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Effects of Post-Anthesis Drought and Irrigation on Grain Yield, Canopy Temperature and ^{13}C Discrimination in Common Wheat, Spelt, and Einkorn

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Abstract: Fluctuations in precipitation and higher evapotranspiration due to rising temperatures are reflected in reduced wheat yields, even in areas with a low historical incidence of drought. In this study, the effects of drought (S) and irrigation (IR) on spelt, einkorn wheat, and two common wheat cultivars were assessed in a field experiment in the years 2018–2021. Water availability was differentiated from the flowering stage using a mobile cover and drip irrigation. Grain yield, canopy temperature, and discrimination of ^{13}C in grain ($\Delta\ ^{13}C$) were monitored. Drought reduced the average grain yield of common wheat to 5.24 t.ha^{-1}, which was 67.00% of the rain-fed control (C) yield, and 62.09% of the irrigated wheat yield. For spelt and einkorn wheat, the average grain yield from stressed plants was 2.02 t.ha^{-1}; this was 79.97% of the C-variant yield, and 70.82% of the IR-variant yield. Higher stand temperatures were an excellent indicator of water deficit in the stressed crops. The relationship between temperature and final grain yield in the monitored variants was always negative. In all years, discrimination of ^{13}C in grain corresponded to water availability; in its effect on yields, the correlation was always positive. Between 2018 and 2020, spelt and einkorn exhibited lower $\Delta\ ^{13}C$ in comparison with common wheat in all variants, suggesting a greater impact of differentiated water supply. The results of the experiment conclusively demonstrated systematic effects of drought after flowering upon yields and other studied characteristics.

Keywords: water availability; supplementary irrigation; root zone; canopy temperature

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1. Introduction

Increased weather variability and a gradual rise in temperatures increase the risk of extreme climate events, especially drought, with resulting impacts on the stability, quantity, and quality of crop production. This threatens food security not only in arid and semi-arid regions but also—according to climate models—in regions previously rarely affected by drought. This applies to transitional climate regions which experience a climate midway between the maritime and continental, such as the Pannonian region in Central Europe, which includes the Czech Republic [1]. Historically, the lands of Czechia have rarely been affected by drought. However, the country has been affected by several dry years in the 21st century so far, and climate change can only lead to a worsening of this problem [2–5].

In the Czech Republic, cereals occupy over 56% of arable land; the profit crop winter wheat accounts for around 33% on its own. Reduced yields due to drought have a large impact on the financial stability of farms [6–9]. In transitional climate conditions, drought-resistant cultivars cannot be grown because they cannot fully take advantage of the favorable moisture conditions in some years or some growth periods. Research on the response of wheat genotypes to different weather conditions and water availability is therefore important for the effective selection of suitable cultivars for specific soil, climate and site conditions, as well as for breeding and selection of genotypes.

In typical soil and climate conditions, drought in cereals and other annual crops occurs most often after the depletion of the winter water supply, during the period of intensive growth, when plants have the largest leaf area and water is required for stem elongation and heading, and for grain growth. When there is low rainfall and high evapotranspiration due to high temperatures, plants are unable to drain sufficient water from the soil and transpire it; the stomata close, photosynthesis decreases, and the plant surface is insufficiently cooled, resulting in overheating and tissue damage. Critical periods of wheat development when plants are vulnerable to damage from high temperatures and drought include the flowering and seed-filling stages [10–12]. Maintenance of photosynthetic leaf activity under adverse conditions is an indicator of genotype resistance. ^{13}C discrimination has been identified as a suitable characteristic for the selection of genotypes with different responses to water deficit; indirect indicators include plant temperature [11,13–15].

The effects of drought on the growth, yield, and grain quality of wheat involve processes and factors which interact with genetically determined traits of wheat plants. Many researchers have sought to evaluate the relationship of genotype plant traits to water availability, especially in terms of drought tolerance, impacts on yield, and yield traits, but often in young plants only, under controllable conditions. Researchers have assumed that older varieties, landraces, or ancient species of wheat would show better resistance to abiotic and biotic stresses, as well as improved nutritional characteristics [16,17].

Under transitional climate conditions, whole years or shorter periods of water deficit alternate unpredictably with times of sufficient rainfall, at least during part of the crop-growing season. Container experiments do not reveal the effects of the gradual depletion of the water supply upon the deep layers of the root zone. To obtain reliable multi-year data in field conditions, and thus enable a comparison of root zone effects caused by different levels of water availability, it is necessary to manipulate the water content by means of irrigation and mobile shelters [18–21].

In this study, as a working hypothesis, we assumed that in the period after flowering, in the stage of grain growth, water deficit would result in a significant yield reduction corresponding to other plant characteristics. We sought to compare, under field conditions, the different effects of drought and adequate-water-supply conditions after flowering on the yield and other characteristics of common wheat cultivars and ancient relatives of wheat. In the period prior to flowering, conditions were the same for plants in all groups; all plants therefore entered the period of differentiated water availability with the same characteristics and the same canopy structures.

