



Nitrogen Use Efficiency and Yield of Wheat Genotypes Affected by Nitrogen Fertilizing and Environmental Conditions in Southern Brazil

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Abstract

Nitrogen (N) is a key nutrient for plant growth and yield, but N fertilizing management is complex due to the influence of the genotype × environment interaction. This study evaluated N use efficiency and yield of wheat genotypes in response to N fertilizer rates and environmental conditions. The experiment was carried out in four environments in southern Brazil [Londrina in rainfed and irrigated conditions (L_{rainfed} and L_{irrig}), Cascavel (C_{rainfed}), and Ponta Grossa (PG_{rainfed})] in a randomized block design with a 2×10 factorial arrangement, i.e. two N rates and ten wheat genotypes. The results showed that the studied wheat features (except shoot dry matter—SDM) were increased mainly due to higher water availability compared to N fertilizing. Increasing N rate from 40 to 120 kg ha⁻¹ N increased the density of fertile spikes by 11.5% in L_{rainfed} , plant lodging by an average of 12 percentage points in L_{rainfed} and L_{irrig} , N concentration in the SDM (NC_{SDM}) by an average of 9% in L_{irrig} , C_{rainfed} and PG_{rainfed} , and N accumulation in the SDM (NA_{SDM}) by an average of 14.6% in L_{irrig} and PG_{rainfed} . Overall, BRS Sanhaço was the genotype more responsive to N rates in terms of grain yield (average increase of 7.3% in C_{rainfed} and PG_{rainfed}), whereas BRS Gralha-Azul, TBIO Sintonia, and Quartzo were the lower ones. The TBIO Toruk took place in the genotype group with the lower N utilization efficiency (NUtE) in all environments, with an average of 25 kg kg⁻¹. TBIO Sinuelo had higher NC_{SDM} , NA_{SDM} , NUtE, and grain yield (averages of 17.3 g kg⁻¹, 163.5 kg ha⁻¹, 40.1 kg kg⁻¹, and 6436 kg ha⁻¹, respectively) across most of the environments. Grain yield had positive correlations with NC_{SDM} , NA_{SDM} , and NUtE. Thus, we conclude that these N traits can be better explored in breeding programmes to achieve genotypes more productive and efficient in N use. In this context, TBIO Sinuelo has the potential to be used as part of an improvement strategy for spring wheat genotypes in southern Brazil.

Keywords Nitrogen fertilizer rates · Nitrogen uptake efficiency · Nitrogen utilization efficiency · *Triticum aestivum* L.

Abbreviations

NUE	Nitrogen use efficiency
NUpE	Nitrogen uptake efficiency
NUtE	Nitrogen utilization efficiency
NC_{SDM}	Nitrogen concentration in the shoot dry matter
NA_{SDM}	Nitrogen accumulation in the shoot dry matter
L_{rainfed}	Londrina in rainfed conditions
L_{irrig}	Londrina in irrigated conditions

C_{rainfed}	Cascavel in rainfed conditions
PG_{rainfed}	Ponta Grossa in rainfed conditions
GS21	Growth stage at the beginning of plant tillering
GS69	Growth stage at anthesis
GS92	Growth stage at grain ripening

Introduction

Wheat (*Triticum aestivum* L.) is among the three most cultivated cereals worldwide, with a global production estimated in 775 million tons in the 2020/21 crop season (USDA, 2021). In Brazil, wheat is the main winter crop with about 90% of its production originating from the South Region, i.e. from the states of Paraná, Santa Catarina, and Rio Grande do Sul (CONAB, 2021). Brazilian wheat production has shown recent expansion. For instance, in the 2020/21 crop

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season, the total sown area (2.34 million hectares of which ~ 97% in rainfed situation) and average grain yield (2550 and 4930 kg ha⁻¹ in rainfed and irrigated conditions, respectively) increased by 14.8% and 5.4%, respectively, resulting in 6.2 million tons of grain, i.e. an increase of 20.9% as compared to the 2019/20 crop season (ANA, 2021; CONAB, 2021). Nonetheless, Brazil has not been self-sufficient in wheat production in the last decades, since the country has imported more than half of its demand for domestic consumption (CONAB, 2020). In fact, Brazilian wheat yield can be considered low, with average of 2516 kg ha⁻¹ from 2010/11 to 2020/21 crop seasons (CONAB, 2021), which makes the country less competitive globally. Therefore, it is essential to increase the current wheat yield at workable costs. This challenge can be achieved by means of well-structured plant breeding programmes combined with improved agronomic management practices such as the use of suitable fertilizing strategies (Corassa et al., 2018).

Nitrogen (N) is the most limiting nutrient for wheat growth and yield in most environmental conditions (Chen et al., 2020; Mandic et al., 2015). This nutrient is a component of plant cell walls, proteins, nucleic acids, chlorophyll, and other organic molecules, being essential for plant physiology (Marschner, 2012). Nitrogen deficiency reduces plant leaf area, photosynthetic rate, tillering capacity, number of fertile spikes per area and, consequently, grain yield (Taiz et al., 2017; Yousaf et al., 2014). On the other hand, excessive N availability can increase plant lodging (Khan et al., 2020; Ma et al., 2016; Peake et al., 2020). Although N fertilizing is among the most important agronomic tools to increase wheat grain yield (Duncan et al., 2018; Lollato et al., 2019; Souza et al., 2021), there are important knowledge gaps to further improve N management in subtropical conditions in southern Brazil. These gaps in determining the optimal N fertilizing practices (i.e. the combination of N rate, timing, source, and placement) are derived from the complex dynamic of N in the soil–plant–atmosphere system (Ferreira et al., 2021; Vieira, 2017). Furthermore, wheat genotypes present significant differences in terms of N use efficiency (NUE), i.e. the plant capacity to uptake N from the soil and use it for grain production (Beche et al., 2014; Lollato et al., 2021; Mansour et al., 2017). Thus, selecting the most adapted wheat genotype for each specific environment is another key tool to maximize crop yield (Munaro et al., 2020; Smutná et al., 2021), particularly considering in the selection process the NUE that is a trait governed by the interaction of multiple genetic and environmental factors (Xu et al., 2012).

