between grain yield and soil water consumption in the 100–200 cm soil layers after anthesis under no irrigation (I0), one irrigation (I1) during the 2020–2021 (**A**) and 2021–2022 (**B**) seasons (* significant at $p < 0.05$; ** significant at $p < 0.01$).

The growth and development of winter wheat mainly relied on stored soil water due to low rainfall after anthesis under water stress conditions. The RLD along the soil profile reflects the uptake of available soil water by winter wheat. Under rainfed conditions, compared with the low-yielding cultivars (CM6002 and SY20), the higher soil water consumption after anthesis of high-yielding cultivars (SM22 and HG35) related to the higher RLD in deeper soil layers. On average, the RLD in the 100–200 cm soil layers of high-yielding cultivars (SM22 and HG35) was 52.5–67.0% higher than that of low-yielding cultivars (CM6002 and SY20), resulting in the soil water consumption below 100 cm soil layers of the former was 54.8–70.3% greater than that of the latter after anthesis in the two seasons. The results indicated that cultivars with higher RLD in deep soil layers had a higher root water uptake ability, and hence, improved soil water utilization under rainfed conditions.

Correlation analysis between either root length (RL) or root weight (RW) in the upper (0–100 cm) and deeper (100–200 cm) soil layers and soil water consumption during the post-anthesis phase among the 10 cultivars was also undertaken under I0 and I2 in the 2020–2022 seasons (Figure 9). Under I0, the RL and RW in the 100–200 cm soil layers had significant and positive relationships with soil water consumption in the same soil layers in both seasons, and the increase in RL in the deep soil layers also improved grain yield and WP (Figure 10). For the I2 treatment, no significant correlations were found between RL and RW with soil water consumption (Figure 9). Meanwhile, the RL and RW in most soil layers were found to have a negative correlation with both grain yield and WP (Figure 10). Thus, cultivars with deep root systems were able to uptake more stored soil water below the 100 cm soil layers during the grain-filling stage and thereby, improve grain yield and WP under rainfed conditions. However, cultivars with a higher proportion of RL and RW did not exhibit increases in soil water availability to crops, and excessive root growth resulted in a waste of resources, which had a negative influence on yield formation under sufficient water supply conditions. The negative relationships between root:shoot ratio and grain yield under I2 also suggested that higher photosynthetic products input in the root system was not conducive to the accumulation of dry matter in grains (Figure 11).

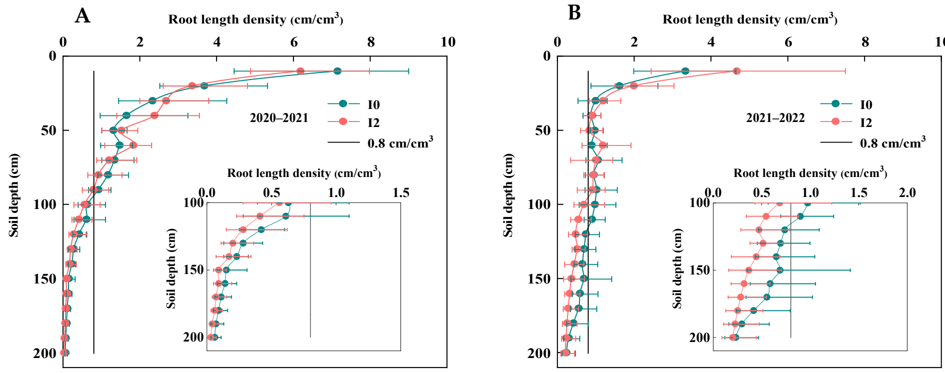

Figure 8. The distribution of mean root length density (RLD) along the soil profile for 10 cultivars during the 2020–2021 (**A**) and 2021–2022 (**B**) seasons under no irrigation (I0) and two irrigations (I2) (Bars represent the range of the RLD among the cultivars sampled).

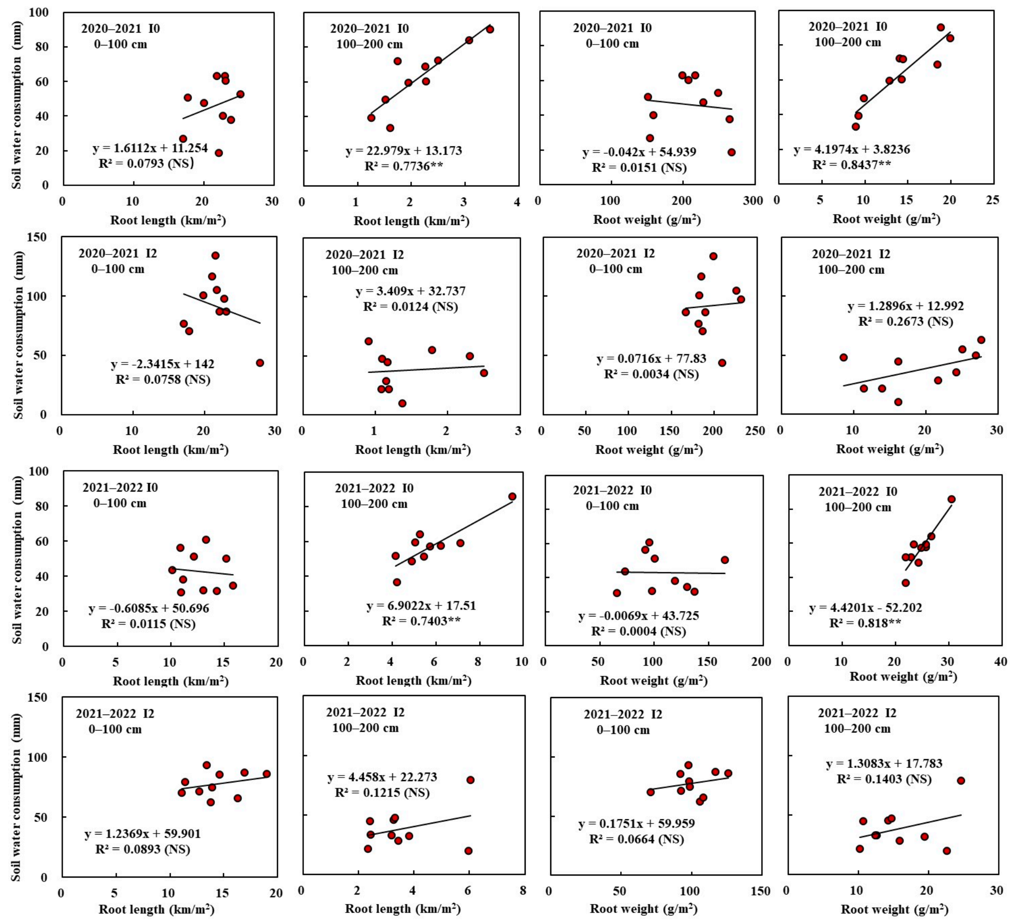

Figure 9. Relationships between root length (RL) and root weight (RW) and soil water consumption in the 0–100 cm and 100–200 cm soil layers at anthesis to maturity under no irrigation (I0) and two irrigations (I2) during the 2020–2022 seasons (** Significant at $p < 0.01$; NS Significant at $p > 0.05$).