2. Materials and Methods

2.1. Site Description

The field trial was performed between 2018 and 2021 in Ruzyně, near Prague, in the Czech Republic (Figure 1). The experimental plots were on deep clay and clay-loam soil formed on loess (Haplic Chernozem soil on loess), the level of ground water is under 6 m depth. The altitude was 340 m, average temperature was 9.6 °C, annual precipitation was 497.5 mm and potential evapotranspiration 720 mm. This soil has a high nutrient content and water capacity. Table 1 shows soil and climatic conditions. Figure 2 gives details of precipitation, temperature, potential evapotranspiration and water balance, calculated as precipitation minus reference evapotranspiration [22], in the experimental years.

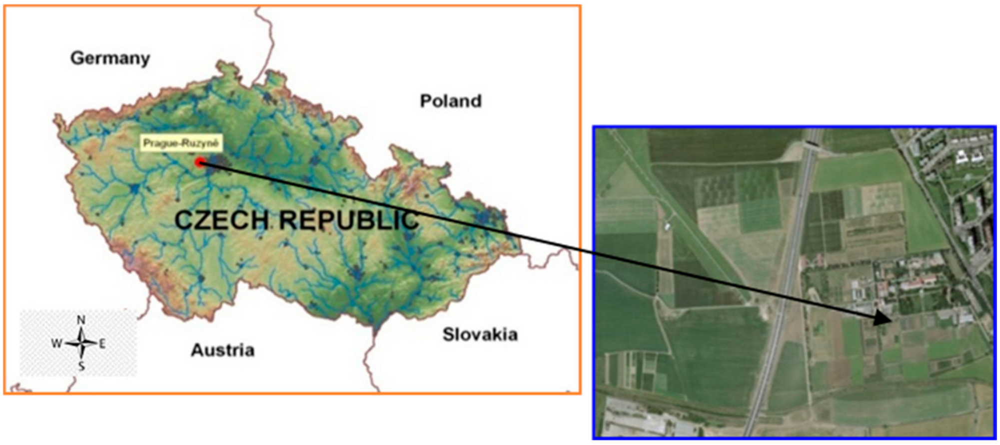

Figure 1. Experimental site.

Table 1. Site characteristics.

Geographic Coordinates	Unit	49°53′29″ N, 15°23′38″ E
Altitude	m a.s.l.	340
Average temperature (1991−2020)	°C	9.6
Average precipitation (1991−2020)	mm	497.5
Available P, K, and Mg [23]		
Topsoil (0–30 cm)		78, 284, 212
Subsoil (30–50 cm)	mg. kg $^{-1}$ soil	29, 180, 210
Deep subsoil (50–130 cm)		2.8, 156, 334
pH/KCl (from top to deep subsoil)	-	6.76, 7.14, 7.19
C_{org} (from top to deep subsoil)	%	1.47, 1.30, 1.07
N_{total} (from top to deep subsoil)	%	0.16, 0.11, 0.04
Soil texture		
Topsoil (0–30 cm)		Silt loam
Subsoil (30–50 cm)	-	Silt loam
Deep subsoil (50–130 cm)		Silt clay loam, Clay loam
Field water capacity (laboratory)	Vol.%	34.5–37.2
Wilting point (laboratory)		15.7–16.2
Maximum water volume observed at spring	Vol.%	
Topsoil (0–30 cm)		29.6
Subsoil (30–50 cm)		31.4
Deep subsoil (50–130 cm)		32.1

2.2. Experimental Design

The experiment had three variants of water supply. Differentiation occurred after the flowering stage. This approach ensured that all plants entered the period of differential water supply in the same physiological state, so that their canopies had the same structure, biomass, and number of ears. In addition, all the plants of each wheat cultivar entered this period with the same depth and size of root systems, as a result of their sharing the same water conditions prior to anthesis. Water deficit (S) was induced using a mobile shelter. The mobile shelter is a metal structure with a special plastic polycarbonate roof and walls, which moves on rails placed on the trial area in early spring, the edge walls protect the vegetation from rain water. Rainwater was drained by gutters outside the experimental area. The cover is moved over the plots only in case of heavier rain (over 3 mm), occurring usually in afternoons, or persistent rain to reduce the effects on microclimate. From flowering stage (BBCH 60–65) onwards, crops were covered during rainfall so that the content of available water in the soil layer to a depth of 90 cm fell to the level of reduced water availability, below 30% of the available water capacity (AWC), when symptoms of water stress already appear. After flowering, during the grain growth stage (BBCH > 70), water content decreased due to water extraction by the roots, up to the wilting point. Considering the low rainfall, and the high water consumption by the plant during stem elongation, it was sufficient for this purpose to drain away any heavier rainfall before flowering. The optimal water supply (IR) was ensured by drip irrigation so that, from the flowering stage, the water content in the 90 cm layer was kept above 70% and under 85% of AWC. The drip hoses were placed in every third row, so the spacing was 37.5 cm. In the years 2018–2021, totals of applied additional irrigation were 234 mm, 224 mm, 186 mm, and 207 mm, respectively. From the S variant, 92 mm, 96 mm, 128 mm, and 175 mm of precipitation were drained away in the four experimental years. Differences in irrigation rates and retained rainfall between wheat cultivars due to different development rates were in the order of millimeters.

