Responses of winter wheat genotypes to reduced rainfall, nitrogen fertilization and pre-crops in Switzerland

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ABSTRACT

Problem: Wheat (*Triticum aestivum* L.) yields may be reduced by projected rainfall decline due to climate change as well as environmental protection demands for less nitrogen (N) fertilizer inputs.

Research question: Therefore, our study aims to determine how projected decreases in rainfall due to climate change and the reduction of N fertilizer inputs might impact the production of different wheat genotypes.

Methods: A field experiment was carried out in a warm-summer humid continental climate in Switzerland with two water treatments: rainfed and rainout shelters to reduce rainfall during grain filling. This was overlaid with two N treatments (non-fertilized and enough N supply to reach 180 kg N ha^{-1}), four winter wheat genotypes, and three pre-crops (barley, *Hordeum vulgare* L.; oilseed rape, *Brassica napus* L.; winter pea, *Pisum sativum* L.) across three field seasons. Grain yield and protein content, yield related components, water-soluble carbohydrates (WSC), N use efficiency (NUE) and N associated traits, were among the assessed variables. Additionally, soil mineral N (Nmin) was measured at beginning of tillering. The three seasons encompassed both average and above average precipitation. The rainout shelter extended the rainfall range to low rainfall during grain filling, compared to the last 30 years.

Results: The reduced rainfall during grain filling had no impact on yield, regardless of crop season, N fertilizer application, pre-crop, initial Nmin, or genotype. N fertilizer applications had no impact on wheat yield when fields had an initial Nmin > 50 kg N ha^{-1}, nor after a poor crop establishment caused by a wet autumn. During a wet season with initial Nmin ≤ 50 kg N ha^{-1}, wheat responded to N fertilizer after a brassica pre-crop, but less so after a legume or a cereal crop. The genotype with a mean of 29% more grains per unit area, yielded up to 8.2 t ha^{-1} in one plot and, on average, about 25% higher than the mean of the other genotypes.

Conclusions: In the short term, wheat production in warm-summer humid continental climates appears resilient to projected rainfall decline from climate change and reductions of N fertilizer inputs, but excessive rainfall during sowing causing poor crop establishment might be much more devastating. The impact on wheat yields observed only on the third year of consecutive cultivation without N fertilizer, suggests the potential for decreasing N supply over a few years.

Implications or significance: This study underscores wheat's short-term resilience to drought and reduced N use, bolstering food security efforts.

1. Introduction

Climate is a key driver of agricultural production, playing a significant role in shaping the variability of global food production (Selvaraju et al., 2011). Fluctuations in temperature, precipitation, and other factors directly influence crop growth, yield, and overall agricultural productivity. These effects, which vary across the globe (Ewert et al., 2015; Nsafon et al., 2020; Pequeno et al., 2021), are estimated to contribute to around one third of the observed global variability in crop yields (Ray et al., 2015). In 2018, crop failures in Europe's breadbasket regions, like the northern European countries, were mainly caused by droughts and heatwaves (Beillouin et al., 2020; Webber et al., 2020).

Heavy precipitation is likely to increase during winter in northern and central Europe, while drought is expected to increase in duration and intensity in southern and, to some extent, central regions of Europe (IPCC, 2014). This is due to changes in rain distribution linked to higher temperatures (Pingale et al., 2014) and more frequent, intense heatwaves. Consequently, there is a higher risk of heat and drought stress as these changes contribute to increased soil water loss through evapotranspiration (Fuhrer et al., 2006). Climate change will worsen and expand these extreme weather conditions (Battisti and Naylor, 2009; IPCC, 2021).

Wheat (*Triticum aestivum* L.) is a staple crop worldwide (Peña-Bautista et al., 2017). Drought has a significant negative impact on its yield (Fuhrer et al., 2006), especially in Europe where it is the main limiting factor for wheat production (Webber et al., 2018). This is a concern for Switzerland, where major wheat-growing areas are expected to experience hotter and dryer summers, with a 43% decrease in precipitation by the end of the century (CH2018, 2018; Fischer et al., 2022). Although an increase in atmospheric carbon dioxide (CO_2) due to climate change could enhance photosynthesis and boost wheat growth, in water deficiency conditions, the carbon fertilization effect declines (Zheng et al., 2020). Drought affects wheat plants in various ways, including reducing CO_2 uptake and photosynthetic performance due to stomatal limitation (Zandalinas et al., 2018). It also disrupts nutrient availability for the plants (Marschner and Rengel, 2012).

Water scarcity during early reproductive phases has a significant impact on wheat yield (Ji et al., 2010) and can affect grain production during seed formation (Onyemaobi et al., 2017). During the grain filling stage, it leads to small grains with lower milling percentage (Steduto et al., 2012). However, the presence of water-soluble carbohydrates (WSC) in the stem, a source of carbon for grain filling, serves as a protective mechanism, offering resilience and buffering yield during reproductive stages (Blum, 1998). In addition to the studied effects of rising temperatures on wheat (Lobell and Gourdji, 2012; Rezaei et al., 2015), the combined stress of heat and drought further impacts photosynthesis (Zahra et al., 2021; Ru et al., 2023a) and grain development, particularly during booting and anthesis stages (Zahra et al., 2021). Farmers aim to attain the optimal-economic yield and remain competitive (McLellan et al., 2018), but uncertain weather conditions significantly impact crop management decisions, including nitrogen (N) fertilization (Asseng et al., 2008; Asseng et al., 2016).

Nitrogen is crucial for crop yield and protein concentration in wheat (Steduto et al., 2012; Zörb et al., 2018), affecting the suitability of grains for various uses, such as baking quality (Zörb et al., 2018). If applied excessively, it may result in abundant vegetative growth, and elevated water consumption, with, often, no proportional increase in grain yield (Steduto et al., 2012). If there is also a low N fertilizer recovery, it can cause off-site pollution of air, groundwater and waterways and climate warming (Zörb et al., 2018). In a study in farms in Switzerland, for example, the mean N balance (N input - N output) was 89 kg N ha^{-1}, as a result of mean N input of 255 kg N ha^{-1}, with significantly differences between farms (Jan et al., 2017). Although it seems high, the Swiss levels of N surplus are considered intermediate compared to other European countries (Spiess and Liebisch, 2020). In response to this situation, the N supply should be reduced to comply with the European Union's Nitrates Directive (91/676/EEC), issued in 1991 (EU Commission, 1991), which aims at preventing water pollution from agricultural nitrates. Although the reduction is necessary, limited N availability during the growth of wheat could compromise its final productivity and quality. A global meta-analysis has shown increases of 37.6% and 49.5% in wheat yield when the N application rate ranged between 0 to 100 kg N ha^{-1} and 100 to 200 kg N ha^{-1}, respectively, compared to non-fertilized conditions, while the grain protein had reasonably increase in all N supplies (Wang et al., 2023). Adequate N supply could also alleviate abiotic stress on wheat, like drought stress (Ru et al., 2023b), by boosting plant growth and biomass accumulation (Agami et al., 2018), and help in a changing climate. However, the N uptake is highly modulated by the soil water availability, thus, in water limited conditions, crops can have water and N limitations simultaneously (Plett et al., 2020).

The impact of water stress could also be reduced through the cultivation of drought tolerant genotypes and effective associated crop management strategies (Farooq et al., 2014). Drought tolerance, defined as the capacity of plants to thrive, develop, and reproduce effectively in intermittent water scarcity or absence, requires self-adaptation in physiology, root structure, and growth, from the part of the plants, to adapt to the soil water gradient (Shi et al., 2022). The drought tolerant genotypes could also perform better under N-limited conditions. In study of Fan and Li (2001), a more drought tolerant winter wheat lines had greater N efficiency than less tolerant ones. Similar results were found by Raya-Sereno et al. (2023). Additionally, crop rotation influences nutrient availability, water, diseases, and soil structure (German et al., 2017). The use of a legume (Williams et al., 2014) or a brassica (Angus et al., 2015) as a "break crop", can boost cereal yield, due to the break of diseases and weeds cycles, and the increase in N availability (Seymour et al., 2012), which often results in higher yields than in a cereal-cereal rotation (Cernay et al., 2018). Also, a cereal-legume rotation can increase water percolation and aeration in soil, promote more efficient nutrient and water use (Zani et al., 2023), and increase wheat grow with limited water and nutrient resources. However, the effect of grain legumes on cereal yields might depend on the N fertilization rate applied to subsequent cereals (Williams et al., 2014).

Global agricultural productivity is constrained by climate change (Ortiz-Bobea et al., 2021). Due to its effects on wheat production, as well as the diverse growing conditions worldwide (Pequeno et al., 2021), there is a need for region-specific adaptations strategies (Zhao et al., 2017; Pequeno et al., 2021). The projected decrease in rainfall coupled with the need for reduced nitrogen fertilizer inputs to meet environmental protection requirements in warm-summer humid continental climates, pose challenges to wheat yields. The complexity of optimal N management, influenced by environmental conditions, cropping systems, and genotype, necessitates exploration of integrated strategies tailored to specific regions. Amidst these challenges, we propose that wheat yield resilience in warm-summer humid continental climates, facing reduced rainfall and nitrogen inputs, can be improved through targeted genotypes, pre-crop selection, and strategic nitrogen management. This is particularly relevant, considering that many cultivated areas may have high residual nitrogen levels from previous agricultural practices (Argento et al., 2022), and that wheat growth is N limited in Swiss conditions (Oberholzer et al., 2014). This study aimed to assess the effects of projected rainfall decline in Switzerland and reduced nitrogen inputs on the yield of four winter wheat genotypes differing in drought tolerance (Touzy et al., 2019), and cultivated after three pre-crops. The main objectives of our study were to test the following hypotheses: (1) projected rainfall during grain filling decreases grain yield of winter wheat in Switzerland; (2) a legume pre-crop, which increases nitrogen availability, is expected to mitigate the decrease in wheat production under reduced N availability more than a brassica or a cereal pre-crop; (3) reduced rainfall and N fertilizer input impacts production differently according to genotype.