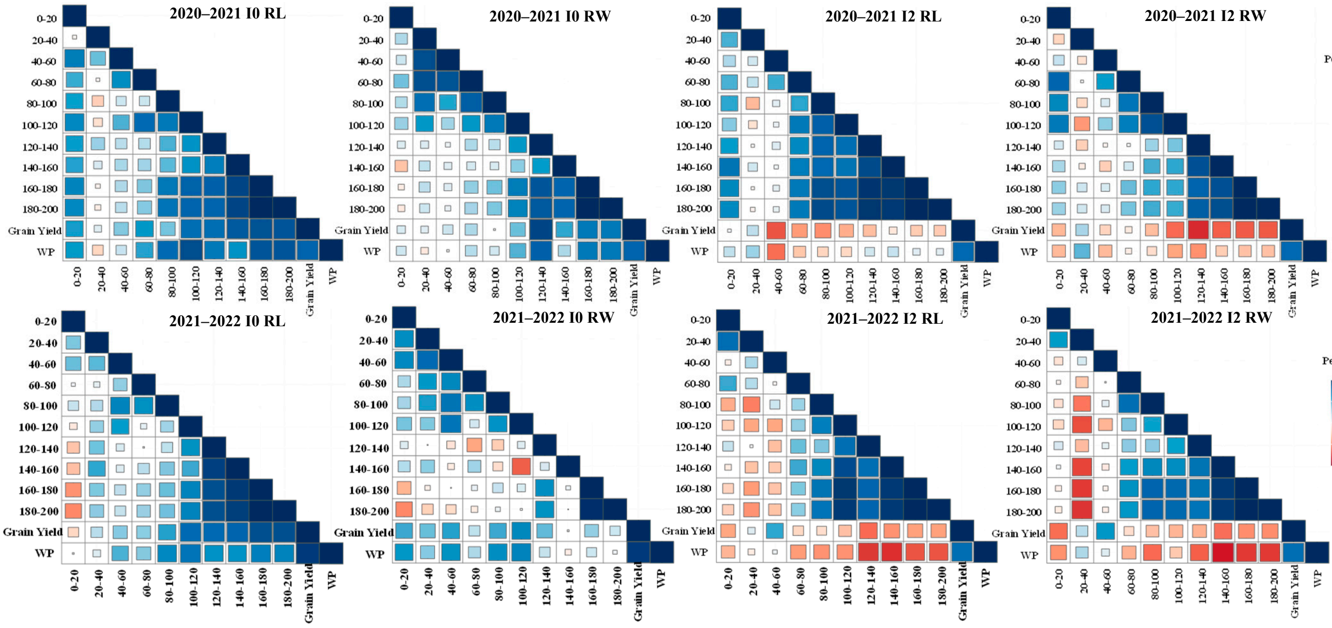

Figure 10. Analysis of correlations between root length (RL) and root weight (RW) in each 20 cm soil layer and grain yield and water productivity (WP) under no irrigation (I1) and two irrigations (I2) during the 2020–2022 seasons.

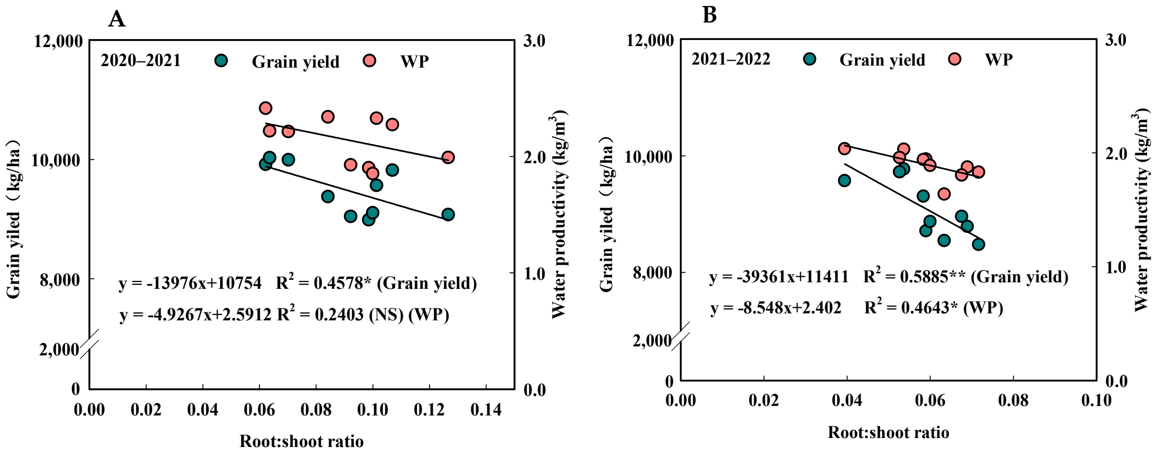

Figure 11. Correlations between root:shoot ratio and both grain yield and water productivity (WP) under two irrigations (I2) during the 2020–2021 (**A**) and 2021–2022 (**B**) seasons (** Significant at $p < 0.01$; * Significant at $p < 0.05$; NS Significant at $p > 0.05$).

3.5.2. Shoot Traits

The rainfall was only 9.6 and 24.4 mm during anthesis to maturity in the two seasons, respectively, significantly lower than the crop water requirements. Cultivars that reduce soil water use before anthesis could increase water availability during the grain-filling stages. According to the correlation analysis, under I0 (Figure 12A,D), the SWD during post-anthesis was positively correlated with post-anthesis dry matter accumulation and Relative leaf water content (RLWC) ($p < 0.01$ in 2020–2021, $p > 0.05$ in 2021–2022), but negatively correlated with canopy temperature (CT). Furthermore, either post-anthesis biomass or RLWC had significant positive correlations with grain yield and WP, while CT had significant negative correlations with grain yield and WP in both seasons. Significant positive relationships between Leaf chlorophyll content (SPAD) with grain yield and WP were found only under I0 in 2021–2022 (Figure 12D). Those results indicated that cultivars were able to absorb more soil water from deeper soil layers (more RLD in deep soil layers) during reproductive stages, resulting in an increase in post-anthesis biomass and RLWC and a lower CT, which ultimately improved grain production and WP (Figure 13). Choosing cultivars with deep root systems was necessary to cope with drought stress under rainfed conditions. However, directly choosing deep-rooted cultivars is difficult as roots grow in opaque soil. The strong negative relationships between CT and RL in the 100–200 cm soil layers (Figure 14) suggested that CT could be used to indirectly identify high-grain-yield cultivars with deeper rooting systems that have a high soil water uptake ability under rainfed conditions in the field.