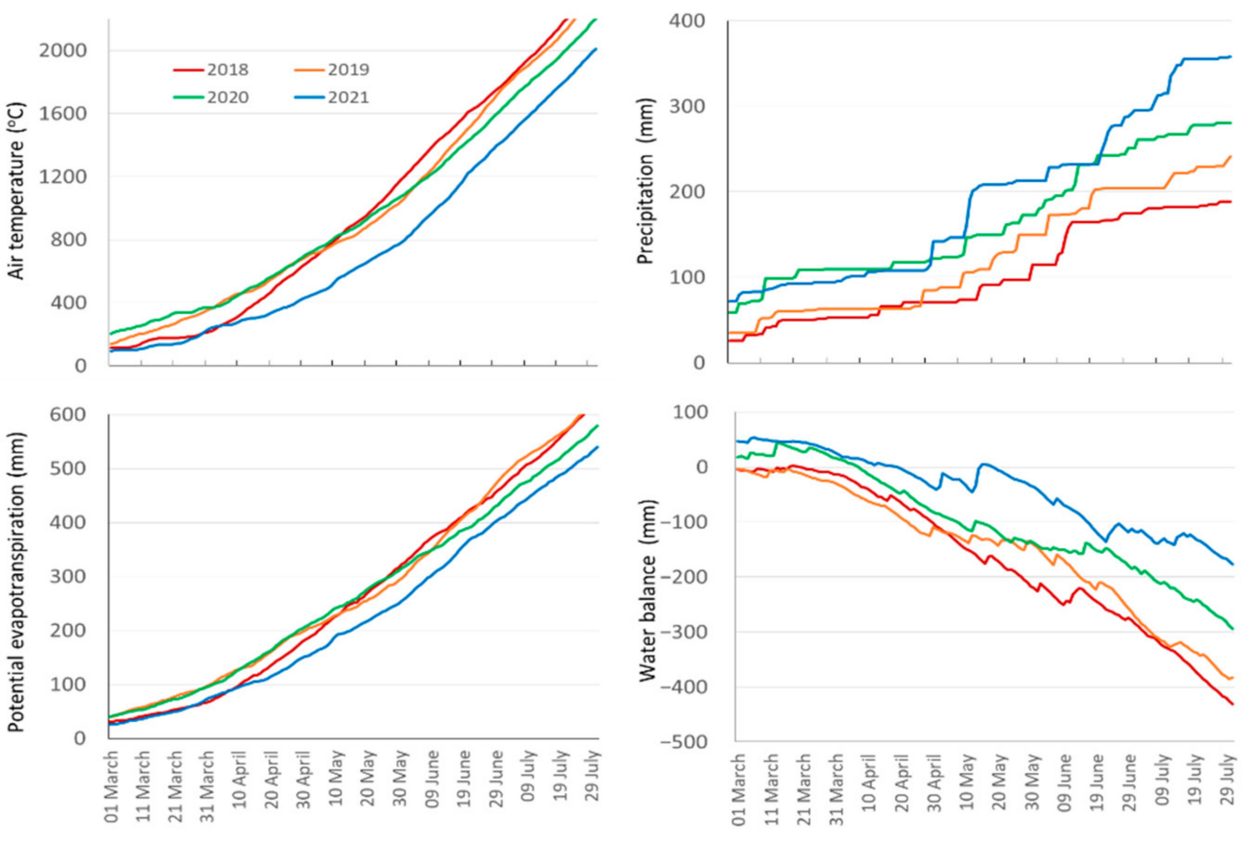

Figure 2. Temperature, precipitation, potential evapotranspiration and water balance, accumulated since 1 January of the given year.

The differentiation of available water content for variants S and IR was determined by a calculation of current evapotranspiration [22] and water balance, corrected for soil moisture monitoring. There is no surface runoff on the near flat field during wheat growth. The groundwater level is deep and the capillary rise from the deeper layers is probably negligible due to the distribution of the roots and according observed apparent depletion from the 0–120 cm layer in previous years. Precipitation during vegetation on this site and soil with a high water capacity does not percolate into deeper layers. Therefore, for the given purpose, the calculation of the water balance and daily change of soil water content (ΔSW) was simplified, as ΔSW = irrigation + precipitation − kc. ETo, where crop coefficient (kc) was based on numerous observations of water depletion by wheat crop in previous years. Soil moisture to depth 120 cm was determined before flowering, twice during grain filling and at maturity. The control (rain-fed) variant (C) depended only on rainfall and water supply in the soil. Precipitation, temperature, humidity, solar radiation, and wind speed were measured at a station 100 m away from the experimental site (www.vurv.cz/meteostanice, accessed on 10 September 2022).

2.3. Examined Species and Cultivars, Sampling and Analysis

In the years 2018 and 2019, the modern Rebel and Ponticus cultivars of common winter wheat (*Triticum aestivum* L.) were monitored; in the years 2020 and 2021 the cultivars Artix and Butterfly were studied (Table 2). In 2018 and 2019, we also monitored spelt wheat (*Triticum spelta* L.), cultivar Rubiota, and in 2020 and 2021 we monitored einkorn wheat (*Triticum monococcum* L.), cultivar Rumona. The row spacing was 12.5 cm. Sowing density was 4.0 million germinating seeds per hectare for common wheat, 2.7 million for spelt, and 3.5 million for einkorn. A total of 100 kg N/ha was applied, of which 40 kg was applied in the spring regeneration stage, at the beginning of tillering (BBCH 20–22) and the remainder at the beginning of heading (BBCH 30–31). The pre-crop was a legume–cereal mixture. Standard tillage and plant protection practices were applied.

Table 2. Characteristic of cultivars.