Nitrogen use efficiency is considered the product of N uptake efficiency (NUpE) and N utilization efficiency (NUtE) (Lollato et al., 2021; Moll et al., 1982; Sharma et al., 2020). The NUpE is a function of root biomass, the morphological ability of the roots to explore soil regions

with abundant availability of nutrients, and the physiological capacity for nutrient uptake (Glass, 2003). Thus, NUpE can be indirectly evaluated by the accumulation of N in the plant biomass. In turn, the NUtE is derived from the crop production per unit of N acquired by the plant (Hawkesford, 2011; Moll et al., 1982). In this context, when plants grow in environments limited in N availability, NUtE plays an important role that determines most of the variation of NUE (Hirel et al., 2007). Therefore, increasing plant NUpE and NUtE allows farmers to improve crop yield with moderate N fertilizing rates near to the maximum economic efficiency (Cai et al., 2021; Mehrabi & Sepaskhah, 2018). Moreover, excessive N fertilizer rates have resulted in serious environmental problems concerning atmospheric, soil, and water enrichment with several forms of N, as a result of N denitrification, volatilization, leaching, and runoff (Ju et al., 2009; Sylvester-Bradley & Kindred, 2009). Thus, improving genotype NUE is a manner to reduce this environmental risk (Meng et al., 2016; Wang et al., 2011).

The influence of environmental conditions and agronomic management practices have been reported to have greater effects on quantitative traits such as NUE than the wheat genotype being grown (Adnan et al., 2021; Bhatta et al., 2017; Ferreira et al., 2021, 2022; Krupnik et al., 2015; Rozbicki et al., 2015). Thus, improvements in NUE are most promptly achieved through the adoption of more efficient management of abiotic stresses, for instance by means of adjustments in irrigation and N fertilizer rates (Mehrabi & Sepaskhah, 2018; Zhang et al., 2015; Zhou et al., 2011). Nonetheless, important genotypic effects on N physiological traits were also reported in the aforementioned studies, which indicates the potential to select wheat genotypes with better NUE considering a wide range of environmental conditions, including soil water and N availabilities. In this context, breeders can increase genetic gains by selecting on physiological traits associated with NUE under multiple N rates as opposed to exclusively selecting on yield per se at a fixed N rate (Brancourt-Humel et al., 2005; Brasier et al., 2019).

Brazilian wheat breeding programmes do not take into account plant traits related to NUE aiming to increase grain yield at reduced N fertilizer requirement. Furthermore, there is a sparse amount of works that studied the genotype × environment interaction effects on wheat NUE in Brazil (Beche et al., 2014; Silva et al., 2014a, 2014b; Todeschini et al., 2016). Thus, we hypothesized that the modern spring wheat genotypes currently cultivated in southern Brazil differ in NUE by environment, and have potential to be added in breeding programmes considering N efficiency traits such as NUpE and NUtE. The objective of this study was to evaluate NUE and yield of wheat genotypes in response to N fertilizer rates and environmental conditions in southern Brazil.

Material and Methods

Environmental Description of the Experimental Sites

The experiment was conducted throughout the 2016 winter growing season in three edaphoclimatic sites in the state of Paraná, southern Brazil: Londrina (23°11'31.4" S 51°10'39.3" W, and 599 m a.s.l.), Cascavel (24°56'20.4" S 53°30'48.6" W, and 697 m a.s.l.), and Ponta Grossa (25°09'05.2" S 50°04'49.0" W, and 875 m a.s.l.). In Londrina, there were rainfed ($L_{rainfed}$) and irrigated (L_{irrig}) conditions, while rainfed was the water management adopted in Cascavel ($C_{rainfed}$) and Ponta Grossa ($PG_{rainfed}$), which resulted in four environmental sites. The trials in L_{irrig} and $L_{rainfed}$ were arranged side by side, separated by 10 m between their edges. All studied sites had been under continuous wheat (winter)–soybean [*Glycine max* (L.) Merrill] (summer) production under no-tillage system for at least ten years prior to the establishment of the experiment.

In Londrina, the experiments were carried out in the experimental field station at the National Soybean Research Centre of the Brazilian Agricultural Research Corporation (*Empresa Brasileira de Pesquisa Agropecuária – Embrapa*). The landscape is smooth-rolling with mild slopes (~15%), and the soil is a basaltic Rhodic Eutrudox according to the USDA Soil Taxonomy (Soil Survey Staff, 2010) [*Latosolo Vermelho eutrófico* according to the Brazilian Soil Classification System (Santos et al., 2018)]. The regional climate is humid subtropical (Cfa) [according to the Köppen climate classification (Köppen, 1931)] with warm and rainy summer, sparse frosts, no defined dry season, and with a mean annual temperature and precipitation of 21.2 °C and 1438 mm (Sibaldelli & Farias, 2019).

In Cascavel, the trial was conducted in the experimental field station at the Assis Gurgacz Foundation University Centre (*Centro Universitário da Fundação Assis Gurgacz – FAG*). In the experimental site, the landscape is flat, and the soil is a Rhodic Hapludox (*Latosolo Vermelho distrófico*). The regional climate is humid subtropical (Cfa) with warm and rainy summer, frequent frosts (from April to September), no defined dry season, and with a mean annual temperature and precipitation of 18.2 °C and 1822 mm.

Finally, in Ponta Grossa, the experiment was carried out in another experimental field station of the Embrapa. The landscape is smooth-rolling with mild slopes (~8%), and the soil in the experimental field is a Rhodic Hapludox. The regional climate is mesothermal humid subtropical (Cfb), with well-distributed rainfall, frequent frosts (from April to September), and a mean annual temperature and precipitation of 17.5 °C and 1500 mm (Nitsche et al., 2019).