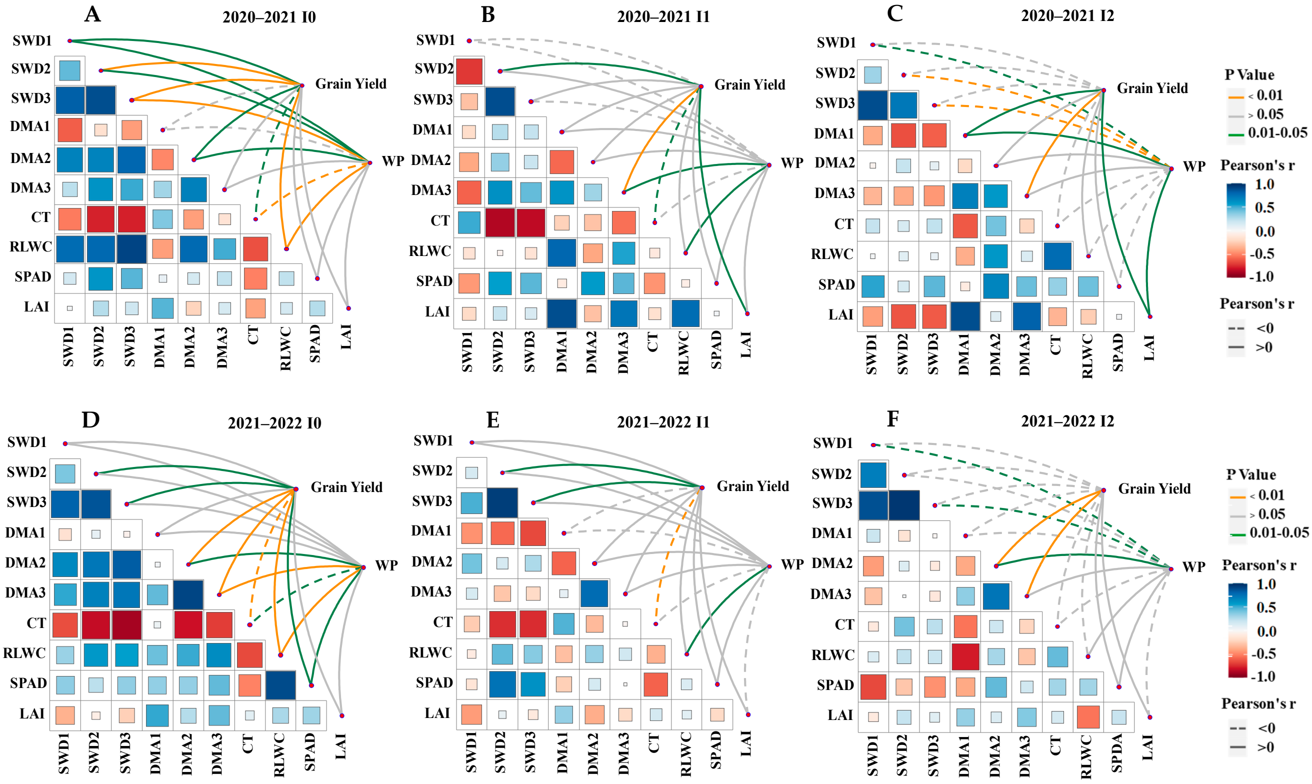

Figure 12. Analysis of correlations between soil water consumption in the 0–100 cm (SWD1), 100–200 cm (SWD2) and 0–200 cm (SWD3) soil layers after anthesis, pre-anthesis dry matter accumulation (DMA1), post-anthesis dry matter accumulation (DMA2), total dry matter accumulation (DMA3), canopy temperature (CT), relative leaf water content (RLWC), chlorophyll relative content (SPAD), leaf area index (LAI), grain yield and water productivity (WP) under no irrigation (I0) (**A**,**D**), one irrigation (I1) (**B**,**E**) and two irrigations (I2) (**C**,**F**) during the 2020–2022 seasons (Dashed lines indicate negative correlations and solid lines indicate positive correlations. Orange, gray and green lines indicate $p < 0.01$, $p > 0.05$ and $p < 0.05$, respectively).

For winter wheat grown under I1 (Figure 12B,E), CT had significant and negative correlations with soil water consumption after anthesis in the 100–200 cm soil layers and grain yield in both seasons. There were significant correlations between leaf area index (LAI) and above-ground biomass and grain yield under I1 in the first season (Figure 12B), but this relationship disappeared in the second season (Figure 12E). The results indicated that cultivars that could increase soil water consumption after anthesis in deep soil layers resulted in a lower CT, which was necessary to cope with drought stress and increase grain production under limited water supply conditions. For winter wheat grown under I2 (Figure 12C,F), irrigation at the jointing and anthesis stages replenished the soil water, thus meeting crop water requirements. No continuous significant correlations were found between CT, RLWC, SPAD and LAI with either soil water consumption, grain yield, or WP.

However, dry matter biomass at maturity was positively correlated with grain yield in each season. Thus, cultivars with more dry matter accumulation tended to produce higher grain yield under sufficient water conditions.

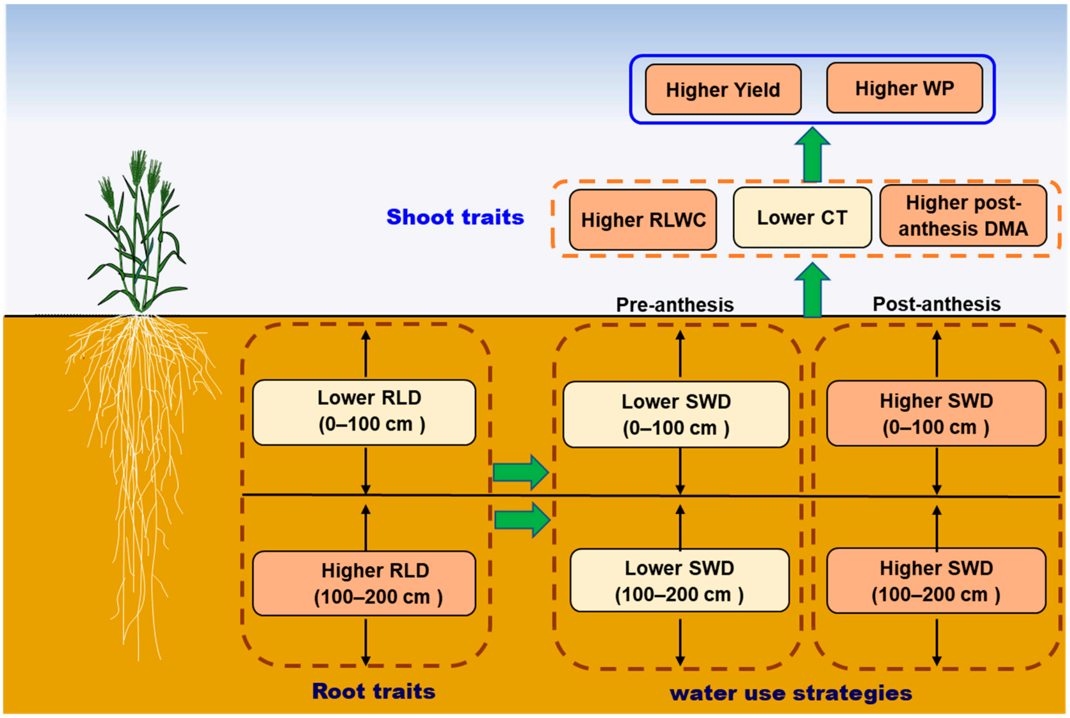

Figure 13. Model of the water use strategies and root and shoot traits of high-yielding cultivars under no irrigation (I0) (RLD: root length density; SWD: soil water depletion; RLWC: relative leaf water content; CT: canopy temperature; DMA: dry matter accumulation; WP: water productivity).

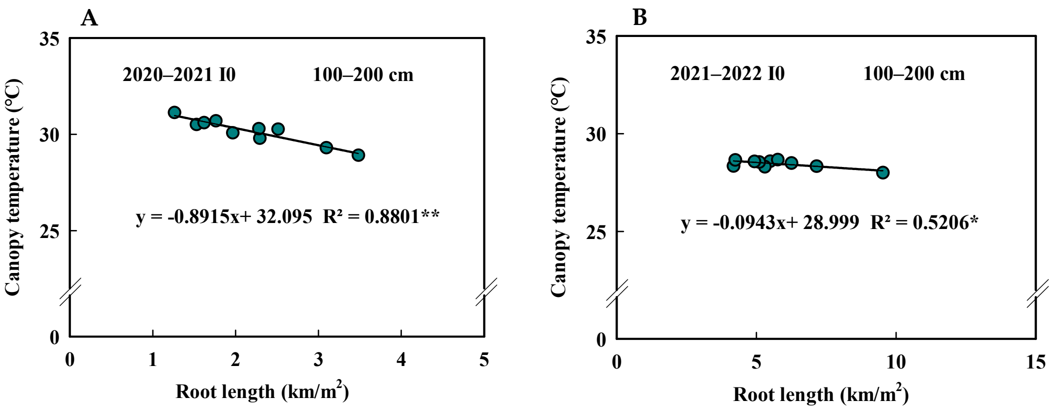

Figure 14. Relationships between canopy temperature (CT) and root length (RL) in the 100–200 cm soil layers under no irrigation (I0) during the 2020–2021 (**A**) and 2021–2022 (**B**) seasons (** Significant at $p < 0.01$; * Significant at $p < 0.05$).