Cultivar	Ponticus	Butterfly	Rebel	Artix	Rumona	Rubiota
Baking quality	E	E	A	B–C	-	-
Earliness	mid early	mid late	mid late	very early	mid late	mid late
TGW	medium	high	medium	medium	medium	small
Maintainer	Dr. Hermann Strube, DE	SELGEN, a.s., CZ	RAGT 2n, FR.	SELGEN, a.s., CZ	VÚRV, v.v.i, CZ	VÚRV, v.v.i, CZ

The experiment had a cross-section design, with blocks of water availability variants, with 2 (S, IR) or 4 (C) replications. Plots were either 5 m × 6 m, or 6 m × 6 m, in size. The harvest plot was 6 m × 2.3 m. For variant S, the size of the plots was 3 m × 3 m. The harvest was carried out with a small-plot combine harvester. At maturity, whole plants were sampled from each plot. Two samples were taken from an area of 0.25 m^2 for HI determination. Plants were cutting at soil surface and HI is the proportion of grain to total dry biomass of the plants. The discrimination of ^{13}C was determined on an elemental analyzer coupled to an isotope-ratio mass spectrometer [20] (EA 3200, Eurovector, Italy; connected with IRMS Isoprime, GV Instruments, UK, in 2018 and 2019) and (EA Vario PYRO cube, Elementar, Germany; with IRMS Isoprime precisION, Elementar, UK, in 2020 and 2021).

2.4. Plant Temperature

The canopy temperature was measured during the grain growth stage (BBCH 73−83) with a handheld FLIR F6 camera (FLIR Systems, USA). Measurements were taken between 12 and 2 p.m., under a cloudless sky, in moderate or negligible wind conditions. The camera was held approximately 50 cm above the canopy at an angle of 45 degrees. Measurement times were always 30−40 min, so that conditions were as even as possible. Measurements were taken repeatedly for each variant on all plots, to reduce the influence of minor variations in conditions at the time of measurement; the resulting temperature values were averages of at least 8 measurements. The temperature values of the measured vegetation area were read using the FLIR Tools program (Teledyne FLIR, Wilsonville, OR, USA).

2.5. Statistical Analysis of Data

Statistical evaluation was performed using the STATISTICA 14 program (StatSoft, Inc., Tulsa, OK, USA). After checking for normality, the effects of different treatment upon different cultivars were analyzed with a two-way factorial analysis of variance (ANOVA); the differences among means were evaluated with Tukey's HSD test (at $p < 0.05$).

The relationship between the grain yield and the investigated characters was evaluated using correlation analysis, and Pearson's coefficient was calculated.

3. Results

3.1. Climatic Conditions during the Trial Period

Climatic conditions were different in each of the experimental years. The driest and warmest year was 2018, and the highest amount of precipitation was in 2021. The water balance corresponded to these conditions (Figure 2). The total doses of irrigation were similar in the experimental years, in line with the experimental objective of replenishing water supply to the target level, to a depth of 90 cm.

3.2. Effect of Drought and Irrigation on Grain Yield

In the individual years from 2018 to 2021, average yields of common wheat cultivars in the rain-fed control were 7.02 t.ha^{-1}, 5.66 t.ha^{-1}, 9.37 t.ha^{-1}, and 8.81 t.ha^{-1}, respectively. For spelt, the yields of the control variant were 2.85 t.ha $^{-1}$ in 2018, and 1.01 t.ha^{-1} in 2019. For einkorn, control yields were 3.31 t.ha^{-1} in 2020, and 3.15 t.ha^{-1} in 2021 (Table 3). Plants subjected to water deficit exhibited significant reductions in yields in all years. For common wheat, average yields were 68.00% of those of the rain-fed control, and 63.10% of the comparable figure for irrigated wheat. For spelt and einkorn, average yields were 78.30% of the control, and 70.40% of the irrigated wheat. Thus, the relative decrease in grain yield due to drought was a little lower for spelt and einkorn than for common wheat cultivars. These old wheat species had significantly lower yields and HI values. The yields of old wheat represented on average 33.45%, 38.52% and 34.53% of the yield of common wheat in variants C, S and IR, respectively.

Table 3. The results of the analysis of the variance (ANOVA) of grain yields.