2. Material and methods

2.1. Field experiments

Three consecutive field seasons of experiments were conducted at the Agroscope research station in Nyon, Switzerland (46.39°N, 6.24°E, 424 m a.s.l.), between September 2017 and July 2021. The experiments were carried out on the same parcel of land, which was divided into seven smaller fields. Three smaller fields were used per season, to allow the installation of a rotational system. In each smaller field, one pre-crop was followed by winter wheat (Supp. Fig. S1). The soil of the field is

Table 1

Soil characteristics of the Calcaric Cambisol where the experiment was carried out. Soil depth, concentration of clay (Cl), silt (Si), sand (Sa), organic matter (OM), pH, phosphorus (P), potassium (K), magnesium (Mg). Standard error of the mean is given after $\pm$. Analysis methods applied by the external lab: pH was measured in water (20 g of soil per 50 ml of extracting solution); P, K and Mg were measured with ammonium acetate and EDTA (AAE10, 5 g of soil per 50 ml of extracting solution). No texture data available for depth of 60 cm or for calculating the standard error of the mean.

Depth (cm)	Cl (%)	Si	Sa	OM (g/100 g)	pH	P (mg kg^{-1})	K	Mg
0 to 30	28	31	41	2.5 ± 0.3	6.6 ± 0.1	37.8 ± 12.3	140.8 ± 13.5	161.6 ± 22.6
30 to 60	-	-	-	1.5 ± 0.3	7.0 ± 0.3	10.2 ± 5.2	113.2 ± 10.0	192.7 ± 45.9

classified as Calcaric Cambisol (WRBSR, 2014). Soil sampling was done with an auger on October 10, 2018. Three samples per depth (0–30 cm and 30–60 cm) were taken in each of the three pre-crop fields during the first season. Eighteen samples were taken in total. Soil samples were sent to an external laboratory (Sol-Conseil, Gland, Switzerland) and analyzed for texture, organic matter, pH measured in water, phosphorus (P), potassium (K) and magnesium (Mg) (Table 1). Nutrient availability was classified as "sufficient" for P, K and Mg by "The Principles of Agricultural Crop Fertilization in Switzerland" (PRIF, Flisch et al., 2017). The seasons are based on the growing season of winter wheat (2018–19, 2019–20 and 2020–21; hereinafter referred to as season "2019″, "2020″ and "2021″, respectively).

The climate of the region is classified as warm-summer humid continental climate (Cfb), according to Köppen's climate classification (Beck et al., 2018). Meteorological data was obtained from the local weather station of MeteoSwiss (named CGI), located approximately 720 m from the field. During the period from 1981- 2021, the mean annual temperature was 10.6 °C, the mean annual precipitation was 997 mm, and the mean annual solar radiation, 12.5 MJ m^{-2} d^{-1}. Mean historical weather conditions during the winter wheat growing season (Oct 1st to July 31st of following year) and the conditions during the years of experiment, are shown in Fig. 1.

Four winter bread wheat genotypes were used, representing a broad range of adaptation to environmental conditions (Table 2) and tolerances to drought (Touzy et al., 2019). The genotypes were selected from high-throughput experiments of Touzy et al. (2019): Apache (drought tolerant), Allez-y (susceptible), Cellule (intermediate tolerance) and CH-Nara (drought tolerant). The genotype CH-Nara was included as the local genotype. Wheat was cultivated every season following barley (*Hordeum vulgare* L., var. KWS Meridian and KWS Orbit), oilseed rape (*Brassica napus* L., var. Visby and Avatar), and winter pea (*Pisum sativum* L., var. Astronaute). Each pre-crop was cultivated according to the local recommendations for the crop and were harvested before sowing of winter wheat.

Additionally, two mineral N fertilization levels were tested: non-fertilized and enough mineral N applied to reach a total supply of

180 kg N ha^{-1} (fertilized), based on the amount of soil mineral N (NO$_3^-$ plus NH$_4^+$, hereafter referred to as Nmin) as in Thompson et al. (2017). This amount is 40 kg N ha^{-1} more than the average N fertilizer applied in winter wheat production in Switzerland (Fossati et al., 2010), and was chosen to avoid limiting production due to N. Furthermore, rainout shelters (present or not present) were used to reduce the amount of rainfall during grain filling. The experimental design was a strip-split plot with 16 treatments in three replicates, totaling 48 plots after each pre-crop, for a total of 144 plots each season. Each plot measured 1.5 m x 1.5 m. The pre-crop represented one whole-plot. The N fertilization and rainout shelter treatments were arranged in horizontal and vertical strips, respectively, across each replicate within the whole-plot, creating crossed main plots. The main plots' intersection was subdivided into four subplots, to which the genotypes were randomly assigned (Supp. Fig. S1).

Table 2

List of the winter wheat genotypes used in this study. Agronomic and physiologic characteristics of the studied winter wheat genotypes: Allez-y, Apache, Cellule and CH-Nara. [a]1 very sensitive, 9 very resistant; [b]1 late, 9 early; [c]1 very short, 9 very tall; [d]1 very small, 9 very large; [e]1 low, 9 high.

Characteristics	Genotypes			
	Allez-y[f]	Apache	Cellule	CH-Nara
Registration year	2011	1998	2012	2007
Country of origin	France	France	France	Switzerland
Cold resistance[a]	8	7	6	-
Precocity at stem extension[b]	1	3	5	4
Precocity at heading[b]	6	7	6.5	6
Height[c]	4	3.5	3.5	3
Awn	no	no	yes	no
Disease resistance[a]				
brown rust	5	4	3	7
yellow rust	5	7	6	9
septoriose	5.5	4.5	5	6.5
Grain size[d]	6	5	3	4
Drought resistance[e]	susceptible	tolerant	intermediate	tolerant

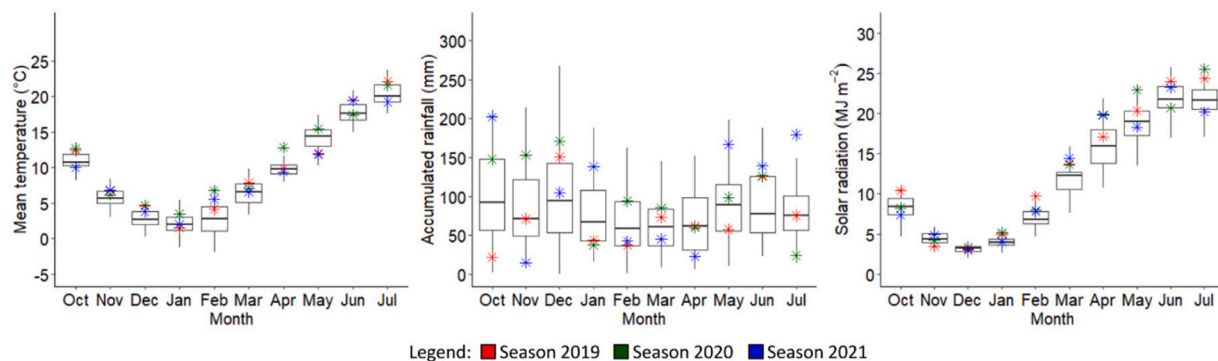*Source*: ARVALIS (2023), [e]Touzy et al. (2019) and [f]Semences de France (2017).

Fig. 1. Weather conditions during winter wheat cropping season (Oct 1st to July 31st) in Nyon, Switzerland. Boxplot of monthly mean temperature (**a**), accumulated rainfall (**b**) and solar radiation (**c**), over the 1981–2021 winter wheat growing seasons in Nyon, Switzerland, and standard error of the means. Weather data corresponding to the years of growing seasons of the field experiments are shown as red, green and blue asterisks for 2019, 2020 and 2021, respectively. Data from MeteoSwiss, the Swiss Federal Office for Meteorology and Climatology.

Table 3

Field experiment operations in winter wheat field experiment. Sowing, harvest, soil mineral N (NO$_3$-N plus NH$_4$-N) to 60 cm depth, N fertilization (ammonium nitrate) and rainout shelter installation and removal dates, and doses for fertilized treatments by season (season 2019, 2020 and 2021), for wheat and pre-crops (barley, oilseed rape, and peas).

Operations	Season 2019	Season 2020	Season 2021
Pre-crops sowing date	Aug-Sep 2017	Aug-Sep 2018	Aug-Sep 2019
Pre-crops harvest date	Jun-Jul 2018	Jun-Jul 2019	Jun-Jul 2020
Wheat sowing date	19 Oct 2018	28 or 30 Oct 2019	18 Oct 2020
Soil mineral-N date	22 Feb 2019	17 Feb 2020	19 Feb 2021
after barley, in kg N ha^{-1}	110	70	20
after oilseed rape, in kg N ha^{-1}	110	70	50
after peas, in kg N ha^{-1}	50	90	30
1st N supply date	-	16 Mar 2020	25 Feb 2021
after barley, in kg N ha^{-1}	-	40	40
after oilseed rape, in kg N ha^{-1}	-	40	40
after peas, in kg N ha^{-1}	-	40	40
2nd N supply date	27 Mar 2019	06 Apr 2020	31 Mar 2021
after barley, in kg N ha^{-1}	30	30	80
after oilseed rape, in kg N ha^{-1}	30	30	50
after peas, in kg N ha^{-1}	90	10	70
3rd N supply date	06 May 2019	04 May 2020	03 May 2021
after barley, in kg N ha^{-1}	40	40	40
after oilseed rape, in kg N ha^{-1}	40	40	40
after peas, in kg N ha^{-1}	40	40	40
Rainout shelter installation date	06 May 2019	13 May 2020	25 May 2021
Diseases analysis date	07 Jun 2019	05-06 Jun 2020	22 Jun 2021
Rainout shelter removal date	28 Jun 2019	07 Jul 2020	12 Jul 2021
Wheat harvest date	22 Jul 2019	13 Jul 2020	19 Jul 2021

Fig. 2. Pre-crops biomass and soil nitrogen at 60 cm soil depth. (**a**) Pre-crops dry biomass (with standard error of the mean) harvested before winter wheat in seasons 2019, 2020 and 2021, and (**b**) soil mineral-N (NO$_3$-N plus NH$_4$-N) up to 60 cm depth in February of 2019 (season 2019), 2020 (season 2020) and 2021 (season 2021), sampled at the beginning of tillering of the winter wheat that followed the pre-crops. Note that biomass samples of the pre-crop peas could not be collected in 2021 due to an early harvest, and the Nmin in 2019 was based in one mixed sample.