4. Discussion

4.1. Choosing Better Cultivars Was Necessary to Increase Grain Yield in the Broad Environment

Water deficit is one of the most critical environmental factors limiting the growth and yield of wheat in arid and semi-arid regions worldwide [46]. Compared with well-water irrigation treatments, drought stress decreased grain yield by 27.4–32.6% [47]. Many studies revealed that cultivars had different responses to drought stress [48,49]. In the present study, the yield variation among the 10 cultivars was up to 21.2–24.6% for I0, 23.7–25.9%

for I1, and 11.6–15.3% for I2 (Figure 3). These results are similar to those of Manschadi and Soltani [16], who revealed that the performance of cultivars is influenced by environmental factors and genotypes and measured yield variations among cultivars of 9.9–46.6% across a wide range of environments. Although there was a significant yield difference among cultivars, the grain production of the high-yielding cultivar (SM22) under I0 was only 5.0–12.9% lower than the average grain yield of the 10 cultivars under I2 in the 2020–2022 seasons (Figure 3). These results suggested that choosing better cultivars was necessary to reduce the adverse effects of drought stress.

4.2. Increasing Soil Water Use in Deep Soil Layers after Anthesis Contributed to High Grain Yield under Water Deficit Conditions

In the semi-arid region of the NCP in China, the mean annual rainfall is about 450–600 mm, with approximately 70–80% of the rainfall occurring from July to September. The relatively abundant rainfall during the summer season replenishes the soil moisture before winter wheat sowing. Although the rainfall during the winter wheat season was far less than crop water requirements, the deep root system of winter wheat can extract more water from the soil profile and contribute substantially to the seasonal ET. In this study, SWD contributed 80.3% and 82.5% of the seasonal ET under I0 and 62.6% and 68.2% under I1 in the 2020–2021 and 2021–2022 seasons, respectively (Figure 5). Previous studies have also shown that approximately 40–60% of crop water use was from the stored soil water before sowing under limited irrigation conditions and up to 60–80% under rainfed conditions [35]. The scarcity and uneven distribution of rainfall during the winter wheat growing season leads to drought stress, especially during the reproductive stage [50]. Soil water very rapidly becomes depleted in the upper profile due to low rainfall and high soil evaporation [51]. The stored soil moisture in deep soil layers is an important water source for winter wheat growth [52]. Our study found that each additional millimeter of water used after anthesis from the 100–200 cm soil layers increased grain yield by 23.6–29.6 kg/ha and 16.4–28.5 kg/ha under I0 and I1, respectively (Figure 7). Similar studies also indicated that making full use of stored soil water can increase grain production in regions with summer-dominant rainfall and stored soil water, such is the case in much of India and northeastern Australia, where rainfall occurs almost entirely in the summer, the rain-fed wheat grown in the winter relies largely on stored soil moisture [31,53,54].

However, in conditions where subsoil water is absent, winter wheat (with a deep root system) could not achieve a high grain yield [55]. A recent path analysis using 5 years of field experimental data showed that it is difficult to obtain high grain production when the soil water storage before sowing is less than 320 mm, even if there is high rainfall during the later growth stage of winter wheat [56]. By contrast, during a very dry season with seasonal rainfall of 60 mm, even if sufficient water was stored in the soil, drought stress had a negative influence on plant growth, and thus, restricted the root system from extracting water from deeper soil, resulting in a decrease in grain yield [57]. The silty loam soil in the NCP is an excellent water reservoir, and the available soil water at the time of sowing winter wheat within 0–2 m is around 500 mm. The stored soil water is precious to crop yield as it could offset the adverse effects of low in-season rainfall [16]. Although the soil water content in the topsoil layers was meager after anthesis, there was a large amount of soil water in the deep soil layers, and over 100 mm of available water remained unused in the root zone at winter wheat harvest [34]. Smaller RLD in the 100–200 cm soil layers restricted the full use of soil water [13]. Choosing cultivars with more RLD in deep soil layers was beneficial to increase soil water extraction and improve grain production of winter wheat under limited water supply conditions [58].

Fang et al. [22] indicated that the seasonal ET was similar among cultivars. However, modern cultivars reduced pre-anthesis water use but increased post-anthesis water uptake under rainfed conditions. In this study, significant positive relationships were found between soil water consumption in the 100–200 cm soil layers after anthesis and grain production under I0 and I1, and negative relationships were observed between soil water consumption before anthesis and grain production under I0 (Table 2). In our study, the winter wheat cultivars were subjected to late-season drought. (Rainfall during anthesis to maturity was lower than the long-term average). Cultivars that had the ability to reduce soil water use during vegetative stages can increase available soil water during anthesis and grain filling. Improved soil water availability during reproductive stages increased the photosynthetic rate and leaf chlorophyll, which enhanced biomass accumulation [20]. This explains why the higher soil water consumption after anthesis of high-yielding cultivars leads to greater post-anthesis dry matter accumulation than that of low-yielding cultivars, particularly in rainfed conditions. Previous studies indicated that 60–90% of the final grain weight was from biomass accumulation after anthesis [59]. Cultivars with higher post-anthesis biomass are generally related to higher grain production [60,61]. In this study, significant positive relationships were also found between post-anthesis dry matter production with grain yield and WP under I0 (Figure 12A,D). Previous studies also indicated that water use during grain filling has a very high conversion efficiency into grain (water use efficiency) [31,54]. Some studies have indicated that most of the increase in grain yield from subsoil water use during the late growth stages was associated with increases in the harvest index (HI) of the crop [20,62]. High-yielding cultivars, which had a higher proportion of water use during the reproductive stage, not only increased dry matter accumulation but also promoted its transfer to the grain of winter wheat [12].

4.3. Root and Shoot Traits Contributing to High Grain Yield

4.3.1. Root Traits

Winter wheat has deep root characteristics that can penetrate down to 2 m, although 55.8–62.2% of the root system is concentrated in the top 0–40 cm soil layers [63]. Some studies indicated that a large root system was not necessary to extract soil water, and a mean RLD of 0.8–1.0 cm/cm^3 was enough to make full use of the available stored soil water [45,64]. In our study, RLD values in the 0–100 cm soil layers were higher than 0.8 cm/cm^3, indicating that the root density was not a limiting factor for soil water uptake in the upper soil layers (Figure 8). Although drought stress conditions promoted root growth in the deep soil profile to improve the soil water supply to the crop [51], the smaller RLD (lower than 0.8 cm/cm^3) below 100 cm soil layers restricted the full utilization of soil water [65].

There were large variations in root distribution among cultivars, and the distribution of roots can influence soil water use [58,66]. Earlier studies revealed that a large root system can result in excessive water use early in the season, which can reduce grain yield when soil water stress occurs during the reproductive stage under water deficit conditions [15,67]. However, a greater distribution of roots in the subsoil layers can increase soil water availability during reproductive stages [12]. The present study revealed significant positive relationships between RL in the 100–200 cm soil layers and post-anthesis water use under rainfed conditions (Figure 9). More RLD in deep soil layers increased the available soil water to wheat, and, therefore, improved grain yield and WP under rainfed conditions (Figures 10 and 13). A similar finding has been also reported for rainfed wheat in Mexico, as high-yield cultivars had greater root distributions in deep soil layers (90–120 cm) [68]. However, under frequent small rainfall events in Mediterranean environments, deep root systems lose their advantage [69].