Soil chemical and physical characterization was performed in soil samples collected in the soil layers of 0–10 and 10–20 cm (Supplementary Table S1). Meteorological variables were recorded throughout the winter growing season in weather stations located less than 800 m from the experimental areas. The water balance was calculated according to the Thornthwaite and Mather (1955) method, and the water deficit and water surplus were presented in ten-day periods (Fig. 1). The accumulated water deficit considered the sum of the ten-day periods with negative water balance throughout the wheat growing season. The meteorological data were used in L_{irrig} for monitoring the need for water supplementation, which was confirmed in the experimental field by means of tensiometers. A self-propelled sprinkler irrigation system applied the supplementary water supply whenever necessary to avoid water deficit in L_{irrig} . There were five 25-mm irrigations during the wheat growing season (Fig. 1b).

Experimental Design and Treatments

Considering a complete 2×10 factorial arrangement, a randomized block design (with three replications) evaluated two N rates (40 and 120 kg ha⁻¹), applied as topdressing fertilizing at the beginning of plant tillering [growth stage GS21 according to the Zadoks' phenological scale (Zadoks et al., 1974)], and ten wheat genotypes (cultivars: BRS Sanhaço, BRS Graúna, BRS Gaivota, BRS Galha-Azul, TBIO Sinuelo, TBIO Mestre, TBIO Sossego, TBIO Sintonia, TBIO Toruk, and Quartzo; henceforth referred to as SAN, GRAU, GAI, GRAL, SINU, MES, SOS, SINT, TOR, and QUA, respectively). The N rates were based on technical indications for wheat crops in the state of Paraná, which consider the results of soil chemical analysis, and the expected grain yield in a range of edaphoclimatic environments (CBPTT, 2016; Foloni et al., 2016). The rates of 40 and 120 kg ha⁻¹ N were chosen considering a wide amplitude between them to maximize plant physiological response of the wheat genotypes, which allowed better ranking of the genotypes in conditions of low and high N availability. The selected wheat genotypes have been widely cultivated in the study region showing greater grain yield and quality. In the state of Paraná, the majority of the wheat genotypes are classified as medium maturing with respect to phenology, except the GRAU genotype that has an early cycle, and SINU and SINT genotypes those cycles range from medium to late or from early to medium, respectively (CBPTT, 2020). Additional information about the genotypes is presented in Supplementary Table S2. In the literature, there is scarce and fragmented information about the effects of N fertilizing and/or environmental conditions on NUE and grain yield for few of these genotypes, which reinforced their use in this study.

The establishment of the trials used no-tillage practices, and wheat was sown few days after soybean harvest.

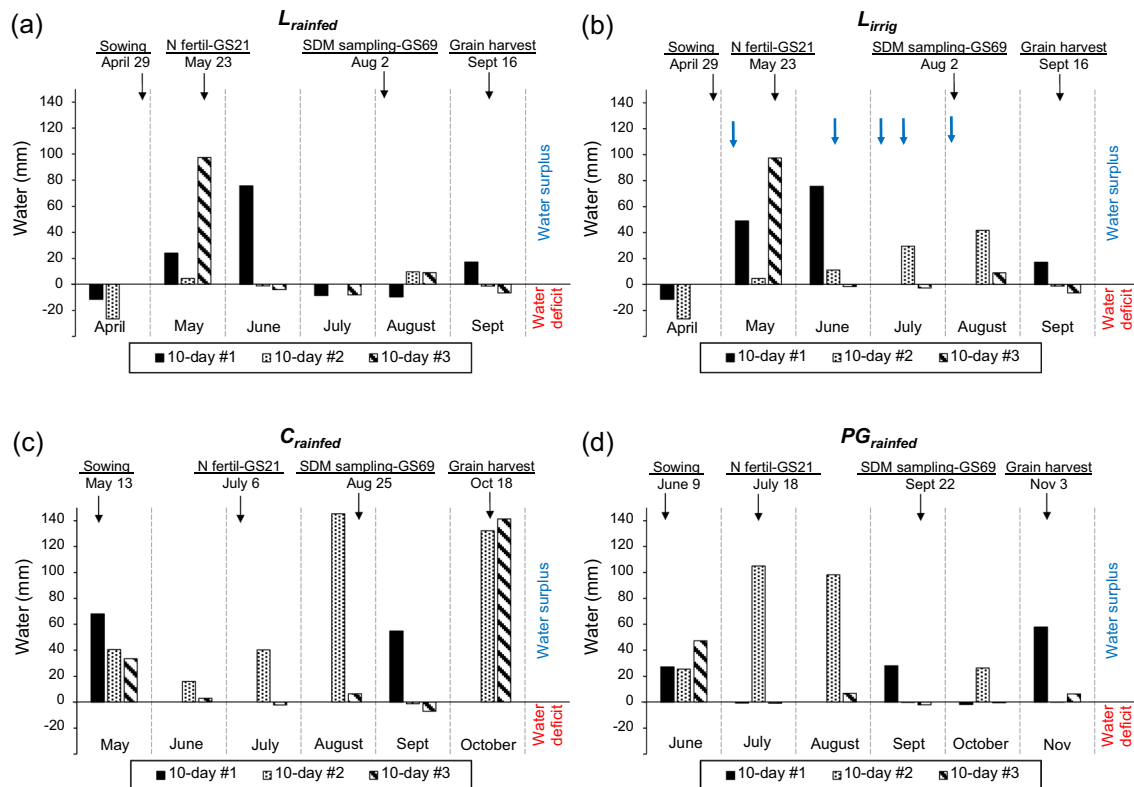


Fig. 1 Ten-day water balance during the 2016 wheat growing season in Londrina (April 29–September 16 = 141 days) in rainfed ($L_{rainfed}$: panel 'a') and irrigated (L_{irrig} : panel 'b') conditions, Cascavel (May 13–October 18 = 159 days) in rainfed ($C_{rainfed}$: panel 'c') situation, and Ponta Grossa (June 9–November 3 = 148 days) in rainfed ($PG_{rainfed}$: panel 'd') condition. In L_{irrig} , five 25-mm irrigations were applied on