Field operations are listed in Table 3. Wheat was sown at a rate of 350 seeds m^{-2} in all seasons. In 2019, due to the high amount of rain and consequent soil humidity, the sowing was split in two days: plots after barley on October 28 and, after peas and oilseed rape, on October 30. Also, in 2019, there was a deficiency in plant emergence in 17 plots (12 after oilseed rape, three after pea and two after barley), which were removed from analysis of season 2020.

Stationary rainout shelters were built and installed to reduce rainfall by up to 40%, based on Kundel et al. (2018), and checked after the trials by the collection of intercepted rainfall with two adapted closed-head plastic drums of 60 L (Supp. Table S1). They were installed before the onset of the grain filling phase and removed just before harvest (Table 3). Each rainout shelter measured 6 m x 3 m and were between 2.0 m - 2.5 m high. One side was shorter than the other to allow the flow of rain to a tube, that would drain the water a few meters from the shelter. The roof of the rainout shelter was a design used by Kundel et al. (2018), with 18 V-shaped clear and UV permeable acrylic glass bands (PLEXIGLAS SUNACTIVE® GS 2458, Bröking Plastex GmbH, Darmstadt, Germany) placed on top, separated by 20 cm (Supp. Fig. S2). Three rainout shelters per pre-crop were installed, each one covered eight plots (Supp. Fig. S1).

To quantify the Nmin, soil samples were collected at the beginning of tillering in February 2019, 2020 and 2021. A representative soil sample was collected in two different locations in each pre-crop plot, for depths 0–30 cm and 30–60 cm. Sampling beyond 60 cm was hampered by the presence of subsurface rock layers on the study site. Each soil sample consisted of an ensemble of three soil cores for each depth, except for 2019, where one sample per depth comprised six soil cores. In 2019, samples were combined, preventing standard error calculation. In 2020 and 2021, two separate samples per pre-crop were analyzed, leading to the inclusion of standard errors in the experimental design. Soil samples were sent to an external laboratory (Sol-Conseil, Gland, Switzerland)
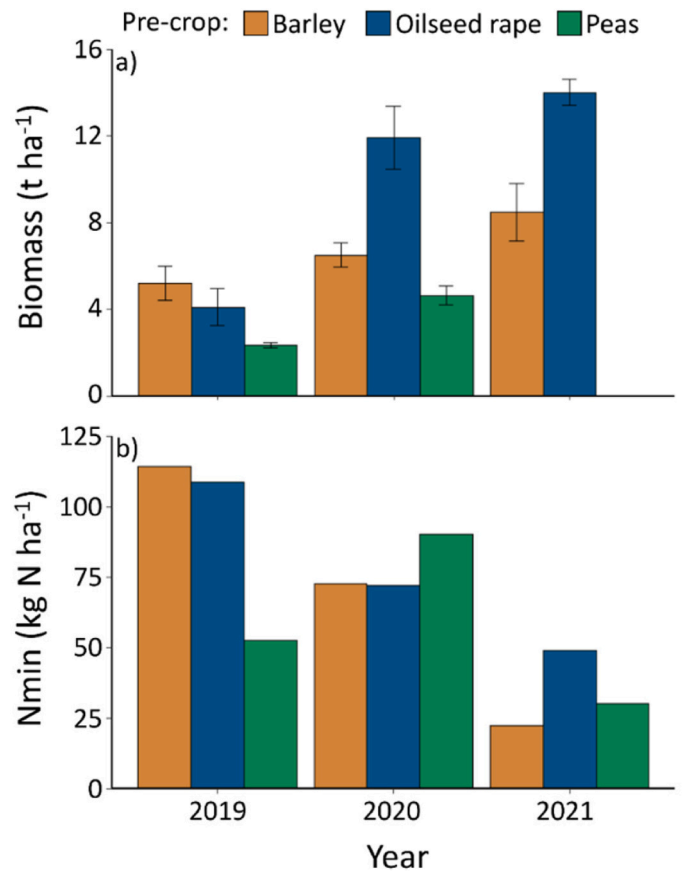
and analyzed for Nmin content. Ammonium nitrate (27% N + 2.5% Mg) was broadcasted twice in season 2019, considering only the timing of second and third application (due to sufficient initial soil mineral N), and three times, on the following seasons, by the time of tillering, stem elongation and heading stages. No other fertilizer was applied. Crop protection operations can be found on Supplementary Table S2. At grain maturity, the plots were partially harvested by hand and winter wheat plants were left over the remaining plants, to avoid mixing samples from neighboring plots. The plots were, then, combine-harvested, and residues were mostly removed from the field and discarded (Table 3).

2.2. Crop analysis

The biomass of barley, oilseed rape and peas were collected at physiological maturity each season. The exception was peas in season 2021 due to an early harvest. Three repetitions of biomass in 1 m^2 were harvested by hand per pre-crop. Samples were weighed fresh and dry. For dry weight, samples were dried at 50 °C until the drying mass was stable. In 2019 and 2020, samples were threshed to separate grains and straws and weighed again, while in 2021, they were weighed before threshing. Means of dry samples were calculated.

Grain yield (at zero percent humidity), yield related components, phenology stages, diseases incidence, water-soluble carbohydrates (WSC), harvest index (HI), N use efficiency (NUE), N harvest index (NHI), N uptake efficiency (NUpE), N utilization efficiency (NUtE), N

balance (N$_{balance}$), and thousand kernel weight (TKW) were analyzed. During the growing season, water stress was quantified through stomatal conductance (g$_s$) and resistance using a leaf porometer (Delta-T Devices, Cambridge, UK).

The severity of diseases in wheat was analyzed during grain filling (June) based on Michel (2001). Three flag leaves per plot were analyzed for brown and yellow rust (*Puccinia recondita* and *Puccinia striiformis*, respectively) and septoria tritici blotch (*Mycosphaerella graminicola*). The percent surface cover of each disease in relation to each leaf area was visually identified (0% for no diseases symptoms and 100% for completely covered by symptoms). Means of percentages were calculated per plot.

The WSC analysis followed the protocol described by Pietragalla and Pask (2012). Fifteen culms per plot were harvested by hand around 10 days after anthesis. Samples were weighed fresh, dried at 60 °C until the drying mass was stable, and weighed again. The peduncles, the spikes, and the rest of the plant material were separated into three different bags per plot, so the material could be weighed and milled separately. One milled repetition of peduncles from the seasons 2019 and 2020 was sent to an external laboratory (SADEF, Aspach-le-Bas, France) and analyzed for WSC, using the methodology of DuBois et al. (1956). All repetitions were measured by near infrared spectroscopy (NIRS) using a ProxiMate (Buchi, Flawil, Switzerland), calibrated for WSC estimation with the laboratory results. Due to an issue during milling of samples, the method could not be used for samples of season 2021, and the values of all three repetitions were measured by NIRS.

For aboveground biomass, HI, NHI, NUpE, and NUtE analysis, 20 plants per plot were harvested approximately seven days before harvest. The samples were weighed, dried until the drying mass was stable, and weighed again. Samples were threshed and the grains and the rest of the plants were weighed and milled separately. One repetition of samples per season was sent to an external lab (SADEF, Aspach-le-Bas, France) and analyzed for N content. All repetitions were measured by NIRS using a ProxiMate for N estimation, calibrated specifically for grains or straw. Protein content of the grain was calculated from the N content using a conversion factor of 5.7 (Schulz et al., 2015). The indices of this study were obtained with equations 1 to 6, as they were considered sufficient for the exploration of the data in this study.

(1) Harvest index (HI) = grain weight [kg] / aboveground biomass [kg].

(2) Nitrogen use efficiency (NUE) = grain yield / (Nmin + N$_{applied}$) (Moll et al., 1982).

(3) Nitrogen harvest index (NHI) = N$_{grain}$ / (N$_{grain}$ + N$_{straw}$).

(4) Nitrogen uptake efficiency (NUpE) = (N$_{grain}$ + N$_{straw}$) / (N$_{soil}$ + N$_{applied}$) (Moll et al., 1982; Hawkesford, 2017).

(5) Nitrogen utilization efficiency (NUtE) = grain yield / (N$_{grain}$ + N$_{straw}$) (Gaju et al., 2011).

(6) Nitrogen balance (N$_{balance}$) = N$_{applied}$ − N$_{harvest}$ (adapted from the soil surface budget method of Oenema et al., 2003).

Where grain yield (kg ha^{-1}) is the grain yield at final harvest, N$_{applied}$ (kg N ha^{-1}) is the total amount of N applied through the season, N$_{grain}$ (kg N ha^{-1}) and N$_{straw}$ (kg N ha^{-1}) are the N content in grains and straw, respectively, from 20 plants, and N$_{harvest}$ (kg N ha^{-1}) is the N content in the grains plus straw at final harvest.