	Factor	2018	2019		2020	2021
	Variant	<0.001	<0.001		<0.001	<0.001
	Wheat cultivar	<0.001	<0.001		<0.001	<0.001
	Variant × Wheat	<0.001	<0.001		0.065	0.01
Variant	**Cultivar**	**Yields (t.ha^{-1})**		**Cultivar**	**Yields (t.ha^{-1})**	
C	Ponticus	7.01 ± 0.32 b	5.98 ± 0.29 b	Artix	9.58 ± 0.64 a	8.94 ± 0.58 ab
	Rebel	7.03 ± 0.16b	5.33 ± 0.39 b	Butterfly	9.16 ± 0.51 ab	8.67 ± 0.44 ab
	Rubiota	2.85 ± 0.12d	1.01 ± 0.10 d	Rumona	3.31 ± 0.35 d	3.15 ± 0.53 c
S	Ponticus	3.85 ± 0.07 c	3.72 ± 0.23 c	Artix	7.78 ± 0.73 bc	6.41 ± 0.025 b
	Rebel	4.12 ± 0.11 c	3.57 ± 0.19 c	Butterfly	6.23 ± 1.43 c	6.27 ± 0.19 b
	Rubiota	2.46 ± 0.025 d	0.86 ± 0.21 e	Rumona	1.76 ± 0.14 e	3.00 ± 0.14 c
IR	Ponticus	7.50 ± 0.22ab	7.12 ± 0.01 a	Artix	9.38 ± 0.14 ab	8.15 ± 0.40 ab
	Rebel	8.19 ± 0.05 a	7.39 ± 0.17 a	Butterfly	9.71 ± 0.59 a	9.00 ± 0.67 a
	Rubiota	3.70 ± 0.30 c	1.16 ± 0.23 d	Rumona	3.16 ± 0.22 de	3.45 ± 0.19 c
			Average data			
	C	5.63 ± 0.54 b	4.11 ± 0.69 b	C	7.35 ± 3.01 a	6.92 ± 2.44 a
	S	3.48 ± 0.77 c	2.72 ± 0.97c	S	5.25 ± 2.61 b	5.22 ± 1.57 b
	IR	6.46 ± 0.77 a	5.22 ± 2.97 a	IR	7.41 ± 2.86 a	6.86 ± 2.67 a
			Average data			
	Ponticus	6.12 ± 1.48 b	5.61 ± 1.26 b	Artix	8.91 ± 0.87 a	7.83 ± 1.13 a
	Rebel	6.45 ± 1.51 c	5.43 ± 1.38c	Butterfly	8.37 ± 1.45 b	7.98 ± 1.19 b
	Rubiota	3.0 ± 0.49 a	1.01 ± 0.20 a	Rumona	2.74 ± 0.69 a	3.20 ± 0.42 a

Note: The cultivar means and means of variants with the same letter at the given year do not differ significantly at $p \leq 0.05$ according to Tukey HSD. Means ± std. deviation are shown.

Significantly higher yields were recorded for irrigated plants, compared to rain-fed crops, in the two drier years of 2018 and 2019. For common wheat, the yields were 11.8% and 28.3% higher in these two years; for spelt, the yields were 29.8% higher in 2018, and 14.8% higher in 2019 (marginal significance).

3.3. Effect of Drought and Irrigation on Canopy Temperature

A higher canopy temperature was a reliable indicator of water deficit. Canopy temperatures revealed significant effects of water supply differentiation for all years and measurement terms, except for one measurement in 2018 (p = 0.46) (Table 4). Based on an average of all years and terms of measurement, common wheat variants C, S and IR had temperatures of 27.07 °C, 28.24 °C, and 24.36 °C, respectively. For spelt and einkorn, the corresponding temperatures were lower than for common wheat, i.e., 26.59 °C (C), and 27.61 °C (S), but slightly higher in irrigated crops (24.94 °C). The temperature differences between the two cultivars of common wheat were mostly insignificant on the control variant, but significant temperature differences were noted on the stressed variant. The average temperature of cultivar Artix was 0.80 °C to 2.34 °C higher than that of Butterfly.

Table 4. Results of the analysis of the variance of the wheat growth temperature.

		2018	**2018**	**2019**	**2019**		**2020**	**2020**	**2021**	**2021**
BBCH		71–73	75–79	77–81	79–82		73–76	76–83	69–72	75–81
	Variant	<0.001	0.046	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001
	Wheat cultivar	<0.001	<0.001	0.28	0.47		<0.001	<0.001	<0.001	<0.001
	Variant × Wheat	0.028	0.035	<0.001	<0.001		0.067	0.024	<0.005	<0.001
Variants	**Cultivar**	**Canopy temperature (°C)**				**Cultivar**	**Canopy temperature (°C)**			
C	Ponticus	32.53 bc	28.97 ab	27.54 a	31.26 ab	Artix	24.40 c	20.30 c	25.88 b	25.30 b
	Rebel	32.70 bc	29.54 a	27.35 a	31.70 a	Butterfly	24.37 c	20.36 c	25.69 bc	25.23 b
	Rubiota	31.23 c	29.08 ab	27.08 a	31.98 a	Rumona	23.32 c	19.15 c	26.10 b	24.74 bc
S	Ponticus	33.95 ab	28.58 ab	27.67 a	31.29 ab	Artix	28.08 a	23.15 a	26.28 b	28.08 a
	Rebel	36.05 a	29.93 a	27.70 a	31.83 a	Butterfly	26.36 b	21.63 b	25.47 bc	25.74 b
	Rubiota	31.50 bc	27.36 bc	27.28 a	31.88 a	Rumona	25.20 bc	21.84 ab	27.55 a	28.16 a
IR	Ponticus	26.20 d	25.97 c	22.33 c	25.58 c	Artix	25.33 bc	21.13 b	24.43 cd	25.46 bc
	Rebel	26.90 d	25.92 c	21.33 c	25.33 c	Butterfly	24.85 bc	20.73 bc	24.65 cd	23.69 c
	Rubiota	26.00 d	26.33 c	24.90 b	30.08 b	Rumona	24.23 c	18.95 c	24.08 d	24.96 bc
						Average data				
	C	32.15 b	29.20 a	27.32 a	31.65 a	C	24.03 c	19.94 b	25.89 b	25.09 b
	S	33.83 a	28.63 a	27.55 a	31.56 a	S	26.55 a	22.21 a	26.43 a	27.33 a
	IR	26.37 c	26.07 b	22.85 b	27.00 b	IR	24.8 b	20.27 b	24.38 c	24.70 c
						Average Data				
	Ponticus	30.89 b	27.84 a	25.85 a	29.38 a	Artix	26.01 a	21.61 a	25.53 a	26.28 a
	Rebel	31.88 a	28.47 a	25.46 a	29.62 a	Butterfly	25.30 a	20.89 ab	26.27 a	24.89 b
	Rubiota	29.58 c	27.59 a	26.42 a	31.31 a	Rumona	23.78 b	20.09 b	25.91 a	25.96 ab

Note: The means of temperature and means of treatments with the same letter at the given year do not differ significantly at $p \leq 0.05$.