May 4, June 17, July 1, July 13, and August 2. The blue arrows in the panel 'b' indicate these irrigations. Dates of the major field operations are also provided in the panels: sowing, N fertilizing at the beginning of plant tillering (Zadoks growth stage GS21), shoot dry matter (SDM) sampling at anthesis (GS69), and grain harvest

The experimental plot was 6 m long by 1.6 m wide (9.6 m²), consisting of nine 0.178 m spaced rows. Wheat was sown in the 2016 crop season ($L_{rainfed}$ and L_{irrig} = April 29; $C_{rainfed}$ = May 13; and $PG_{rainfed}$ = June 9) using a sowing density of 350 viable seeds m⁻². The seeds were placed in furrows with approximately 4 cm depth, using a sowing-fertilizer drill developed for experimental plots and no-tillage system. The base fertilizing was performed in the aforementioned furrows with 250 kg ha⁻¹ of the formulated fertilizer 08–28–16 (N–P₂O–K₂O) (CBPTT, 2016; Foloni et al., 2016). In the phenological GS21, the topdressing fertilizing used ammonium nitrate (32% N) as source of N.

Weeds, insects and fungi diseases were controlled with commercial pesticides, in accordance with regional technical recommendations for wheat crops (CBPTT, 2016).

Wheat Growth and Yield, and Nitrogen Uptake and Utilization Efficiency by Plants

When wheat plants were at anthesis (GS69), shoot dry matter was evaluated by harvesting two rows 0.5 m long (0.178

m²) in each experimental plot. The shoot dry matter was determined after drying the samples in a heater with forced air circulation at 65 °C for 72 h. Anthesis was chosen for this evaluation because it is the phenological stage with the highest N accumulation in the wheat plant biomass (Lollato et al., 2021; Wiethölter, 2011).

The dried biomass samples were ground in a stainless steel Wiley mill, passed through a 0.1 mm sieve, to determine N concentration in the shoot dry matter (NC_{SDM}) by Kjeldahl method (Silva, 2009). Nitrogen accumulation in the shoot dry matter (NA_{SDM} ; kg ha⁻¹) at anthesis (i.e. an indirect measurement of NUpE) was estimated from NC_{SDM} (g kg⁻¹) and shoot dry matter (kg ha⁻¹) (Eq. 1):

$$NA_{SDM} = \frac{\text{Shoot dry matter} \times NC_{SDM}}{1000} \quad (1)$$

Wheat grain yield (GY) was determined by harvesting plants at ripening (GS92) using a self-propelled combine developed for a small plot of cereals (Wintersteiger). Harvested area covered seven rows wide by 6 m long in each plot.

Grain moisture content was evaluated, recorded, and adjusted to 13% for yield calculation.

Nitrogen utilization efficiency (NUE; kg kg^{-1}) for grain yield was estimated according to Crusciol et al. (2003) by means of the Eq. (2) (GY at GS92, and NA_{SDM} at GS69; both in kg ha^{-1}):

$$NUE = \frac{GY}{NA_{SDM}} \quad (2)$$

The density of fertile spikes (spikes m^{-2}) was evaluated at GS69. Plant lodging was estimated by a visual scoring system (adapted from EMBRAPA, 2009) that consists of notes taken at maturity (GS92) and recorded on a scale from 0 to 10 (where 0 is upright and 10 is completely lodged), which were converted to percentages of lodging.

Statistical Analyses

The statistical analyses were performed using the R statistical software (R Core Team, 2021), individually for each environment. The Shapiro–Wilk's test evaluated the normality of residuals, and the Bartlett's test assessed the variance homogeneity. According to these tests, no data transformation was needed. Since all of the assumptions required for a valid analysis of variance (ANOVA) were met, F-test was performed. When the ANOVA resulted in a significant P -value ($P \leq 0.05$), the means of the two treatments from the factor 'N rates' were compared by the Student–Newman–Keuls' test ($P < 0.05$). The means from the factor 'wheat genotypes' were grouped by the Scott–Knott's clustering algorithm ($P < 0.05$). When the subject factors (i.e. the main effects) were significant but the interaction was not, the multiple comparisons among treatment means were performed within each factor. On the other hand, when the two-way interaction between factors was significant, the comparisons among treatment means for one factor were performed individually within each level of the other factor (Wei et al., 2012). Finally, the wheat features evaluated in the four environments were submitted to Pearson's correlation analysis.

Results

Changes in Wheat Growing Seasons in Response to Weather Conditions

The experiment was replicated in four environmental conditions in the 2016 crop season in southern Brazil: two in Londrina that differed in terms of water management ($L_{rainfed}$ and L_{irrig}), one in Cascavel ($C_{rainfed}$), and one in Ponta Grossa ($PG_{rainfed}$) (Fig. 1, and Supplementary Fig. S1).

In Londrina, the wheat growing season reached a period of 141 days, which had mean values of average, maximum, and minimum temperatures of 17.6 ± 3.2 , 22.9 ± 3.8 , and 12.9 ± 3.5 °C (mean \pm standard deviation), and accumulated precipitation of 465.3 mm (Fig. S1a). In addition, the treatments in L_{irrig} were sprinkled with five 25-mm irrigations (at 6th, 50th, 64th, 76th, and 96th day) that raised the total water supply to 590.3 mm and decreased the accumulated water deficit from 31.4 mm ($L_{rainfed}$; Fig. 1a) to 4.3 mm (Fig. 1b). After wheat sowing, a seven-day drought period occurred, followed by a four-day rainy period with an accumulation of 55.4 mm (Fig. S1a). Moreover, there were two distinguished drought periods: the first from 40th day (mid tillering stage; GS25) to 78th day (end of culm elongation; GS39) (i.e. 39 days without rainfall), and the second from 80 to 111th day (soft dough stage; GS85) (i.e. 32 days with an accumulated of 12.4 mm). The topdressing N fertilizing was performed on the 25th day, which was preceded by 33.7 mm of rainfall (considering five consecutive days), and followed by 190.8 mm in the 14 days after fertilizing (Fig. S1a). Throughout the grain-filling period (i.e. from anthesis to grain ripe), there was accumulated precipitation of 70 mm and mean values of average, maximum, and minimum temperatures of 18.7 ± 3.4 , 24.6 ± 4.3 , and 13.4 ± 3.5 °C. The occurrence of frost was not recorded during the crop season.