3. Statistical analysis

Statistical analysis was carried out in R (version 4.1.3, R Core Team, 2021), using a linear statistical model and principal component analysis (PCA) to assess differences between main factors and their interactions. Water, N fertilization, and genotype treatments, as well as the interaction between them, were considered as fixed factors. Main plots (water and N fertilization) and subplots (genotypes) were considered as random effects for the analysis of variance (ANOVA, function "aov" from the R package "stats"). Standard errors in Supplementary Material were estimated with the function "emmeans" from R package of same name

(Lenth, 2022), and are not shown in some cases because the functions in this package first determine whether the results are uniquely estimable, and standard errors are not estimated when there is at least one missing value. Post-hoc Tukey's test (function "emmeans") was used to uncover specific differences between three or more group means when an ANOVA test was significant ($P \leq 0.05$). The treatment means different at $P < 0.05$ were considered statistically significant. A PCA was used to reduce the dimensions of the dataset and better visualize correlations between variables using the function "prcomp" in R. The PCA included all the sources of variation at a similar level. The results were plotted using the function "autoplot", from the R package "ggfortify". Genotypes were highlighted in plots in order to assess differences between them. Only the first two principal components were illustrated in the plot since they accounted for most of the variation.

4. Results

4.1. Pre-crops and soil Nmin

The total dry biomass of the pre-crops (harvested before winter wheat sowing) increased each year, while the Nmin tended to decrease (Fig. 2). In season 2019, barley had the greatest average biomass (5.2 t ha^{-1}), followed by oilseed rape (4.0 t ha^{-1}), and peas (2.3 t ha^{-1}). Oilseed rape had the greatest biomass in following seasons, with approximately 11.9 t ha^{-1} in season 2020 and 14.0 t ha^{-1}, in season 2021. Biomass samples of pre-crop peas could not be collected in season 2021 due to an early harvest. In February, the Nmin in the upper 0.6 m of soil was poorer after peas in season 2019 (52.7 kg N ha^{-1}) and greater in 2020 (90.2 kg N ha^{-1}) than after other pre-crops. The Nmin after barley and oilseed rape were similar in seasons 2019 (114.4 and 108.7 kg N ha^{-1}, respectively) and 2020 (72.6 and 72.0 kg N ha^{-1}, respectively). In 2021, the average Nmin after oilseed rape was the greatest (49.2 kg N ha^{-1}).

4.2. Winter wheat analysis

4.2.1. Effects of rainfall and rainout shelters

Accumulated rainfall during the period considered optimal for sowing and establishment of winter wheat in each season is shown in Fig. 3. From October 1st until sowing, the accumulated rainfall was 5 mm in season 2019, 145 mm in season 2020 and 85 mm in season 2021 (Supp. Fig. S3). Due to the high amount of rainfall and soil humidity in season 2020 (October 2019), the sowing of winter wheat occurred 10 days later than the other seasons and under supraoptimal soil moisture conditions, contributing to a poor crop establishment. Despite the higher initial rainfall, the season 2020 was intermediate in accumulated rainfall from sowing to harvest (854 mm), also similar to the mean for wheat growing season in the region (838 mm, Oct 1st to Jul 31st, 1981–2021). Season 2021 had the greatest rainfall (925 mm), while 2019 had the least (648 mm).

During grain filling from 15th May to 15th July (based on the field experiments), the accumulated rainfall was 168 mm (2019), 207 mm (2020), and 331 mm (2021, Fig. 3). Average accumulated rainfall during grain filling for the 1982–2021 period was 182 mm. Therefore, the three seasons in the experiment covered average to wet rainfall years. Furthermore, the rainout shelter created three additional weather conditions extending the rainfall range to low rainfall during grain filling, compared with the last 30 years. The accumulated rainfall with the rainout shelters, assumed as a maximum reduction of 40% of the incident rainfall (based on results shown in Supp. Table S1), were 101 mm (2019), 124 mm (2020), and 199 mm (2021). Despite that, the shelter treatment had no significant effect on yield ($P > 0.05$) regardless of season, pre-crop, N fertilizer application, or genotype (Fig. 4). Also, no difference between shelter treatments could be identified by the analysis of winter wheat aboveground biomass ($P > 0.05$, Supp. Tab. S3, S5 and S7) or g$_s$ ($P > 0.05$, Supp. Tab. S9) in any date of analysis.
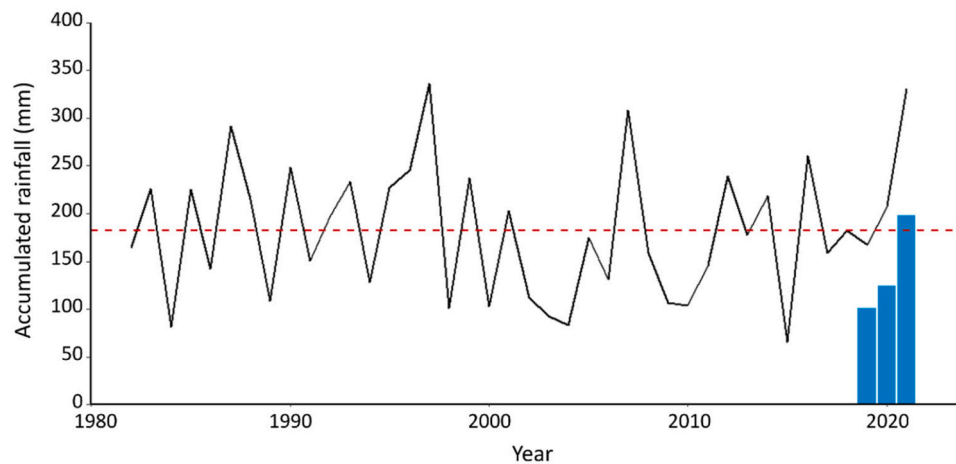
Fig. 3. Historical accumulated rainfall during wheat grain filling in Nyon, Switzerland. Accumulated rainfall (black line) between 1982–2021 and its average (182.3 mm, red line) between 15th May to 15th July, which is the usual wheat grain filling period at Nyon. Accumulated rainfall with rainout shelter (assumed as a maximum reduction of 40% of the incident rainfall) in the wheat experiments from seasons 2019 to 2021 (rainfall during wheat grain filling, blue bars).

4.2.2. Effects of nitrogen supply and genotype

No significant differences of wheat yield between fertilized (total supply of 180 kg N ha^{-1}) and non-fertilized (Nmin only) treatments were found in seasons 2019 and 2020 ($P > 0.05$, Fig. 5), years where initial soil Nmin was ≥ 50 kg N ha^{-1}. The exception was CH-Nara after peas in season 2019. In 2019, yields for both N treatments were around 4.7 t ha^{-1}, while in 2020, average yield in non-fertilized treatment was 2.5 t ha^{-1} and, in fertilized, 2.6 t ha^{-1}. In 2021, the disparity between N treatments were more evident, from 3.0 t ha^{-1} in non-fertilized treatment to 4.2 t ha^{-1}, in fertilized. Further, when comparing no N treatments to fertilized treatments, wheat had greater average yields after oilseed rape (4.4 t ha^{-1} for non-fertilized v. 5.6 t ha^{-1} for fertilized) compared to barley (1.5 t ha^{-1} for non-fertilized v. 3.0 t ha^{-1} for fertilized) and peas (3.0 t ha^{-1} for non-fertilized v. 4.2 t ha^{-1} for fertilized).

Genotype had the most consistent impact on wheat grain yield across seasons ($P < 0.05$). In seasons 2019, 2020 and 2021, the average yields of four genotypes were 4.7 t ha^{-1}, 2.6 t ha^{-1}, and 3.6 t ha^{-1}, respectively. Cellule had the greatest average yields in all seasons, and yielded a maximum of 8.2 t ha^{-1} with 180 kg N ha^{-1}, in one single plot after oilseed rape in 2021 (data not shown). Allez-y had the second greatest average yields in 2019 (4.8 t ha^{-1}) and 2021 (3.6 t ha^{-1}), and CH-Nara in 2020 (2.7 t ha^{-1}). Apache yielded lower in 2019 (4.0 t ha^{-1}) and around in 2020 and 2021 (2.4 t ha^{-1} and 3.3 t ha^{-1}, respectively).

4.2.3. Wheat diseases

The presence and severity of brown and yellow rust as well as septoria on the flag leaf during grain filling varied between seasons and pre-crops (Fig. 6). Season 2019 had the lowest disease incidence, only brown rust and septoria were observed. Septoria presented the lowest incidence in 2019, going from 2.2% after barley to 2.5%, after both oilseed rape and peas, while brown rust went from 6.4% after barley to 9.7%, after oilseed rape. The intermediate level of disease incidences occurred in 2021, with identified symptoms of only yellow rust (from 4.7% after barley to 12.6% after peas) and septoria (from 12.4% after peas to 18.1% after barley). In 2020, the plants presented symptoms of all three diseases and incidences generally higher than other seasons. The septoria disease presented the highest incidences in flag leaves, from 19.9% after oilseed rape to 28%, after barley, followed by brown rust, with incidences between 14.8% (after oilseed rape) and 22.3% (after peas). Yellow rust was less observed this season, with incidences going from 7.4% (after oilseed rape) to 15.7% (after barley). The highest percentage of disease incidence occurred, thus, after barley (septoria), followed by peas (brown rust) and oilseed rape (septoria), all in 2020.