We found that the relationship between temperature and final grain yield was dependent upon the state of the crop at the time of measurement, especially for the control variant with fluctuating water supply. Correlation coefficients of the relationships between canopy temperatures and yields were always negative, and mostly insignificant (Table 5). For common wheat, the correlation coefficient varied between −0.39 and −0.84; for spelt and einkorn, the figure varied between −0.56 and −0.99, in individual years and in terms of measurement.

Table 5. Correlation between grain yield and grain ^{13}C discrimination or canopy temperature.

		2018		2019		2020		2021	
Yield vs. ^{13}C discrimination	common wheat,	0.98 **		0.97 **		0.98 **		0.86 *	
	spelt, eincorn	0.98		0.99*		0.86 *		0.78	
	Term of	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Yield vs. Canopy temperature	common wheat,	−0.81 *	−0.63	−0.84 *	−0.84	−0.68	−0.62	−0.39	−0.75
	spelt, eincorn	−0.96	−0.56	−0.9	−0.84	−0.91	−0.99 *	−0.99 *	−0.72

Note: *—significant at 0.05 level, **—significant at 0.01 level.

3.4. The Effect of Drought and Irrigation on ^{13}C Discrimination

Grain ^{13}C discrimination (Δ ^{13}C) clearly differentiated stressed plants from irrigated crops in all years and corresponded to the effect of drought and irrigation on yields (Table 6). For all wheat, across all the experimental years, the average Δ ^{13}C values were 19.51‰, 17.78‰, and 20.51‰, for variants C, S, and IR, respectively. For all the variants, the Δ ^{13}C values for each year from 2018 to 2021 were 17.92‰, 18.59‰, 20.59‰, and 20.65‰, respectively, in agreement with annual weather conditions.

Table 6. Results of analysis of variance of ^{13}C discrimination in grain of three wheat genotypes.

		2018	2019		2020	2021
ANOVA	Variant	<0.001	<0.001		<0.001	<0.001
	Wheat cultivar	<0.001	<0.001		<0.001	0.008
	Variant × Wheat	0.264	0.101		<0.001	<0.001
Variant	**Cultivar**			**Cultivar**		
C	Ponticus	18.50 bc	19.04 b	Artix	20.75 bc	21.04 ab
	Rebell	18.93 ab	18.90 b	Butterfly	20.35 c	20.67 b
	Rubiota	16.98 d	17.64 c	Rumona	19.58 d	21.38 ab
S	Ponticus	16.46 d	17.58 c	Artix	19.23 de	19.97 d
	Rebell	16.67 d	16.91 cd	Butterfly	18.64 e	19.56 d
	Rubiota	15.06 e	16.60 d	Rumona	17.48 f	18.95 e
IR	Ponticus	19.76 ab	20.87 a	Artix	21.14 ab	21.35 ab
	Rebell	19.92 ab	20.24 a	Butterfly	20.61 c	20.90 ab
	Rubiota	19.04 abc	19.36 ab	Rumona	21.23 ab	21.47 a
				Average data		
	C	18.14 b	18.53 b	C	20.23 b	21.03 a
	S	16.06 c	17.03 c	S	18.45 c	19.49 b
	IR	19.57 a	20.16 a	IR	20.99 a	21.24 a
				Average data		
	Ponticus	18.24 a	19.16 a	Artix	20.37 a	20.79 a
	Rebell	18.51 a	18.68 a	Butterfly	19.87 b	20.38 a
	Rubiota	17.03 b	17.87 b	Rumona	19.43 b	20.60 a

Note: The means of Δ ^{13}C and means of treatments with the same letter at the given year do not significantly differ at $p \leq 0.05$.

The effect of the variants was highly significant in all years. Differences in precipitation in the experimental years were manifested by significant differences in Δ ^{13}C between variant C and IR in the dry years 2018 and 2019, while in the wet years of 2021 and partially 2020, the effect of irrigation was not significantly different from the rain-fed control variant.

Similarly, in 2020 and 2021, the yields of the variants under irrigation were not significantly different from the yields of the control variant (Table 6).

The values of grain Δ ^{13}C positively correlated with yields of both common and ancient wheat for all years from 2018 to 2021, though less closely in 2021 when more significant rainfall occurred. For common wheat, the correlation coefficients were 0.98, 0.97, 0.95, and 0.86, respectively, for each of the experimental years; for spelt and einkorn, the corresponding figures were 0.98, 0.99, 0.86, and 0.78.

The Δ ^{13}C values of Artix were higher than those of Butterfly at all levels of water availability, but yields were higher for Artix only in 2020. The Δ ^{13}C values of cultivars Ponticus and Rebel (2018−2019) typically exhibited no significant differences.