Although roots play a key role in water uptake, an increase in root production may have a negative influence on grain yield due to the substantial metabolic costs associated with higher root growth [70]. Earlier studies have revealed that more than 50% of the photosynthate was allocated to the root system instead of grains, and a root system with large biomass would result in a yield penalty [23]. The present study found that the RLD in the upper soil layers was higher than 3 cm/cm^3 (Figure 8), in theory, exceeding the threshold value required to absorb soil water [64]. Having an extensive root system in topsoil layers did not increase the soil water absorbed by winter wheat. However, maintaining this large root system requires an abundance of photosynthetic assimilates, which negatively affects grain yield [20]. In the present study, under rainfed conditions, negative relationships were found between RL in the 0–20 cm soil layers and grain yield in 2021–2022, and between RL in the 20–40 cm soil layers and WP in 2020–2021 (Figure 10). The negative relationships between RL, RW in most soil layers and the root:shoot ratio with grain yield under I2 also indicated higher allocations of dry matter to the root system were not conducive to increasing grain production under a sufficient water supply (Figures 10 and 11) [52]. Furthermore, previous studies indicated that plants with more roots in topsoil were more sensitive to drying of the topsoil, which then promoted the production of ABA and triggered ROS (reactive oxygen species) generation, and thus, decreased the photosynthetic rate and transpiration rate, thereby negatively affecting dry matter accumulation [71]. A reduction in root biomass in the upper soil layers not only saved soil water before anthesis but also decreased root respiration. Ma et al. [72] indicated that root pruning at the jointing stage was an effective measure to improve the HI and grain yield of winter wheat by reducing the root biomass in topsoil layers. Conversely, there were positive relationships between grain yield and RL in the 100–200 cm soil layers under rainfed conditions in this study (Figure 10). The advantages brought by root growth in the subsoil profile offset the cost in carbon products [20].

In the current study, there were no significant relationships between either RL or RW in 0–100 cm soil layers with grain yield under rainfed conditions (Figure 10). This differs from the observation of Ehdaie et al. [73], who conducted an experiment in PVC tubes and found a positive correlation between root biomass in the 0–80 cm soil layers and grain production under terminal drought conditions. These relationships may be influenced by differences in growth environment conditions, soil water content and genotypic variations. Results from this study also showed that the contribution of RL to grain yield was higher than that of RW under rainfed conditions (Figure 10). In fact, cultivars with a higher specific root length (SRL, m root per g dry root mass) may be more useful in increasing grain production [74], because higher SRL implies longer and thinner roots with more branching, which increases the root surface area of contact with the surrounding soil [70].

4.3.2. Shoot Traits

When crops experience water stress, the stomata close, leaves often roll and senescence occurs [75]. Stay-green traits, such as leaf chlorophyll concentration, leaf photosynthetic rate and LAI, reflect root water uptake ability. They can be used as a selection criterion to improve grain yield under drought conditions [76–78]. Lu et al. [13] showed that cultivars with higher SPAD at the late grain-filling stage always had higher grain yield under water deficit conditions. However, in the present study, the relationship between SPAD and grain yield was inconsistent in both seasons (Figure 12). Balota et al. [79] also indicated that there were no consistent relationships between SPAD and grain yield. Further, Hasanuzzaman et al. [80] showed that chlorophyll density per unit area may increase owing to reduced leaf growth and increased leaf thickness of stressed plants, which had a negative influence on grain production. The results of this study indicated that RLWC at the grain-filling stage had positive correlations with grain yield and WP under I0 (Figure 12A,D). Cultivars with a higher RLWC exhibit the utilization of deeper soil water. However, there was high leaf-to-leaf variation for SPAD and RLWC, so analyses of these traits require a large number of replicates to achieve reliable results, and these measurements are often time-consuming and labor-intensive for large-scale screening [81].

CT reflects transpiring leaf area incorporating the whole crop canopy, which contains a large number of genotypes and can be readily measured using infrared technology on cloudless days [82,83]. Pinto and Reynolds [83] showed that cooler canopy genotypes can absorb 35% more water from the 30–90 cm soil layers than warmer canopy genotypes under drought conditions. The current study found that CT was negatively correlated with soil water consumption in the 100–200 cm soil layers after anthesis and grain yield under water deficit conditions in both seasons (Figure 12), suggesting high-yielding cultivars promoted water absorption from deep soil layers, which ultimately, decreased the CT when soil water is available at depth [21]. Previous studies have also shown a negative correlation between CT and grain yield, indicating that CT is considered an effective trait for choosing high-yielding cultivars under water deficit conditions [69]. However, under well-irrigated conditions, some studies demonstrated that warmer canopies are associated with slower transpiration and water use and produce higher grain yield [84].

4.3.3. Using Shoot Traits to Choose More RLD in Deep Soil Layers under Water Deficit Conditions

Despite the apparent importance of choosing cultivars with higher RLD in deep layers to capture available soil water under rainfed conditions, it is difficult to measure root traits in realistic field conditions because roots occur beneath the soil surface [31]. Some researchers used pots, PVC tubes, or greenhouse experiments to study the performance of winter wheat cultivars in relation to their root systems [27]. However, seedling roots under controlled conditions may not exhibit the developmental features of mature roots in the field [28,85]. Previous studies indicated that cultivars with cooler CT during grain filling related to a more excellent distribution of roots in deep soil layers under drought-prone environments [21,81]. In this study, the strong negative relationships between CT and RL in the 100–200 cm soil layers suggested that CT could be used to indirectly choose high-grain-yielding cultivars with higher RLD in deep soil layers that have a higher soil water uptake ability after anthesis under deficit water supply conditions (Figure 14). A recent study successfully used CT at the grain-filling stage to identify cultivars with greater RLD in deep soil layers in field conditions and found that the deeper-rooted cultivar yielded 5.0% more than the smaller RLD cultivar [13].

5. Conclusions

Our study demonstrated that there was a large yield variation among cultivars. Choosing high-yielding cultivars has the advantage of reducing yield loss caused by drought stress. Under water deficit conditions, the high-yielding cultivars were able to reduce water use during vegetative stages and increase water use during reproductive stages, especially water use from deeper soil layers. This water use strategy allows more soil water to be available during the grain-filling stage. Higher RLD in deeper soil layers, higher RLWC and lower CT could all be used as indicators for choosing high-yielding cultivars. Under sufficient water supply conditions, reducing water use after anthesis improved WP. The above-ground biomass showed a positive correlation with grain yield, while an increased allocation of dry matter to root systems led to reduced yield. Thus, cultivars with higher dry matter accumulation and lower root:shoot ratios have the potential to improve grain yield under sufficient water supply conditions in the NCP.