4.2.4. Understanding differences between genotypes

A PCA was used to identify associations among variables (Fig. 7). The PCA allowed to consider 15 crop and soil variables (i.e., grain number per m^2, ears per m^2, grains per ear, yield, NUE, NUpE, NUtE, N$_{balance}$, aboveground biomass, HI, NHI, TKW, WSC, g$_s$ and grain protein content of wheat) in two dimensions (the number of PCs selected). For g$_s$, data from one date per season with consistent and/or greatest variety effect ($P < 0.05$, Supp. Tab. S9) was considered in the PCA (2019: 27 June, 2020: 23 June, 2021: 01 June). The two principal components (PC 1 and PC 2) accounted for 53.4% of variance for all seasons analyzed together. All variables except for grain protein, N$_{balance}$ and g$_s$, are positively correlated to PC 1. Grains per ear, biomass, HI, NUpE, NHI, N$_{balance}$, TKW and WSC are negatively correlated to PC 2. The percentages of features contributions to PC1 and PC2 can be found in Supplementary Fig. S4. Means of all variables are shown by pre-crop and season in Supplementary Table S3 to Table S8.

The PCA also revealed a strong positive relationship between the yield and grain number (Fig. 7), even when seasons were analyzed separately (Supp. Fig. S5). Cellule yielded $\approx 25\%$ more than the mean of the other genotypes (3.5 t ha^{-1}) and had the highest mean grain number per m^2 (12804 grains m^{-2}). Mean grain numbers of Allez-y, Apache and CH-Nara were 10472 grains m^{-2}, 9677 grains m^{-2} and 9905 grains m^{-2}, respectively. Also, although not closely correlated to yield, Cellule also presented the greatest results for the yield components: ears per m^2 (603.9) and grains per ear (21.6). They were both affected by genotype, but ears per m^2 was also affected by N treatments, especially in 2021 ($P < 0.05$, Supp. Tab. S3, S5 and S7). Ears per m^2 of Allez-y (566.9 ears m^{-2}) was the second greater, followed by Apache (554.8 ears m^{-2}) and CH-Nara (517.3 ears m^{-2}). On the other hand, CH-Nara followed Cellule on the number of grains per ear (19.5 grains ear^{-1}), while Allez-y and Apache presented similar results (18.4 grains ear^{-1} and 18.3 grains ear^{-1}, respectively).

Additionally, when seasons were analyzed together, a positive correlation could be identified between WSC, TKW and aboveground biomass (Fig. 7). This correlation was also found in 2019, when seasons were analyzed separately (Supp. Fig. S5). CH-Nara, drought tolerant genotype, had the greatest mean of WSC (48.7 g kg^{-1}) and biomass (0.703 kg), and its TKW (36.0 g) was among the greatest (36.1 g for Allez-y, 34.6 g for Apache and 35.0 g for Cellule). The means of WSC for Allez-y (drought susceptible), Apache (tolerant) and Cellule (intermediate) were 39.0 g kg^{-1}, 40.8 g kg^{-1} and 43.1 g kg^{-1}, respectively, while the means of biomass were 0.672 kg, 0.661 kg and 0.680 kg (Supp. Tab. S3, S5 and S7).
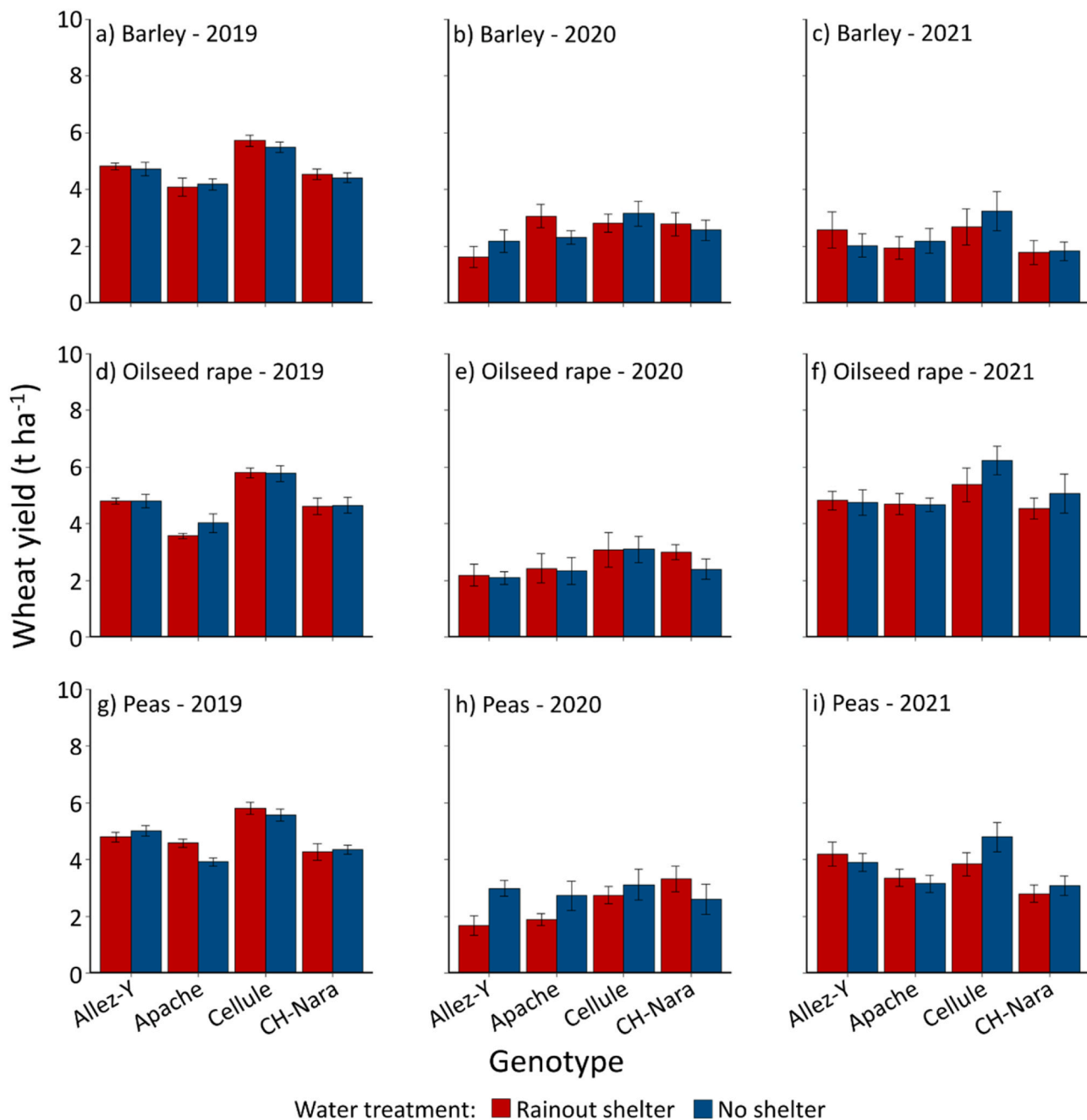
Fig. 4. Responses of winter wheat genotypes to reduced rainfall. Winter wheat genotype average yields (with standard error of the mean) response to pre-crops (**a, b, c**) barley, (**d, e, f**) oilseed rape and (**g, h, i**) peas, during different cropping seasons indicated by wheat harvest year of (**a, d, g**) 2019, (**b, e, h**) 2020 and (**c, f, i**) 2021. Rainfed conditions (no shelter) indicated by blue bars and rainout shelters indicated by red bars. N fertilizer treatments are averaged as there were very few statistical differences between N treatments (Supp. Tab. S3, Tab. S5 and Tab. S7).

Furthermore, although not seen when seasons were analyzed together (Fig. 7), results have shown a close relationship between grain protein content and $N_{balance}$ in 2019 and 2021 (Supp. Fig. S5). Grain protein was consistently affected by genotype ($P < 0.05$), and it was somehow affected by N treatments, specially in 2019 and 2021 (Supp. Tab. S3, S5 and S7). CH-Nara had the greatest grain protein content (14.0%), followed by Allez-y (12.0%), Apache (11.8%) and Cellule (11.4%). As for the $N_{balance}$, the effects were not consistent, with more significance ($P < 0.05$) in 2019 and 2020 for genotype, and, for N treatments, in all seasons after peas (Supp. Tab. S4, S6 and S8). $N_{balance}$ was greater for Apache (-43.2 kg N ha^{-1}), followed by Allez-y (-55.6 kg N ha^{-1}), CH-Nara (-60.8 N ha^{-1}) and Cellule (-67.1 kg N ha^{-1}).