The wheat growing season in $C_{rainfed}$ extended in 159 days with mean values of average, maximum, and minimum temperatures of 16.8 ± 4.2 , 23.1 ± 5.2 , and 11.7 ± 4.3 °C, and total precipitation of 717.6 mm (Fig. S1b). The precipitation was well distributed throughout the wheat growing cycle, which resulted in a low accumulated water deficit of 10.3 mm (Fig. 1c). Wheat sowing was followed by an accumulation of 106 mm from 3rd to 20th day (Fig. S1b). Nitrogen fertilizing in the 55th day was succeeded by 70 mm of rainfall during 11 days (from 55 to 65th day). During the grain-filling period, there were an accumulated precipitation of 293.6 mm and mean values of average, maximum, and minimum temperatures of 19.2 ± 3.9 , 26.4 ± 5.3 , and 13.3 ± 3.9 °C (Fig S1b). There were no frosts during the wheat growing cycle.

In $PG_{rainfed}$, the wheat growing cycle had 148 days with mean values of average, maximum, and minimum temperatures of 15.4 ± 3.9 , 21.6 ± 4.5 , and 10.3 ± 4.5 °C, and total precipitation of 520.4 mm (Fig. S1c). The rainfall distribution was regular, which resulted in an accumulated water deficit of only 5.7 mm (Fig. 1d). Wheat sowing was followed by an eight-day drought period with only 0.2 mm of rainfall (Fig. S1c). Then, there was 87.8 mm across five consecutive days. The topdressing N fertilizing was performed on the 40th day of the growing season, which was preceded by 125.4 mm of rainfall in six successive days (Fig. S1c). After N fertilizing, there was a 20-day drought period with 2.8 mm of rainfall. Over the

grain-filling period, there was an accumulated precipitation of 95 mm, and mean values of average, maximum, and minimum temperatures of 18.0 ± 3.1 , 24.2 ± 3.9 , and 13.7 ± 3.0 °C. There were five events of frost after sowing (from the 1st to the 5th day).

Wheat Growth and Yield

The density of fertile spikes averaged 423, 513, 577, and 535 spikes m^{-2} in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$, respectively (Table 1). In Londrina, the water supply by irrigation increased the density of spikes by an average of 21.3% (from $L_{rainfed}$ to L_{irrig}). Whereas comparing the rainfed environments, $C_{rainfed}$ and $PG_{rainfed}$ showed 36.4% and 26.5% more spikes m^{-2} than that of $L_{rainfed}$. Increasing the topdressing N fertilizing from 40 to 120 kg ha^{-1} N increased the density of spikes by 11.5% in $L_{rainfed}$. The Scott–Knott's test assembled the genotypes in two groups in each environment. Comparing these groups, the increases in the density

of spikes ranged from 20.2% (in L_{irrig}) to 29.8% (in $L_{rainfed}$). The genotypes SAN, MES, SOS and QUA belonged to the group with the higher density of spikes in all environments, whereas the TOR genotype always was grouped within the other group. The genotypes GRAU, GAI, GRAL, SINU and SINT showed lower genetic stability for this crop trait, interchanging between the groups depending on the environment.

Plant lodging was highly influenced by the environmental conditions (Table 1). It averaged 44.2%, 63.7%, 7.3%, and 0% in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$. Thus, irrigation increased plant lodging by 19.5 percentage points in Londrina; whereas in $C_{rainfed}$, plant lodging was 7.4 times lower than the average of Londrina (i.e. $L_{rainfed}$ and L_{irrig}). Increasing N rate from 40 to 120 kg ha^{-1} increased plant lodging by 10.3, 13.7, and 3.0 percentage points in $L_{rainfed}$, L_{irrig} , and $C_{rainfed}$. The lodging variability among the genotypes allowed clustering them into three groups per environment (except for $PG_{rainfed}$). Thus, plant lodging ranged from 53.3% (in $C_{rainfed}$) to 87.5% (in $L_{rainfed}$) in the first group with more

Table 1 Multiple comparisons between treatment means for nitrogen (N) rate and wheat genotype, and significance of the analysis of variance of the main effects (N rate and genotype) and their interaction for density of fertile spikes, plant lodging, and grain yield in

four environments: Londrina in rainfed ($L_{rainfed}$) and irrigated (L_{irrig}) conditions, and Cascavel ($C_{rainfed}$) and Ponta Grossa ($PG_{rainfed}$) only in rainfed situation