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References

1. Wulff, B.B.H.; Dhugga, K.S. Wheat—The cereal abandoned by GM Genetic modification of wheat for disease resistance could help stabilize food production. *Science* **2018**, *361*, 451–452. [CrossRef] [PubMed]
2. Kettlewell, P.; Byrne, R.; Jeffery, S. Wheat area expansion into northern higher latitudes and global food security. *Agric. Ecosyst. Environ.* **2023**, *351*, 108499. [CrossRef]
3. Rahimi-Moghaddam, S.; Deihimfard, R.; Azizi, K.; Roostaei, M. Characterizing spatial and temporal trends in drought patterns of rainfed wheat (*Triticum aestivum* L.) across various climatic conditions: A modelling approach. *Eur. J. Agron.* **2021**, *129*, 126333. [CrossRef]
4. Clarke, D.; Hess, T.M.; Haro-Monteagudo, D.; Semenov, M.A.; Knox, J.W. Assessing future drought risks and wheat yield losses in England. *Agric. For. Meteorol.* **2021**, *297*, 108248. [CrossRef]
5. Saddique, Q.; Liu, D.L.; Wang, B.; Feng, P.Y.; He, J.Q.; Ajaz, A.; Ji, J.M.; Xu, J.T.; Zhang, C.; Cai, H.J. Modelling future climate change impacts on winter wheat yield and water use: A case study in Guanzhong Plain, northwestern China. *Eur. J. Agron.* **2020**, *119*, 126113. [CrossRef]
6. Kunz, K.; Hu, Y.C.; Boincean, B.; Postolatii, A.; Schmidhalter, U. Evaluating the impact of a 2.5–3°C increase in temperature on drought-stressed German wheat cultivars under natural stress conditions. *Agric. For. Meteorol.* **2023**, *332*, 109378. [CrossRef]
7. Mwadzingeni, L.; Shimelis, H.; Dube, E.; Laing, M.D.; Tsilo, T.J. Breeding wheat for drought tolerance: Progress and technologies. *J. Integr. Agric.* **2016**, *15*, 935–943. [CrossRef]
8. Lorite, I.J.; Castilla, A.; Cabezas, J.M.; Alza, J.; Santos, C.; Porras, R.; Gabaldón-Leal, C.; Muñoz-Marchal, E.; Sillero, J.C. Analyzing the impact of extreme heat events and drought on wheat yield and protein concentration, and adaptation strategies using long-term cultivar trials under semi-arid conditions. *Agric. For. Meteorol.* **2023**, *329*, 109279. [CrossRef]
9. Zahra, N.; Wahid, A.; Hafeez, M.B.; Ullah, A.; Siddique, K.H.M.; Farooq, M. Grain development in wheat under combined heat and drought stress: Plant responses and management. *Environ. Exp. Bot.* **2021**, *188*, 104517. [CrossRef]
10. Blum, A. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Res.* **2009**, *112*, 119–123. [CrossRef]
11. Thapa, S.; Xue, Q.W.; Jessup, K.E.; Rudd, J.C.; Liu, S.Y.; Pradhan, G.P.; Devkota, R.N.; Baker, J. More Recent Wheat Cultivars Extract More Water from Greater Soil Profile Depths to Increase Yield in the Texas High Plains. *Agron. J.* **2017**, *109*, 2771–2780. [CrossRef]
12. Yang, W.J.; Liu, W.J.; Li, Y.L.; Wang, S.W.; Yin, L.N.; Deng, X.P. Increasing rainfed wheat yield by optimizing agronomic practices to consume more subsoil water in the Loess Plateau. *Crop J.* **2021**, *9*, 1418–1427. [CrossRef]
13. Lu, Y.; Yan, Z.Z.; Li, L.; Gao, C.S.; Shao, L.W. Selecting traits to improve the yield and water use efficiency of winter wheat under limited water supply. *Agric. Water Manag.* **2020**, *242*, 106410. [CrossRef]
14. Figueroa-Bustos, V.; Palta, J.A.; Chen, Y.; Stefanova, K.; Siddique, K.H.M. Wheat cultivars with contrasting root system size responded differently to terminal drought. *Front. Plant Sci.* **2020**, *11*, 1285. [CrossRef] [PubMed]
15. Figueroa-Bustos, V.; Palta, J.A.; Chen, Y.; Siddique, K.H.M. Early season drought largely reduces grain yield in wheat cultivars with smaller root systems. *Plants* **2019**, *8*, 305. [CrossRef] [PubMed]
16. Manschadi, A.M.; Soltani, A. Variation in traits contributing to improved use of nitrogen in wheat: Implications for genotype by environment interaction. *Field Crops Res.* **2021**, *270*, 108211. [CrossRef]
17. Ali, S.; Xu, Y.; Ma, X.; Ahmad, I.; Jia, Q.; Akmal, M.; Hussain, Z.; Arif, M.; Cai, T.; Zhang, J.; et al. Deficit irrigation strategies to improve winter wheat productivity and regulating root growth under different planting patterns. *Agric. Water Manag.* **2019**, *219*, 1–11. [CrossRef]
18. Wu, Y.C.; Zhou, S.L.; Wang, Z.M.; Zhang, X. Residual subsoil nitrogen utilization under water-saving cultivation in winter wheat. *Acta Ecol. Sin.* **2005**, *25*, 1869–1873. (In Chinese)
19. Fang, Q.; Zhang, X.Y.; Chen, S.Y.; Shao, L.W.; Sun, H.Y. Selecting traits to increase winter wheat yield under climate change in the North China Plain. *Field Crops Res.* **2017**, *207*, 30–41. [CrossRef]
20. Li, H.T.; Li, L.; Liu, N.; Chen, S.Y.; Shao, L.W.; Sekiya, N.; Zhang, X.Y. Root efficiency and water use regulation relating to rooting depth of winter wheat. *Agric. Water Manag.* **2022**, *269*, 107710. [CrossRef]
21. Lopes, M.S.; Reynolds, M.P. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Funct. Plant Biol.* **2010**, *37*, 147–156. [CrossRef]
22. Fang, Y.; Liang, L.; Liu, S.; Xu, B.; Siddique, K.H.M.; Palta, J.A.; Chen, Y. Wheat cultivars with small root length density in the topsoil increased post-anthesis water use and grain yield in the semi-arid region on the Loess Plateau. *Eur. J. Agron.* **2021**, *124*, 126243. [CrossRef]
23. Lambers, H.; Atkin, O.K.; Scheureater, I. Respiratory patterns in root in relation to their function. In *Plant Roots: The Hidden Half*; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, 1996; pp. 323–362.
24. Vain, S.; Tamm, I.; Tamm, Ü.; Annusver, M.; Zobel, K. Negative relationship between topsoil root production and grain yield in oat and barley. *Agric. Ecosyst. Environ.* **2023**, *349*, 108467. [CrossRef]
25. Wasson, A.; Bischof, L.; Zwart, A.; Watt, M. A portable fluorescence spectroscopy imaging system for automated root phenotyping in soil cores in the field. *J. Exp. Bot.* **2016**, *67*, 1033–1043. [CrossRef]
26. Wasaya, A.; Zhang, X.Y.; Fang, Q.; Yan, Z.Z. Root phenotyping for drought tolerance: A review. *Agronomy* **2018**, *8*, 241. [CrossRef]