The relationship between HI, as well as g_s, and other features were not strong in PCA (Fig. 7) and varied when seasons were analyzed separately (Supp. Fig. S5). HI was significantly affected by genotype the first two seasons ($P < 0.05$), with greatest values in 2020 (Supp. Tab. S3, S5 and S7), and was not affected by N or water treatments ($P > 0.05$). In 2019, CH-Nara had the greatest HI (0.45 kg kg^{-1}), followed by Cellule (0.44 kg kg^{-1}), Apache (0.43 kg kg^{-1}) and Allez-y (0.42 kg kg^{-1}). In 2020, Cellule had greatest HI (0.50 kg kg^{-1}), followed by both CH-Nara (0.49 kg kg^{-1}), Apache (0.49 kg kg^{-1}), and Allez-y had the lowest (0.46 kg kg^{-1}). In 2021, CH-Nara had the lowest HI (0.46 kg kg^{-1}), while other genotypes had HI around 0.47 kg kg^{-1}. As for g_s, the results were rather inconsistent among seasons. It was affected by N treatments only in 2021, while by genotypes, at least one date of measurements per
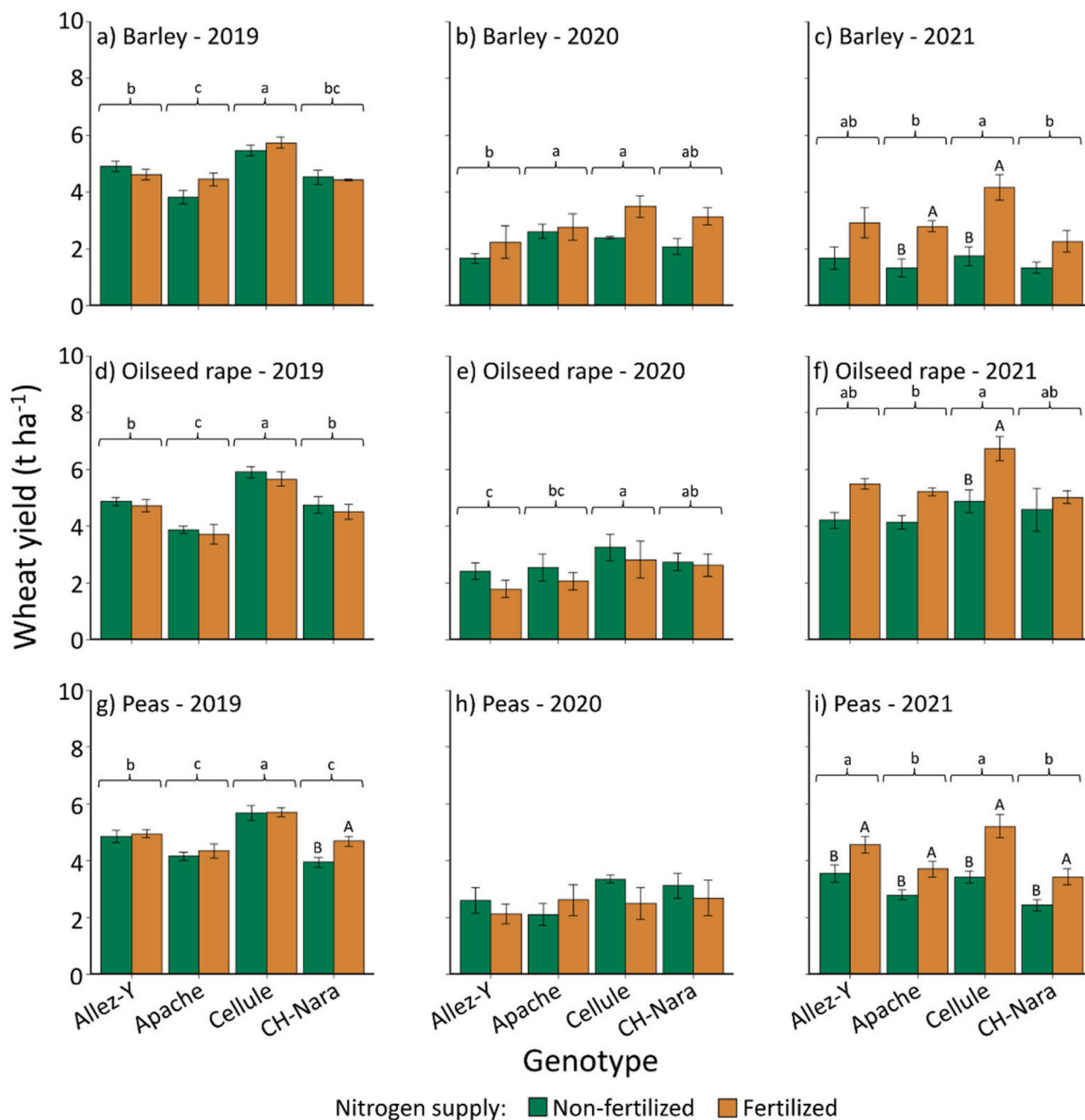
Fig. 5. Responses of winter wheat genotypes to nitrogen supply. Winter wheat genotype average yield (with standard error of the mean) response to pre-crops (**a, b, c**) barley, (**d, e, f**) oilseed rapes and (**g, h, i**) peas, during different cropping seasons indicated by wheat harvest year of (**a, d, g**) 2019, (**b, e, h**) 2020 and (**c, f, i**) 2021, grown under non-fertilized (orange bars) and fertilized (green bars) N treatments. Means with different uppercase letter within N treatments (non-fertilized compared to fertilized) are significantly different at p < 0.05. Same letter within genotypes (Allez-y, Apache, Cellule and CH-Nara) indicates no significant differences (*P* < 0.05). Mineral N fertilizer was applied to reach a total soil supply of 180 kg N ha^{-1} to 60 cm depth. Shelter treatments are averaged as there were no statistical differences between water treatments (Supp. Tab. S3, Tab. S5 and Tab. S7).

pre-crop in 2019 (all dates after barley, and 27 May and 27 Juin after oilseed rape and peas) and 2021 (all dates after oilseed rape, 16 Juin after barley and 01 June after peas). In 2020, the factor genotype was only significant (*P* < 0.05) after peas on 23 Juin (Supp. Tab. S9). Considering only the date per season used for the PCA, Allez-y had the greatest g$_s$ (145.1 mmol m^{-2} s^{-1}), followed by CH-Nara (123.4 mmol m^{-2} s^{-1}), Cellule (115.3 mmol m^{-2} s^{-1}) and Apache (113.6 mmol m^{-2} s^{-1}).

NUE and NUpE were consistently closely related between each other (Fig. 7, Supp. Fig. S5), while relationships between NUtE, as well as NHI, and other features were less evident (Fig. 7) and varied with season

(Supp. Fig. S5). The four of them were affected by N treatment after peas, independently of season (*P* < 0.05, Supp. Tab. S4, S6 and S8). NUtE was also affected by N treatments after barley and oilseed rape in all seasons (*P* < 0.1). NUE was affected by N treatments after barley and oilseed rape in 2019 and 2021 (*P* < 0.05), while NUpE, was less significantly affected (*P* < 0.05, after barley) or not affected (*P* > 0.05, after oilseed rape). In general, NUE, NUpE and NUtE means were greater for non-fertilized compared to fertilized treatments, while NHI means were more similar (Supp. Tab. S4, S6 and S8). NHI was not affected by N treatments after barley in all seasons, and after oilseed rape in 2020 and 2021 (*P* > 0.05, Supp. Tab. S4, S6 and S8). Furthermore, NUE, NUpE,
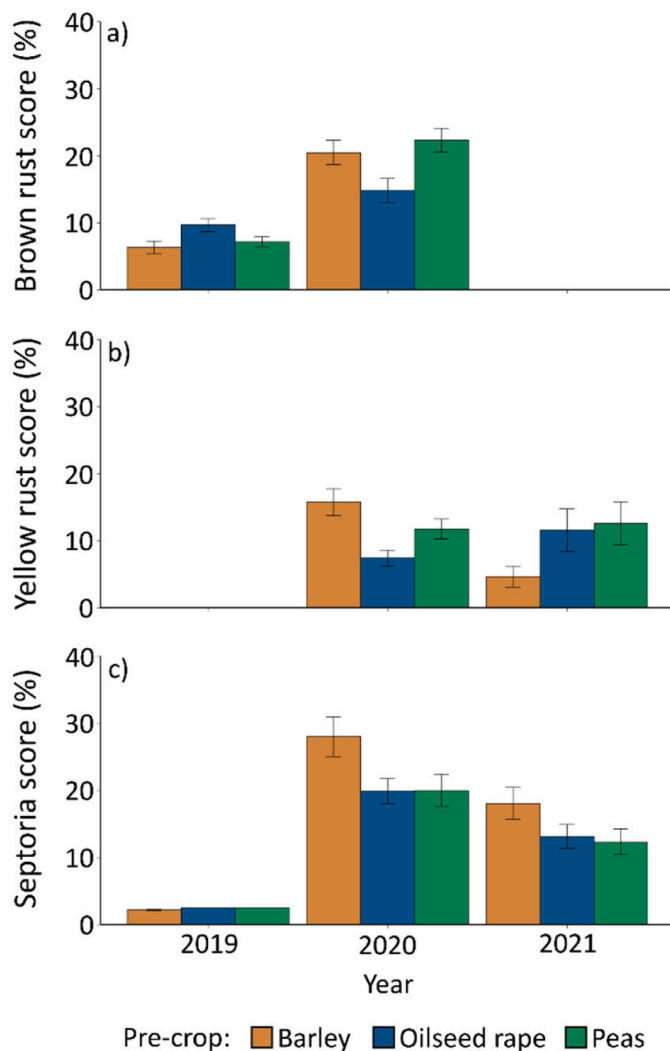
Fig. 6. Incidence of foliar diseases in wheat. Severity score of (**a**) brown rust, (**b**) yellow rust and (**c**) *septoria tritici* blotch in 2019, 2020, and 2021, after each pre-crop. The severity was measured on the flag leaf during wheat grain filling in June. Error bars show standard error of the mean.

Fig. 7. Principal component analysis (PCA) of winter wheat genotype variables. The figure contains the first two principal components, PC 1 and PC 2, and their respective scores explaining variation within the data of all seasons analyzed together. Arrows indicate the strength of the trait influence on the first two PCs. Factors included wheat grain number per m^2 (Grain number), ears per m^2 (Ears m^{-2}), grains per ear (grains ear^{-1}), grain yield (Yield), grain N use efficiency (NUE), N uptake efficiency (NUpE), N utilization efficiency (NUtE), N balance ($N_{balance}$), aboveground biomass (Biomass), harvest index (HI), N harvest index (NHI), thousand kernel weight (TKW), water-soluble carbohydrates (WSC), stomatal conductance (g_s) and grain protein content (Grain Protein %). Data means shown in Supplementary Tables S3 to Table S9.