Factor	Treatment	Density of fertile spikes (spikes m^{-2})				Plant lodging (%)				Grain yield (kg ha^{-1})			
		$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$PG_{rainfed}$	$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$PG_{rainfed}$	$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$PG_{rainfed}$
N rate (kg ha^{-1})	40	425 a	511 a	565 a	506 b	39.0 b	56.8 b	5.8 b	0.0	3726 a	5398	6613	6020
	120	421 a	514 a	588 a	564 a	49.3 a	70.5 a	8.8 a	0.0	3800 a	5390	6860	6700
Genotype	BRS Sanhaço	472 a	527 a	616 a	587 a	52.5 b	55.0 b	0.0 c	0.0	3448 b	5352	7523	7083
	BRS Graúna	416 a	468 b	521 b	515 a	45.8 b	75.8 a	2.0 c	0.0	3972 a	5763	6745	6385
	BRS Gaivotá	381 b	415 b	596 a	589 a	31.7 b	21.7 c	2.5 c	0.0	2992 b	4783	6505	6227
	BRS Gralha-Azul	460 a	454 b	620 a	537 a	87.5 a	99.2 a	53.3 a	0.0	3744 a	5304	6250	7345
	TBIO Sinuelo	418 a	504 b	622 a	581 a	31.7 b	45.0 b	0.0 c	0.0	4693 a	5923	8125	7002
	TBIO Mestre	442 a	579 a	628 a	595 a	53.3 b	84.2 a	1.7 c	0.0	4059 a	5092	7109	6744
	TBIO Sossego	438 a	569 a	610 a	530 a	50.0 b	75.0 a	3.3 c	0.0	4386 a	5913	7080	6428
	TBIO Sintonia	475 a	579 a	530 b	480 b	39.2 b	92.5 a	7.8 b	0.0	3790 a	5571	5933	6151
	TBIO Toruk	302 b	489 b	441 b	406 b	6.67 c	3.3 c	0.0 c	0.0	2499 c	4775	4723	3294
	Quartzó	427 a	545 a	582 a	530 a	43.3 b	85.0 a	2.5 c	0.0	4047 a	5459	7376	6939
Source of variation	Df	Significance of the analysis of variance											
Block	2	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns
N rate (N)	1	ns	ns	ns	**	*	*	***	-	ns	ns	**	***
Genotype (G)	9	*	***	*	***	***	***	***	-	***	***	***	***
N × G	9	ns	ns	ns	ns	ns	ns	ns	-	ns	*	*	*
CV (%)		19.0	12.5	17.3	11.9	36.3	31.5	41.6	-	15.9	7.2	4.7	4.8

CV= coefficient of variation

Df= degrees of freedom (note: df from error=38)

ns, *, **, and ***=not significant, and significant at $P \leq 0.05$, ≤ 0.01 , and ≤ 0.001 , respectively, by the F-test. Means followed by different lowercase letters in the column, individually for N rate or genotype factors, differ from each other by the Student–Newman–Keuls' test ($P < 0.05$) or Scott–Knott's test ($P < 0.05$), respectively. Comparisons with significant interaction between the main effects have further interpretations in Fig. 2

susceptible genotypes; whereas it ranged from 1.5% (in $C_{rainfed}$) to 12.5% (in L_{irrig}) in the third group, which genotypes are considered more tolerant to lodging. Overall, the GRAL genotype showed the highest plant lodging (average of 60%) and the TOR genotype the lowest one (average of 2.5%) across the environments where this damage occurred.

The environments had a greater influence on wheat grain yield, which averaged 3763, 5394, 6737, and 6360 $kg\ ha^{-1}$ in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Table 1). In Londrina, irrigation increased grain yield by an average of 43% (from $L_{rainfed}$ to L_{irrig}). In rainfed conditions, grain yields in $C_{rainfed}$ and $PG_{rainfed}$ were 79% and 69% higher than that of $L_{rainfed}$. Significant 'N rate' effect was identified only by decomposing its interaction with the factor 'genotype' (Fig. 2). Thus, increasing N rate from 40 to 120 $kg\ ha^{-1}$ increased grain yield by averages of 14.4% for the genotypes SAN and SINU in L_{irrig} (Fig. 2a), 19.2% for SAN and TOR in $C_{rainfed}$ (Fig. 2b), and 15.5% for SAN, GRAU, GAI, GRAL, MES and SOS in $PG_{rainfed}$ (Fig. 2c). Thus, the SAN genotype was the more responsive to N fertilizing considering these three environments, whereas the genotypes GRAL, SINT and QUA were not influenced by N rates. The clustering test assembled the genotypes in three groups in $L_{rainfed}$, where the TOR genotype had the least grain yield (2499 $kg\ ha^{-1}$), SAN and GAI genotypes yielded on average 3220 $kg\ ha^{-1}$, and the others genotypes showed higher grain yields (average of 4099 $kg\ ha^{-1}$) (Table 1). In the other environments (L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$), there was a genotype \times N rate interaction that showed a great diversity of genotype clusters by N rate (Fig. 2). Overall, the TOR genotype was the least productive (average of 3823 $kg\ ha^{-1}$), and SINU yielded more (average of 6436 $kg\ ha^{-1}$).

The shoot dry matter at anthesis stage averaged 9608, 9074, 10,088, and 8193 $kg\ ha^{-1}$ in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Table 2). Therefore, irrigation decreased the shoot dry matter by an average of 5.6% (from $L_{rainfed}$ to L_{irrig}) in the environment of Londrina. Evaluating the rainfed environments, the shoot dry matter in $C_{rainfed}$ was on average 5% higher than that of $L_{rainfed}$; while in $PG_{rainfed}$ it was 14.7% lower also compared to $L_{rainfed}$. There were no effects of the factors 'N rate' and 'genotype' on shoot dry matter production.

Nitrogen Uptake and Utilization Efficiency by Wheat Plants

The NC_{SDM} at anthesis stage averaged 13.3, 16.6, 17.8, and 17.9 $g\ kg^{-1}$ in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Supplementary Table S3). Thus, the additional water supply raised the NC_{SDM} by an average of 24.8% (from $L_{rainfed}$ to L_{irrig}), whereas under rainfed conditions the NC_{SDM} was on average 34.2% higher in $C_{rainfed}$ and $PG_{rainfed}$ as compared to that of

$L_{rainfed}$. Increasing N rate from 40 to 120 $kg\ ha^{-1}$ increased the NC_{SDM} by averages of 7.5%, 8.2%, and 11.2% in L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Table S3), and by 29.1% and 26% for the genotypes GRAU and SINU in $L_{rainfed}$ (Supplementary Fig. S2). The clustering test assembled the genotypes in three groups in L_{irrig} , and two groups in $C_{rainfed}$ and $PG_{rainfed}$ (Table S3). The TOR genotype always belonged to the group with higher NC_{SDM} (Table S3 and Fig. S2), whereas GRAU, SINT and QUA genotypes were clustered in the last group in L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$.