27. Becker, S.R.; Byrne, P.F.; Reid, S.D.; Bauerle, W.L.; McKay, J.K.; Haley, S.D. Root traits contributing to drought tolerance of synthetic hexaploid wheat in a greenhouse study. *Euphytica* **2016**, *207*, 213–224. [CrossRef]
28. Rich, S.M.; Jack, C.; Richard, R.; Michelle, W. Root phenotypes of young wheat plants grown in controlled environments show inconsistent correlation with mature root traits in the field. *J. Exp. Bot.* **2020**, *71*, 4751–4762. [CrossRef]
29. Li, H.T.; Shao, L.W.; Liu, X.W.; Sun, H.Y.; Chen, S.Y.; Zhang, X.Y. What matters more, biomass accumulation or allocation, in yield and water productivity improvement for winter wheat during the past two decades? *Eur. J. Agron.* **2023**, *149*, 126910. [CrossRef]
30. Li, X.X.; Ingvordsen, C.H.; Weiss, M.; Rebetake, G.J.; Condon, A.G.; James, R.A.; Richards, R.A. Deeper roots associated with cooler canopies, higher normalized difference vegetation index, and greater yield in three wheat populations grown on stored soil water. *J. Exp. Bot.* **2019**, *70*, 4963–4974. [CrossRef]
31. Wasson, A.P.; Richards, R.A.; Chatrath, R.; Misra, S.C.; Prasad, S.V.; Rebetzke, G.J.; Kirkegaard, J.A.; Christopher, J.; Watt, M. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *J. Exp. Bot.* **2012**, *63*, 3485–3498. [CrossRef]
32. Ti, J.S.; Yang, Y.H.; Pu, L.L.; Wen, X.Y.; Yin, X.G.; Chen, F. Ecological compensation for winter wheat fallow and impact assessment of winter fallow on water sustainability and food security on the North China Plain. *J. Clean. Prod.* **2021**, *328*, 129431. [CrossRef]
33. Yang, X.L.; Wang, G.Y.; Chen, Y.Q.; Sui, P.; Pacenka, S.; Steenhuis, T.S.; Siddique, K.H.M. Reduced groundwater use and increased grain production by optimized irrigation scheduling in winter wheat–summer maize double cropping system—A 16-year field study in North China Plain. *Field Crops Res.* **2022**, *275*, 108364. [CrossRef]
34. Zhang, X.Y.; Qin, W.L.; Xie, J.N. Improving water use efficiency in grain production of winter wheat and summer maize in the North China Plain: A review. *Front. Agric. Sci. Eng.* **2016**, *3*, 25–33. [CrossRef]
35. Fang, Q.; Zhang, X.Y.; Shao, L.W.; Chen, S.Y.; Sun, H.Y. Assessing the performance of different irrigation systems on winter wheat under limited water supply. *Agric. Water Manag.* **2018**, *196*, 133–143. [CrossRef]
36. Jabro, J.D.; Stevens, W.B.; Iversen, W.M. Comparing two methods for measuring soil bulk density and moisture content. *Open J. Soil Sci.* **2020**, *10*, 233–243. [CrossRef]
37. Allen, R.G.; Pereira, L.S.; Raes, D.; Smith, M. *Crop Evapotranspiration—Guidelines for 16 Computing Crop Water Requirements*; FAO Irrigation and Drainage Paper 56; FAO: Rome, Italy, 1998.
38. Liu, C.M.; Zhang, X.Y.; Zhang, Y.Q. Determination of daily evaporation and evapotranspiration of winter wheat and maize by large-scale weighing lysimeter and micro-lysimeter. *Agric. Forest. Meteorol.* **2002**, *111*, 109–120. [CrossRef]
39. Zadoks, J.C.; Chang, T.T.; Konzak, C.F. A decimal code for the growth stages of cereals. *Weed Res.* **1974**, *14*, 415–421. [CrossRef]
40. Zegaoui, Z.; Planchais, S.; Cabassa, C.; Djebbar, R.; Belbachir, O.A.; Carol, P. Variation in relative water content, proline accumulation and stress gene expression in two cowpea landraces under drought. *J. Plant Physiol.* **2017**, *218*, 26–34. [CrossRef] [PubMed]
41. Tennant, D. A test of a modified line intersect method of estimating root length. *J. Ecol.* **1975**, *63*, 995–1001. [CrossRef]
42. Liang, S.S.; Li, L.; An, P.; Chen, S.Y.; Shao, L.W.; Zhang, X.Y. Spatial soil water and nutrient distribution affecting the water productivity of winter wheat. *Agric. Water Manag.* **2021**, *256*, 107114. [CrossRef]
43. Zhang, X.Y.; Chen, S.Y.; Sun, H.Y.; Pei, D.; Wang, Y.M. Dry matter, harvest index, grain yield and water use efficiency as affected by water supply in winter wheat. *Irrig. Sci.* **2008**, *27*, 1–10. [CrossRef]
44. Hordofa, A.T.; Leta, O.T.; Alamirew, T.; Chukalla, A.D. Response of winter wheat production to climate change in Ziway Lake Basin. *Sustainability* **2022**, *14*, 13666. [CrossRef]
45. Zhang, X.Y.; Chen, S.Y.; Sun, H.Y.; Wang, Y.M.; Shao, L.W. Root size, distribution and soil water depletion as affected by cultivars and environmental factors. *Field Crops Res.* **2009**, *114*, 75–83. [CrossRef]
46. Couëdel, A.; Edreira, J.I.R.; Lollato, R.; Archontoulis, S.; Sadras, V.; Grassini, P. Assessing environment types for maize, soybean, and wheat in the United States as determined by spatio-temporal variation in drought and heat stress. *Agric. For. Meteorol.* **2021**, *307*, 108513. [CrossRef]
47. Zhao, H.X.; Zhang, P.; Wang, Y.Y.; Ning, T.Y.; Xu, C.L.; Wang, P. Canopy morphological changes and water use effciency in winter wheat under different irrigation treatments. *J. Integr. Agric.* **2020**, *19*, 1105–1116. [CrossRef]
48. Dorrani-Nejad, M.; Kazemipour, A.; Maghsoudi-Moud, A.A.; Abdolshah, R. Wheat breeding for early heading: Does it improve grain yield under drought stress and well-watered conditions? *Environ. Exp. Bot.* **2022**, *200*, 104902. [CrossRef]
49. Thapa, S.; Reddy, S.K.; Fuentealba, M.P.; Xue, Q.; Rudd, J.C.; Jessup, K.E.; Devkota, R.N.; Liu, S. Physiological responses to water stress and yield of winter wheat cultivars differing in drought tolerance. *J. Agron. Crop Sci.* **2018**, *204*, 347–358. [CrossRef]
50. Li, J.P.; Zhang, Z.; Liu, Y.; Yao, C.S.; Song, W.Y.; Xu, X.X.; Zhang, M.; Zhou, X.N.; Gao, Y.M.; Wang, Z.N.; et al. Effects of micro-sprinkling with different irrigation amount on grain yield and water use efficiency of winter wheat in the North China Plain. *Agric. Water Manag.* **2019**, *224*, 105736. [CrossRef]
51. Jha, S.K.; Gao, Y.; Liu, H.; Huang, Z.D.; Wang, G.S.; Liang, Y.P.; Duan, A.W. Root development and water uptake in winter wheat under different irrigation methods and scheduling for North China. *Agric. Water Manag.* **2017**, *182*, 139–150. [CrossRef]
52. Xu, C.L.; Tao, H.B.; Tian, B.J.; Gao, Y.B.; Ren, J.H.; Wang, P. Limited-irrigation improves water use efficiency and soil reservoir capacity through regulating root and canopy growth of winter wheat. *Field Crops Res.* **2016**, *196*, 268–275. [CrossRef]
53. Manschadi, A.M.; Christopher, J.; deVoil, P.; Hammer, G.L. The role of root architectural traits in adaptation of wheat to water-limited environments. *Funct. Plant Biol.* **2006**, *33*, 823–837. [CrossRef] [PubMed]
54. Lilley, J.M.; Kirkegaard, J.A. Benefits of increased soil exploration by wheat roots. *Field Crops Res.* **2011**, *122*, 118–130. [CrossRef]