NUtE and NHI were, generally, not affected by N treatment $\times$ genotype interactions, but they were consistently affected by genotype ($P < 0.05$), except for season 2021, after oilseed rape ($P > 0.05$). When all seasons were considered together, Cellule had greatest means of NUE (49.3 kg kg^{-1}), NUpE (1.20) and NutE (39.4 kg kg^{-1}), followed by Allez-y (NUE = 44.6 kg kg^{-1} and NUpE = 1.15). Allez-y and Apache had similar NUtE (36.5 kg kg^{-1} and 36.9 kg kg^{-1}, respectively), while CH-Nara, the lowest (33.1). Apache and CH-Nara had similar NUE (39.0 kg kg^{-1} and 39.1 kg kg^{-1}, respectively), and varying NUpE (1.0 for Apache and 1.20 for CH-Nara). Further, CH-Nara had the greatest mean of NHI (0.76), followed by Cellule (0.74), Apache (0.73) and Allez-y (0.72).

5. Discussion

5.1. Effect of reduced rainfall on winter wheat

Although wheat can be sensitive to water limitation at both vegetative and reproductive (i.e., grain filling) stages (Daryanto et al., 2017), our study found that the level of rainfall reduction (up to 40%) during grain filling did not impact grain yields, aboveground biomass or g_s. Similar results were found by Sun et al. (2006) and Zhang et al. (2008),
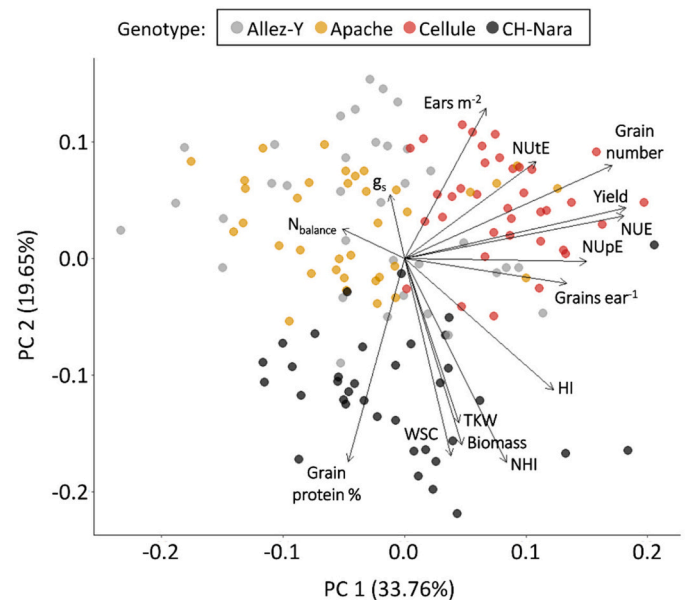
in which no differences were observed in wheat grain yields between treatments with and without irrigation during grain filling, in North China Plain. The wheat water needs during growing season varies between 450 and 650 mm (FAO, 1986). According to Pennington et al. (2023), the water needs during the grain filling phase of a winter wheat yielding 5 t ha^{-1} are 2 mm day^{-1}, 2.5–3.5 mm day^{-1}, and 1–2.5 mm day^{-1} at the onset, middle and end of grain filling, respectively when mean air temperatures ranges from 12 to 15 °C (May), 17 to 19 °C (June), and 19 to 22 °C (July). Thus, the water demand during grain filling in our study can be estimated in the range of 124–177 mm, which is lower than the rainfall occurred during grain filling (168, 207, and 331 mm in 2019, 2020, and 2021, respectively). This suggests that rainfall restrictions higher than 26%, 40%, and 62% in 2019, 2020, and 2021 would have been necessary to impose water limitations during grain filling if available soil water at anthesis had been null. However, rainfall before the grain filling period (Fig. 1) allowed winter wheat to grow without water limitation (Fig. 4) even in 2019, which was the year with lower rain during grain filling. This suggests that without increases in evapotranspiration, reductions in precipitation of around 40% (CH2018, 2018; Fischer et al., 2022) may not reduce significantly grain yield and grain protein in this environment. In the study of Kundel et al. (2018), a greater reduction in rainfall (−65%, from 201.1 mm to 70.6 mm) with rainout shelters of same design, did not affect winter wheat aboveground biomass neither four, eight or 13 weeks after their installation. These results were also attributed to the rainfall reduction level, which was not sufficient to dry out the soil within the duration of their experiment (Kundel et al., 2018). Greater intercepted rainfall levels might have changed our results, considering that the largest decrease in Swiss wheat production over the last 60 years was due to excessive rainfall during wheat anthesis and grain filling period in 2016, causing waterlogging, decreased solar radiation and high incidence of plant diseases (Nóia Júnior et al., 2023a).

Also, our findings partially align with the results of Klem et al. (2018), in which precipitation was totally intercepted. In their study, rainout shelters were installed between the middle of stem elongation and early milk ripening stages of winter wheat, and only affected yields and aboveground biomass in one of the two seasons examined, regardless of N supply levels (0 kg N ha^{-1} or 140 kg N ha^{-1}). In the affected season, based on soil moisture data, the water deficit occurred earlier and more it was more severe, and was followed by lower precipitation until the end of vegetative phase, compared to the unaffected season (Klem et al., 2018). Other research by Liu et al. (2016) indicated that a drought-resistant winter wheat genotype had increased yields under mild drought conditions (80 mm of irrigation) during reviving-jointing, jointing-anthesis and grain filling, but yields decreased under moderate (60 mm) and severe drought (40 mm) in all stages, while the yield of a drought-susceptible genotype was affected in all drought treatments during jointing-anthesis and grain filling. Although Brisson et al. (2010) found that drought stress may be more critical to grain yield during stem elongation than during grain filling (which might be more affected by heat stress), this may not be the case for our region. In Switzerland, climate change is expected to produce heavier rainfall especially during winter and spring, as well as hotter and dryer summer, with reduction of up to 43% in precipitation by 2099 (CH2018, 2018).

Although we attribute the lack of shelter effect to a non-limiting water supply despite the reduction in rain, we identified limitations in the design and installation of the rainout shelters that should be considered in future studies. Rainout shelters have been used for decades to intercept rainfall during the cropping season and create variable water conditions within a field experiment (Arkin et al., 1976; Kant et al., 2017; Steward et al., 2019). Various studies on drought stress have utilized them in different crop production scenarios, intercepting partial precipitation (Lai et al., 2022), total precipitation (Klem et al., 2018), or combining rainout shelters with irrigation (Zhao et al., 2022). In our study, although the rainout shelters were able to intercept 33–38% of the rainfall (Supp. Table S1), the experiment was limited by the release of the intercepted amount up to three meters away, which could have allowed a reflux of water onto the plots below the shelters. This differed from the study of Kundel et al. (2018), in which the intercepted rainfall was collected in 310 L rain barrels and removed from the experimental site. It is also worth noting that our rainout shelters were designed without lateral cover, allowing oblique rainfall to reach the covered plots. However, lateral covers may introduce artifacts and create artificial microclimates. While the use of border zones is considered a better option, it would have reduced the number of plots and treatments that these rainout shelters can cover. Additionally, we installed the shelters without the lower side facing the prevailing wind direction on the site, which was contrary to the setup of Kundel et al. (2018). This study illustrates the difficulties and the importance of accurately creating projected climate change conditions to determine their effects on crop production. Crop simulation models assist in designing multiple water-limited experiments and evaluating climate change effects on wheat yield. Robust calibration depends on comprehensive experiments like the one discussed. However, these models may not fully consider field nuances, such as the observed effects of excess rainfall in this study (Nóia Júnior et al., 2023b; Kim et al., 2024). Therefore, interpreting the results of their climate change impact projections on crop yield requires careful consideration. Hence, for more robust projections, crop simulation models should always be integrated with field experiments (Helman and Bonfil, 2022), like the one conducted in this study.

5.2. Nitrogen supply to the crop and N use

Previous studies have demonstrated that N supply could be used to alleviate the effects of drought stress, on crop growth and development (Zhang et al., 2007; Xiong et al., 2018; Moghaddam et al., 2023; Ru et al., 2023b). In our study, mineral N fertilizer applications (non-fertilized or Nmin, and fertilized to reach 180 kg N ha^{-1}) had no impact on wheat yield in the first two seasons (Fig. 5). These results can be attributed to the Nmin greater than 50 kg ha^{-1} in 2019 (Fig. 2). In 2020, grain yields were unaffected by the N treatment due to the Nmin greater than 50 kg ha^{-1} and a poor crop establishment caused by a wet autumn. They also highlight the importance of analyzing the Nmin before fertilization in wheat production to avoid excessive fertilizer inputs, and cause environmental issues. Wheat N fertilizer recovery is low, thus applying N in excess can cause off-site pollution of air, groundwater and waterways and climate warming (Zörb et al., 2018). The Nmin at the beginning of wheat development is frequently used to determine the N supply that will be applied during the growing season (Thompson et al., 2017), thus, it can vary according to the pre-crop, and if crop residues are left in the field. The Nmin after a legume was reported to be higher than non-legumes, due to its N fixation capacity (Preissel et al., 2015). In contrast to Preissel et al. (2015) and Raya-Sereno et al. (2023), in our study the Nmin after peas was lower than after barley in 2019, and after brassica in 2019 and 2021. This could be a result of the N inputs from fertilizers applied to barley and the brassica pre-crop, compared with no N fertilizer applied in peas, which were done according to the local recommendations for these crops. Despite that, the Nmin after peas (53–90 kg N ha^{-1}) was similar to the values reported by Preissel et al. (2015).