The NA_{SDM} at anthesis averaged 127, 150, 179, and 145 $kg\ ha^{-1}$ in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Table 2). Therefore, it was on average 40.9% and 14.2% higher in $C_{rainfed}$ and $PG_{rainfed}$ as compared to that of $L_{rainfed}$. Furthermore, in Londrina, irrigation increased the NA_{SDM} by an average of 18.1%. Increasing N rate from 40 to 120 $kg\ ha^{-1}$ increased the NA_{SDM} by 12.8% and 16.4% in L_{irrig} and $PG_{rainfed}$ (Table 2). The factor 'genotype' influenced the uptake of N in $C_{rainfed}$, where the NA_{SDM} of the genotypes SINU, SOS and TOR was on average 17.6% higher than that of the other genotypes. Considering the average of all environments by genotype, the NA_{SDM} ranged from 141 $kg\ ha^{-1}$ for SINT to 164 $kg\ ha^{-1}$ for SINU.

The NUtE for grain yield averaged 30.9, 37.1, 38.4, and 45.4 $kg\ kg^{-1}$ in $L_{rainfed}$, L_{irrig} , $C_{rainfed}$, and $PG_{rainfed}$ (Table 2). Thus, in Londrina, the water supply by irrigation increased the NUtE by 20%. In rainfed conditions, the NUtE increased by averages of 24.3% and 46.9% in $C_{rainfed}$ and $PG_{rainfed}$, as compared to that of $L_{rainfed}$. Nitrogen fertilizing influenced the NUtE only in L_{irrig} for some genotypes, where the N rate of 120 $kg\ ha^{-1}$ decreased the NUtE by 28.6% and 45.5% for GRAL and TOR, as compared to that of 40 $kg\ ha^{-1}$ N (Fig. 3). The genetic differences among the genotypes allowed clustering them into two groups per environment (Table 2). The TOR genotype took place within the group with the lower NUtE in all environments, and GAI and GRAL genotypes also were clustered in this group in $L_{rainfed}$ (Table 2 and Fig. 3). The group of the more efficient genotypes had 28.7%, 30.7%, 42%, and 48.2% higher NUtE in $L_{rainfed}$, L_{irrig} (within 120 $kg\ ha^{-1}$ N), $C_{rainfed}$, and $PG_{rainfed}$, as compared to that of the other group.

Discussion

Environmental Influence on Wheat Growth and Yield, and N Uptake and Utilization by Plants

The water management in Londrina ($L_{rainfed}$ and L_{irrig}) and the different edaphoclimatic conditions in the three sites [Londrina, Cascavel ($C_{rainfed}$), and Ponta Grossa ($PG_{rainfed}$)] resulted in four distinct environments. Briefly, Londrina had higher temperatures and lower accumulated rainfall