55. Christopher, J.T.; Manschadi, A.M.; Hammer, G.L.; Borrell, A.K. Developmental and physiological traits associated with high yield and stay-green phenotype in wheat. *Aust. J. Agric. Res.* **2008**, *59*, 354–364. [CrossRef]
56. Dong, Z.Y.; Zhang, X.D.; Li, J.; Zhang, C.; Wei, T.; Yang, Z.; Cai, T.; Zhang, P.; Ding, R.X.; Jia, Z.K. Photosynthetic characteristics and grain yield of winter wheat (*Triticum aestivum* L.) in response to fertilizer, precipitation, and soil water storage before sowing under the ridge and furrow system: A path analysis. *Agric. For. Meteorol.* **2019**, *272*, 12–19. [CrossRef]
57. Thapa, S.; Xue, Q.W.; Jessup, K.E.; Rudd, J.C.; Liu, S.Y.; Devkota, R.N.; Baker, J.A. Soil water extraction and use by winter wheat cultivars under limited irrigation in a semi-arid environment. *J. Arid Environ.* **2020**, *174*, 104046. [CrossRef]
58. Rezzouk, F.Z.; Gracia-Romero, A.; Kefauver, S.C.; Nieto-Taladriz, M.T.; Serret, M.D.; Araus, J.L. Durum wheat ideotypes in Mediterranean environments differing in water and temperature conditions. *Agric. Water Manag.* **2022**, *259*, 107257. [CrossRef]
59. Masoni, A.; Ercoli, L.; Mariotti, M.; Arduini, I. Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. *Eur. J. Agron.* **2007**, *26*, 179–186. [CrossRef]
60. Kirkegaard, J.A.; Lilley, J.M.; Howe, G.N.; Graham, J.M. Impact of subsoil water use on wheat yield. *Aust. J. Agric. Res.* **2007**, *58*, 303. [CrossRef]
61. Moradi, L.; Siosemardeh, A.; Sohrabi, Y.; Bahramnejad, B.; Hosseinpanahi, F. Dry matter remobilization and associated traits, grain yield stability, N utilization, and grain protein concentration in wheat cultivars under supplemental irrigation. *Agric. Water Manag.* **2022**, *263*, 107449. [CrossRef]
62. Passioura, J.B. Grain yield, harvest index, and water use of wheat. *J. Aust. Inst. Agric. Sci.* **1977**, *43*, 117–120.
63. Hu, Y.J.; Ma, P.H.; Wu, S.F.; Sun, B.H.; Feng, H.; Pan, X.L.; Zhang, B.B.; Chen, G.J.; Duan, C.X.; Lei, Q.; et al. Spatial-temporal distribution of winter wheat (*Triticum aestivum* L.) roots and water use efficiency under ridge–furrow dual mulching. *Agric. Water Manag.* **2020**, *240*, 106301. [CrossRef]
64. Barraclough, P.B.; Weir, A.H. Effects of a compacted subsoil layer on root and shoot growth, water use and nutrient uptake of winter wheat. *J. Agric. Sci.* **1988**, *110*, 207–216. [CrossRef]
65. An, S.Q.; Liu, G.S.; Guo, A.H. Consumption of available soil water stored at planting by winter wheat. *Agric. Water Manag.* **2003**, *63*, 99–107. [CrossRef]
66. Hodgkinson, L.; Dodd, I.C.; Binley, A.; Ashton, R.W.; White, R.P.; Watts, C.W.; Whalley, W.R. Root growth in field-grown winter wheat: Some effects of soil conditions, season and genotype. *Eur. J. Agron.* **2017**, *91*, 74–83. [CrossRef]
67. Ahmed, M.A.; Passioura, J.; Carminati, A. Hydraulic processes in roots and the rhizosphere pertinent to increasing yield of water-limited grain crops: A critical review. *J. Exp. Bot.* **2018**, *69*, 3255–3265. [CrossRef] [PubMed]
68. Lopes, M.S.; Reynolds, M.P. Drought Adaptive Traits and Wide Adaptation in Elite Lines Derived from Resynthesized Hexaploid Wheat. *Crop Sci.* **2011**, *51*, 1617–1626. [CrossRef]
69. Palta, J.A.; Chen, X.; Milroy, S.P.; Rebetzke, G.J.; Dreccer, M.F.; Watt, M. Large root systems: Are they useful in adapting wheat to dry environments? *Funct. Plant Biol.* **2011**, *38*, 347–354. [CrossRef] [PubMed]
70. Ahmadi, S.H.; Sepaskhah, A.R.; Zarei, M. Specific root length, soil water status, and grain yields of irrigated and rainfed winter barley in the raised bed and flat planting systems. *Agric. Water Manag.* **2018**, *210*, 304–315. [CrossRef]
71. Batool, A.; Akram, N.A.; Cheng, Z.G.; Lv, G.C.; Ashraf, M.; Afzal, M.; Xiong, J.L.; Wang, J.Y.; Xiong, Y.C. Physiological and biochemical responses of two spring wheat genotypes to non-hydraulic root-to-shoot signalling of partial and full root-zone drought stress. *Plant Physiol. Biochem.* **2019**, *139*, 11–20. [CrossRef]
72. Ma, S.C.; Xu, B.C.; Li, F.M.; Liu, W.Z.; Huang, Z.B. Effects of root pruning on competitive ability and water use efficiency in winter wheat. *Field Crops Res.* **2008**, *105*, 56–63. [CrossRef]
73. Ehdaie, B.; Layne, A.P.; Waines, J.G. Root system plasticity to drought influences grain yield in bread wheat. *Euphytica* **2012**, *186*, 219–232. [CrossRef]
74. Aziz, M.M.; Palta, J.A.; Siddique, K.H.M.; Sadras, V.O. Five decades of selection for yield reduced root length density and increased nitrogen uptake per unit root length in Australian wheat varieties. *Plant Soil.* **2017**, *413*, 181–192. [CrossRef]
75. Nguyen, T.H.; Langensiepen, M.; Gaiser, T.; Webber, H.; Ahrends, H.; Hueging, H.; Ewert, F. Responses of winter wheat and maize to varying soil moisture: From leaf to canopy. *Agric. For. Meteorol.* **2022**, *314*, 108803. [CrossRef]
76. Rebetzke, G.J.; Jimenez-Berni, J.A.; Bovill, W.D.; Deery, D.M.; James, R.A. High-throughput phenotyping technologies allow accurate selection of stay-green. *J. Exp. Bot.* **2016**, *67*, 4919–4924. [CrossRef] [PubMed]
77. Christopher, M.; Chenu, K.; Jennings, R.; Fletcher, S.; Butler, D.; Borrell, A.; Christopher, J. QTL for stay-green traits in wheat in well-watered and water-limited environments. *Field Crops Res.* **2018**, *217*, 32–44. [CrossRef]
78. Mahmood, Y.A.; DeSilva, J.; King, J.; Foulkes, M.J. Leaf photosynthesis traits and associations with biomass and drought tolerance in amphidiploid and ancestral wheat genotypes. *Eur. J. Agron.* **2023**, *147*, 126846. [CrossRef]
79. Balota, M.; Green, A.J.; Griffey, C.A.; Pitman, R.; Thomason, W. Genetic gains for physiological traits associated with yield in soft red winter wheat in the Eastern United States from 1919 to 2009. *Eur. J. Agron.* **2017**, *84*, 76–83. [CrossRef]
80. Hasanuzzaman, M.; Shabala, L.; Brodribb, T.J.; Zhou, M.; Shabala, S. Assessing the suitability of various screening methods as a proxy for drought tolerance in barley. *Funct. Plant Biol.* **2017**, *44*, 253–266. [CrossRef] [PubMed]
81. Rebetzke, G.J.; Rattey, A.R.; Farquhar, G.D.; Richards, R.A.; Condon, A.T.G. Genomic regions for canopy temperature and their genetic association with stomatal conductance and grain yield in wheat. *Funct. Plant Biol.* **2013**, *40*, 14–33. [CrossRef]
82. Graß, R.; Böttcher, U.; Lilienthal, H.; Wilde, P.; Kage, H. Is canopy temperature suitable for high throughput field phenotyping of drought resistance of winter rye in temperate climate? *Eur. J. Agron.* **2020**, *120*, 126104. [CrossRef]

83. Pinto, R.S.; Reynolds, M.P. Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. *Theor. Appl. Genet.* **2015**, *128*, 575–585. [CrossRef] [PubMed]
84. Pinter, P.J.; Zipoli, G.; Reginato, R.J.; Jackson, R.D.; Idso, S.B.; Hohman, J.P. Canopy temperature as an indicator of differential water use and yield performance among wheat cultivars. *Agric. Water Manag.* **1990**, *18*, 35–48. [CrossRef]
85. Watt, M.; Moosavi, S.; Cunningham, S.C.; Kirkegaard, J.A.; Rebetzke, G.J.; Richards, R.A. A rapid, controlled-environment seedling root screen for wheat correlates well with rooting depths at vegetative, but not reproductive, stages at two field sites. *Ann. Bot.* **2013**, *112*, 447–455. [CrossRef] [PubMed]