Spelt and einkorn showed lower Δ ^{13}C in comparison with common wheat, by 1.35 ‰ and 0.99 ‰ (einkorn) and 0.69 ‰ (spelt), suggesting a greater impact of differentiated water supply. The wetter weather in 2021 (difference −0.18 ‰) reduced the differences between wheat types (Figure 3, Table 6).

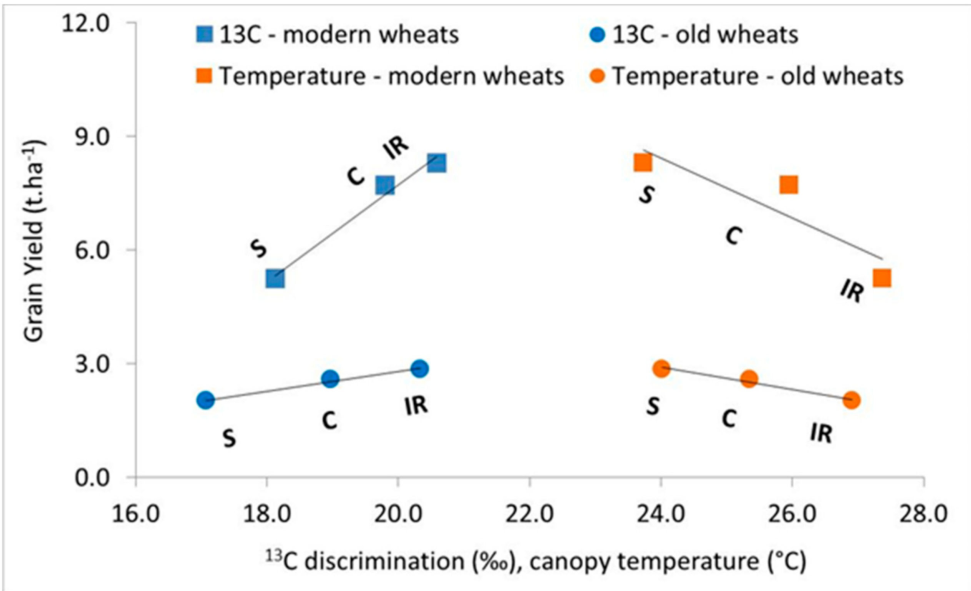

Figure 3. The relationships between grain yield and grain ^{13}C discrimination or canopy temperature averaged over experimental years. The yield data represent average of experimental years and cultivars; temperature data are averages of two measuring terms, experimental years and cultivars.

4. Discussion

4.1. Grain Yield

Effects of post-anthesis drought on yields were strong and significant in all years, although crops in all variants experienced identical conditions prior to flowering. This finding confirms that, even under transitional climate conditions, during the relatively short period of grain filling, water deficit is a significant factor affecting yields. In contrast, irrigation during this period had a significant positive effect compared to rain-fed vegetation only in the drier years of 2018 and 2019. The grain yield does not depend only on precipitation and water balance, but also on root growth and the use of water resources in the deep layers of the subsoil [24]. Under the given soil conditions, the roots of winter wheat reach below 1-m depth and are thus able to use the water reserve from the winter period [25,26]. However, root depth varies across years, in response to autumn growth and weather conditions for overwintering, thus introducing another element of variability in the response of wheat to the water supply.

Observations revealed slight differences in the responses of different wheat species to drought conditions. Compared to the rain-fed control, the relative yield reduction in common wheat was 13% higher than the corresponding figure for spelt and einkorn.

In this regard, relevant findings in the literature are rather inconsistent; for example, Pandey et al. [17] reported improved tolerance of terminal heat stress in crosses of spring wheat in comparison with spelt wheat. In contrast, Csákvári et al. [16] found that modern winter wheat had a better yield and grain quality compared to einkorn. Fang et al. [27] attributed the improved yields of modern wheat cultivars in their experiment to improved root system traits. In comparison with common wheat cultivars, the potential benefits of better drought tolerance in wheat ancestors are reduced by the low HI of these genotypes.

The water content in the root zone of the rain-fed variants varied (depending on the water depletion by crop, distribution, and amount of precipitation) between the irrigated and stressed stands but was mostly closer to the S variant (not presented).

It should be mentioned that both spelt and einkorn plants are taller than common wheat by several tens of centimeters. These plants tended to lodge already during the stem elongation stage, especially the irrigated variants, but also some rain-fed variants. This may have impaired leaf function and grain growth [28]. Together with the low HI and overall low yield potential, these differences in response to drought might alternatively be interpreted as demonstrating the inability of spelt and einkorn to exploit better moisture conditions in the C and IR variants.

4.2. Canopy Temperature

Water deficit, or water stress, causes stomata to close and increases the temperature of the canopy; contrarily, an adequate water supply allows transpiration without restriction and cools the surface of plants [10,11]. The higher temperature of stressed plants was confirmed in this experiment. Measurements with a hand-held thermal camera can reliably indicate a lack of water (Table 4). The differences in the temperatures of the irrigated and rain-fed stands were not always conclusive, as they depend on the current availability of water in the root zone of the control crop. The relationship between temperature and grain yield was mostly moderate-to-strong, except for the rainy year 2021. Katimbo et al. [29] reported that CWSI (a stress index based on the difference between canopy and air temperature) was more sensitive to soil water depletion when depletion exceeded 80% of available water content.