Additionally, the use of a "break crop" in rotational systems, like peas (Williams et al., 2014) and brassica (Angus et al., 2015), can improve cereal yield by breaking the cycles of diseases and weeds, and increasing N availability, among other benefits (Seymour et al., 2012). Although our wheat foliar diseases results varied between seasons and pre-crops, with no clear pattern (most likely due to the also variable water availability), both oilseed rape and peas are considered favorable pre-crops for winter wheat for different reasons (Sieling and Christen, 2015). According to Sieling and Christen (2015), winter wheat obtained greater grain and straw yields, as well as higher N uptake, after oilseed rape and peas than after cereals. On the other hand, regarding yield, the literature shows conflicting results. In France, no differences were found between oilseed rape and peas on the subsequent wheat yields (Sieling and Christen, 2015), and wheat yields were around 0.8 t ha^{-1} to 1.0 t ha^{-1} lower after oilseed rape than after leguminous crops (Brisson et al., 2010). Our results partially disagree with this result since during a generally wet season (2021) with low initial Nmin, wheat responded to additional N fertilizer after oilseed rape, obtaining yields + 38% and + 120% greater than the legume and cereal crops, respectively. Although only replicate in time and susceptible to the season effect, the results of the study could have been affected by the annual climate variability of the region. In a study by Kirkegaard et al. (1994), although different break crops consistently increased subsequent wheat vegetative growth, the wheat yields depended on season conditions.

Despite that, in 2021, wheat yields were greater after peas than after barley, in both N treatments. These results are in agreement with those of Cernay et al. (2018), in which grain legume-cereal rotation yielded more than cereal-cereal rotation. Also, the effect of grain legumes on cereal yields is suggested to depend on the N fertilization rate applied to subsequent cereals (Williams et al., 2014). However, the positive effects of grain legumes on yields of subsequent cereals are only relevant under low N input conditions and are considered negligible when the mean N fertilization exceeds 153 kg N ha^{-1} (Cernay et al., 2018). This may explain the greatest differences between pre-crops found in non-fertilized treatments. Thus, it is important to identify the most adequate approach for specific production conditions, since, according to LeGouis et al. (2020), the use of less favorable pre-crops, combined with decrease in use of N fertilizer and changes in climate conditions, have affected wheat production across Europe. In Switzerland, winter wheat producers may consider crop rotation with legume crops or oilseed rape to maintain yield levels with less N supply.

Considering N uptake is also highly regulated by the soil water availability, in water limited conditions, crops can have water and N limitations simultaneously (Plett et al., 2020). In our study, NUE, NUpE,

NUtE and NHI were not affected by water treatment, but they were affected by genotype and N treatment. Similar results were found by Cohan et al. (2019) and Manschadi and Soltani (2021). Additionally, unlike other studies (Cormier et al., 2013; Cohan et al., 2019), NUE, NUpE, NUtE and NHI were, in general, not affected by genotype × N interactions (Supp. Tab. S4, S6 and S8), indicating that the genotypes could be used to address the effect of genotype on the traits in the studied conditions. Cellule (intermediate drought tolerance) had the greatest NUE, as well as generally greater NUpE and NUtE, than both susceptible (Allez-y) and tolerant to drought (Apache and CH-Nara) genotypes. However, CH-Nara presented higher capacity to allocate the accumulated N to the grain, with mostly greater NHI than the other genotypes. These results partially agree with the study of Fan and Li (2001), in which more drought tolerant winter wheat lines had greater N efficiency than less tolerant ones. According to Manschadi and Soltani (2021), it is important to characterize winter wheat genotypes for N-related traits, because more season-specific N management is needed to minimize N inputs in unfavorable seasons in a changing climate.

5.3. Wheat yield, quality, and physiological traits

Genotype had the most consistent impact on wheat grain yield and other traits, such as grain number per m^2, N and protein grain content, HI, and WSC (Sup. Mat. Tab. S5 to S10). These results highlight the importance of accounting for genotype specificities in studies of climate change effects on crop production. Golba et al. (2018) found that in a warm-summer humid continental climate condition, the number of ears per m^2 is the most important yield component for obtaining a high grain yield. Our results show mostly moderate correlations between grain yield and number of ears per m^2, however, in our conditions, the number of grains per m^2 was more closely associated to grain yield (Fig. 7). This is illustrated by the genotype Cellule, which consistently presented both higher yields (+ 25%) and number of grains (+ 29%) than the average for Allez-y, Apache and CH-Nara combined. Also, our results are consistent with studies of Fischer (2011) and Pedro et al. (2012), in which crop yield was better related to grain number per unit area than other yield components (Pedro et al., 2012). Given the consistent superiority of the genotype with the higher number of grains per m^2, genotypes with greater number of grains per m^2 may not only be an option to achieve high levels of productivity, but also to do so under varying levels of N and water availability.

Besides the grain yield, the protein content in the grains is also a relevant factor in the payment for bread wheat to producers in Switzerland (Swiss Granum, 2020). Grain protein can also be used to determine the N adequacy in crop production, with a transition zone between N deficiency and sufficiency being 11.1% and 12.0% of protein (Goos et al., 1982). Under our conditions, CH-Nara had the greatest protein content (+ 12.8% and + 15.2% in non-fertilized and fertilized treatments, respectively), since it consistently had higher grain N content, and greatest N sufficiency in both N supplies. Similar results for CH-Nara were found by Caldelas et al. (2023). This did not occur with the other genotypes, whose grain protein levels below the transition zone in non-fertilized treatment (10.9% for Allez-y, 10.6% for Apache, and 10.4% for Cellule) could represent a N deficiency. Although some wheat genotypes have presented different results (Monaghan et al., 2001), grain protein content in cereals is shown to be strongly and negatively correlated with grain yield (Simmonds, 1995; Feil, 1997). Both variables are also susceptible to genotype x environment interactions (Oury and Godin, 2007), and their relationship can be hidden by environmental effects (Oury et al., 2003), making it difficult to analyze it. In study of Yan et al. (2022), only grain yield was affected by irrigation, while in study of Li et al. (2021), both grain yield and protein were affected by irrigation, as well as by season. On the other hand, management strategies could be applied to improve the relationship grain yield and protein. The late N application (after flag leaf visible), for example, was found to be neutral for grain yield, but improved grain protein (Giordano et al., 2023), and

the mixed application of controlled-release urea and normal urea, increased both (Zhang et al., 2022).

The HI (aboveground biomass partitioning to the grain) was affected by genotype, particularly in 2019 and 2020, but not by N or water treatments. These results reflect a marked genetic influence of the trait, as found in studies of Dai et al. (2016) and Burton et al., (in press). In our study, the genotypes CH-Nara and Cellule had the greatest HI in 2019 and 2020, showing a higher carbon translocation efficiency than the other genotypes. HI is an indicator of plant efficiency in agriculture (Austin et al., 1980). However, although HI can be rather stable in a given climate zone (Hay, 1995), it can also be reduced by abiotic stress, such as drought (Thapa et al., 2019). Low yields resulted from reductions in both biomass production and HI under water-limited conditions during jointing, anthesis and grain filling phases of wheat growth (Thapa et al., 2019). Since HI is among the components that could contribute to higher yields under different water regimes (Xue et al., 2014), it is a useful crop indicator for the analysis of the effects of limited water availability due to climate change.

Another trait that was proposed as relevant for reduced rainfall is WSC (Asseng and Van Herwaarden, 2003). We hypothesized that WSC could also be relevant for reduced N conditions. The genotypes Apache and Cellule and, in some cases, Allez-y, demonstrated small variations in WSC in peduncles of stems ≈ 10 days after anthesis (DAA). These similarities could be explained by both the absence of water stress in this study and the timing of the sampling. Liu et al. (2020) found greatest differences between concentration of WSC in peduncles of two genotypes (with different drought tolerances) at ≈ 14 DAA under drought stress, and ≈ 21 DAA in well-watered conditions, with almost no differences between all water conditions and genotypes around 7 DAA. Also, CH-Nara had consistently the greatest amounts of WSC (mean of 48.7 g kg^{-1}), with no apparent correlation to grain yield, only with aboveground biomass and TKW (Fig. 7). These results are contrary to the positive correlation between WSC and grain yield found by Xue et al. (2008), which occurs especially in water-limiting conditions (Asseng and Van Herwaarden, 2003). WSC can already contribute to yields when photosynthesis declines by 10–20% in favorable conditions (Dreccer et al., 2013), but up to 50% or more in severe terminal drought (Rattey et al., 2009). Additionally, findings of Dreccer et al. (2013) suggest that high stem WSC levels could contribute to yields when genotypes present lower grain numbers per m^2, trait that, in our study, was strongly correlated to grain yields. Therefore, high WSC concentration is also a trait of interest for ensuring wheat grain yields, particularly in water-limited environments (Ruuska et al., 2006; Foulkes et al., 2007; Xue et al., 2008), since adverse effects on wheat grain yields are likely to become more severe, due to projected rainfall variability with frequent droughts resulted from climate change (Dias de Oliveira et al., 2013).

6. Conclusions

Despite the limitations of using rainout shelters to intercept rainfall in field experiments, our research suggests that winter wheat production in Switzerland may not be severely affected by the projected rainfall decline. On the other hand, excessive rainfall during certain growth stages (like sowing, causing poor crop establishment) might be much more devastating. The lack of N fertilizer impact on wheat yields when Nmin was greater than 50 kg ha^{-1}, highlights the importance of measuring it before fertilization, and suggests the possibility of decreasing N supply over a few years when it reaches this threshold. Grain numbers per m^2 and WSC proved to be traits contributing to ensure grain yields under reduced N and varying rainfall conditions in Switzerland. Due to a higher grain number per unit area, the genotype Cellule (intermediate drought tolerant) showed the highest yield, while CH-Nara (drought tolerant), had greater grain N and protein content, as well as WSC. Overall, our experiment provides important insights for managing reduced N and understanding varying rainfall conditions during grain filling in Switzerland.

CRediT authorship contribution statement

Paola de F. Bongiovani: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Senthold Asseng :** Formal analysis, Supervision, Writing – review & editing. **Emmanuel Frossard:** Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing. **Rogério de S. Nóia Júnior:** Formal analysis, Investigation, Writing – review & editing. **Nicolas Vuille-dit-Bille:** Data curation, Investigation, Methodology, Project administration. **Juan M. Herrera:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Amanda Burton:** Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2024.109272.

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