Interpreting temperature differences between examined crops in terms of yield reduction due to drought is not simple, as the morphologies of individual cultivars and species, leaf positions, and responses to drought differ. In the water-deficit condition, we observed significant leaf curling in the Butterfly cultivar in comparison with Artix. The observed wheat plants also exhibited different development rates. Spelt and einkorn wheat developed more slowly, were taller, and presented narrower leaves and smaller ears. However, Anderegg et al. [30] reported that temporal trends in wheat canopy temperature had high repeatability and were largely independent of canopy structure and phenology. This is in line with our finding that, despite different rates of development, and different shoot and ear morphologies, the canopy temperatures of einkorn and spelt did not significantly differ from those of common wheat cultivars.

At the level of individual cultivars, differences in canopy temperature and $\Delta\ ^{13}C$ did not always correspond to yield differences. The significantly higher temperatures of stressed (also IR) plants of the Artix cultivar compared to Butterfly in 2020 corresponded to lower grain $\Delta\ ^{13}C$ values but not to higher yields in stressed Artix plants, indicating a different response to drought (Tables 3–6). Thakur et al. [21] on fifteen diverse genotypes of wheat released for cultivation under different environmental conditions (water shortage, irrigation) found that canopy temperature was correlated with grain weight regardless of water stress treatment. They concluded that precise phenotyping for canopy temperature at a sensitive growth stage would help in exploring QTLs for cooler canopy temperature as a potential trait for heat stress tolerance in wheat. Temperature, as a possible trait for selection, has been considered in several studies such as Gautam et al. [31].

Due to the need to measure temperature under identical meteorological conditions, measurements in our experiment were taken at the same time chronologically, rather than at the same stage of growth. This might contribute to occasionally consistent results. Our experience of monitoring canopy temperature showed that, even a tiny change in conditions, such as a small gust of wind, or a near-negligible formation of cloud, can affect the temperature of the stand in a matter of seconds. For this reason, we conclude that the measurement of stand temperature, if performed at stable conditions, is suitable for indicating differences in plant response to water availability. However, to obtain reliable data on the relationship between temperature and yield responses to water shortage in different wheat cultivars, continuous temperature measurement during the grain growth period may produce more fully representative results [29,32,33].

4.3. Grain ^{13}C Discrimination

Discrimination of ^{13}C in all years and for all observed wheat reliably distinguished grain from plants with a water shortage from those with optimal supply of water during the grain growth period. The differences between the rain-fed control and the irrigated variant were significant in the dry years (2018 and 2019) but mostly insignificant in the years with higher rainfall (2020 and 2021) (Table 6). These results confirmed that the grain $\Delta\,^{13}$C value integrates conditions over a longer period and functions as a proxy for water availability [20,34,35].

Mostly strong correlations between grain yields and grain $\Delta\,^{13}$C values confirm the fundamental influence of water availability on the gas exchange between the atmosphere and plant leaves via stomata, and consequently a direct impact on yield. The observed differences between species and cultivars of wheat indicate certain dependencies, as we found in our comparison of the relative effects of stress on Artix and Butterfly in 2020 and 2021. However, this interpretation requires more detailed studies of yield formation processes, especially the remobilization and reutilization of carbon assimilated prior to anthesis, for grain filling under different water regimes [36,37].

The strong relationship between $\Delta\,^{13}$C, canopy temperature, and grain yield (Figure 3) offers additional possibilities for phenotyping wheat genotypes in terms of short-term and long-term effects of water availability on yields. To the best of our knowledge, few studies have investigated the relationship of $\Delta\,^{13}$C with temperature, or other optical features of vegetation [38,39]. Fisher et. al. [40] described a relationship between higher yield and lower temperature, and between yield and Δ^{13}C, in grains of different spring wheat cultivars bred between 1962 and 1988. Garriga et. al. [41] measured grain Δ^{13}C and used hyperspectral canopy reflectance to estimate grain yield in 384 cultivars of wheat; the best model explained 78% and 60% of yield and $\Delta\,^{13}$C data variability, respectively. Contrarily, Royo et al. [42] concluded, from a field experiment with rain-fed and irrigated durum wheat, that $\Delta\,^{13}$C was the trait that best assessed genotype differences in yield within trials, while reduced canopy temperature during the anthesis and grain-filling periods was a poor indicator in this regard.

5. Conclusions

The results of a four-year field trial with induced water shortage and irrigation of common wheat, spelt and einkorn showed a strong demonstrable effect of drought in the period after flowering, during grain growth, on yield, post-anthesis temperature, and grain ^{13}C discrimination. Thus, the working hypothesis was confirmed. Old wheat species, spelt and einkorn, achieved significantly lower yields than common wheat cultivars, however, the canopy temperature and grain $\Delta\,^{13}$C did not correspond with the great yield gap. Spelt and einkorn showed a slightly weaker reduction of yield under water stress in comparison with better water supply but the interpretation of the observations will demand a deeper understanding of related processes. The determination of canopy temperature and $\Delta\,^{13}$C of the grain provides the possibility for screening the short-term and long-term response of genotypes to different levels of soil water availability or determining the influence of various agronomy measures on plant water availability and management.

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