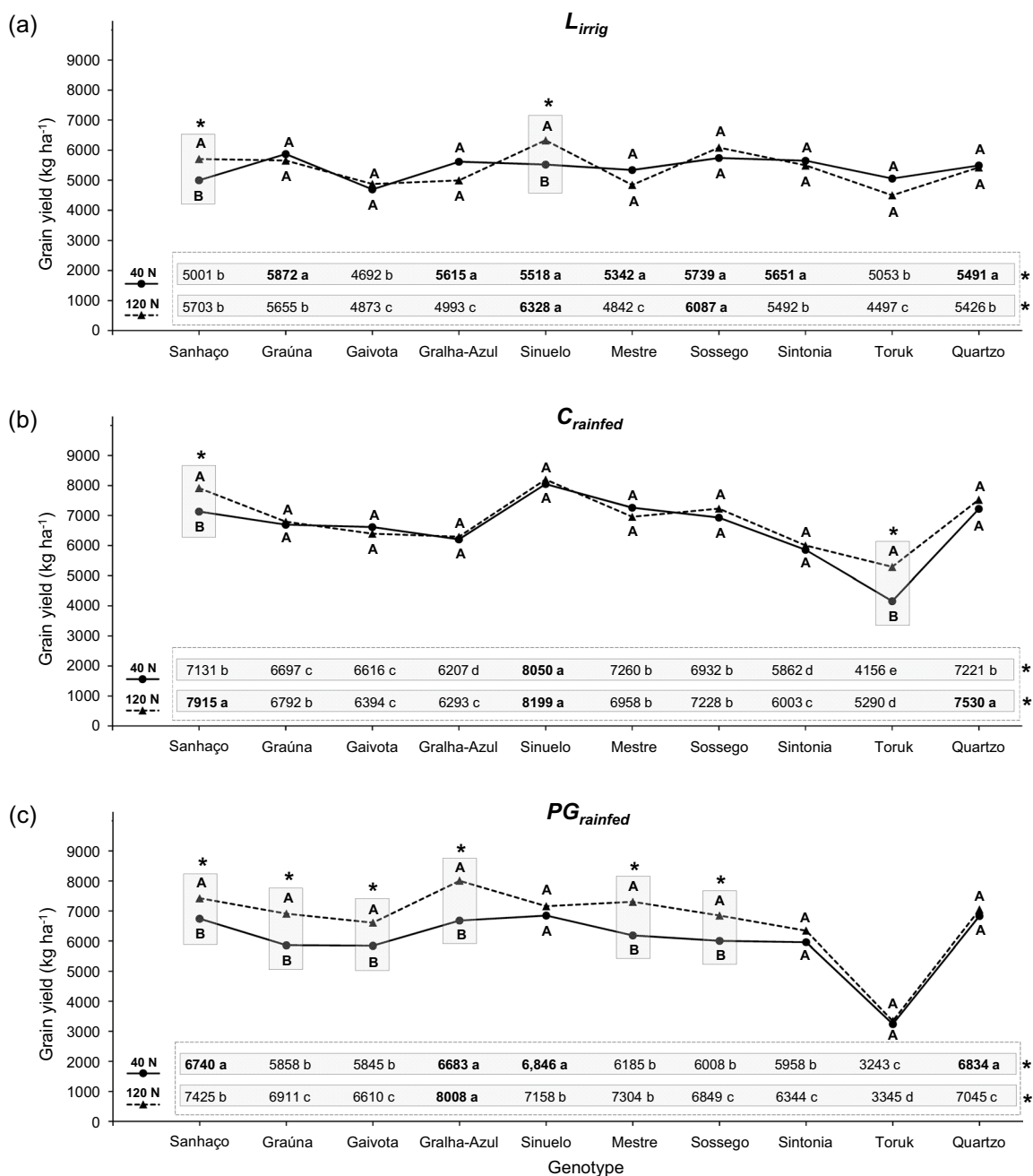


Fig. 2 Comparisons between treatment means when the two-way interaction between the main factors was significant, i.e. 'nitrogen (N) rate×genotype' for grain yield in Londrina in irrigated (L_{irrig} : panel 'a') condition, Cascavel in rainfed ($C_{rainfed}$: panel 'b'), and Ponta Grossa in rainfed ($PG_{rainfed}$: panel 'c'). Individually for each N rate (40 or 120 kg ha⁻¹, i.e. 40 N or 120 N), values within the box comparing genotypes (BRS Sanhaço, BRS Graúna, BRS Gaivota, BRS Gralha-

Azul, TBIO Sinuelo, TBIO Mestre, TBIO Sossego, TBIO Sintonia, TBIO Toruk, and Quartzo) followed by different lowercase letters differ (*) from each other by the Scott–Knott's test ($P < 0.05$). Individually for each genotype, symbols (black circle and black triangle) comparing N rates followed by different capital letters differ (*) from each other by the Student–Newman–Keuls' test ($P < 0.05$)

experienced during the crop growing cycle, which had the shortest period (141 days). In $L_{rainfed}$, the periods of water deficit achieved higher values, affecting the phenological stages of seedling growth, culm elongation, flowering,

and grain filling, besides the uptake of N. In turn, in L_{irrig} the seedling growth was also influenced by the water deficit, but the other phenological stages were not affected by drought. Compared to Londrina, the $C_{rainfed}$ environment

Table 2 Multiple comparisons between treatment means for nitrogen (N) rate and wheat genotype, and significance of variance of the main effects (N rate and genotype) and their interaction for shoot dry matter (SDM) at anthesis, N accumulation in the SDM, and N utilization efficiency (NUE) for grain yield in four environments: Londrina in rainfed ($L_{rainfed}$) and irrigated (L_{irrig}) conditions, and Cascavel ($C_{rainfed}$) and Ponta Grossa ($P_{rainfed}$) only in rainfed situation

Factor	Treatment	Shoot dry matter ($kg\ ha^{-1}$)				N accumulation in the SDM ($kg\ ha^{-1}$)				NUE for grain yield ($kg\ kg^{-1}$)			
		$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$P_{rainfed}$	$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$P_{rainfed}$	$L_{rainfed}$	L_{irrig}	$C_{rainfed}$	$P_{rainfed}$
N rate ($kg\ ha^{-1}$)	40	9474 a	8909 a	10,232 a	8006 a	121 a	141 b	175 a	134 b	32.4 a	39.1	38.7 a	46.4 a
	120	9743 a	9239 a	9944 a	8380 a	134 a	159 a	184 a	156 a	29.4 a	35.1	38.0 a	44.4 a
Genotype	BRS Sanhaço	8272 a	8614 a	9494 a	8052 a	115 a	145 a	179 b	147 a	30.2 a	37.6	42.7 a	50.5 a
	BRS Graúna	10,314 a	9476 a	10,019 a	8287 a	129 a	145 a	170 b	140 a	32.4 a	40.7	40.2 a	47.3 a
	BRS Gaivota	9101 a	8221 a	10,183 a	8614 a	130 a	135 a	172 b	142 a	23.8 b	35.7	38.3 a	45.1 a
	BRS Gralha-Azul	10,847 a	9382 a	9125 a	8287 a	140 a	152 a	166 b	155 a	27.2 b	36.0	37.7 a	48.1 a
	TBIO Sinuelo	10,941 a	9228 a	10,651 a	7678 a	155 a	158 a	200 a	141 a	30.3 a	37.8	40.8 a	51.5 a
	TBIO Mestre	9696 a	8680 a	9644 a	8474 a	133 a	146 a	174 b	148 a	31.3 a	35.0	40.9 a	47.1 a
	TBIO Sossego	9916 a	9003 a	10,459 a	8614 a	123 a	148 a	188 a	148 a	36.7 a	40.6	38.3 a	44.5 a
	TBIO Sintonia	9888 a	9827 a	9775 a	9036 a	115 a	146 a	158 b	145 a	38.4 a	39.5	37.7 a	43.4 a
	TBIO Toruk	7631 a	8553 a	11,217 a	6742 a	120 a	174 a	213 a	145 a	21.3 b	30.8	23.2 b	24.7 b
	Quartzo	9476 a	9757 a	10,314 a	8146 a	113 a	148 a	173 b	139 a	37.3 a	37.2	43.7 a	51.7 a
Source of variation	Df	Significance of the analysis of variance											
Block	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
N rate (N)	1	ns	ns	ns	ns	ns	**	ns	**	ns	*	ns	ns
Genotype (G)	9	ns	ns	ns	ns	ns	ns	**	ns	*	ns	***	***
N×G	9	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns
CV (%)		23.6	15.4	12.6	23.9	23.1	15.5	13.0	20.6	28.1	16.3	12.8	20.6

CV = coefficient of variation

Df = degrees of freedom (note: df from error = 38)

ns, *, **, and *** = not significant, and significant at $P \leq 0.05$, ≤ 0.01 , and ≤ 0.001 , respectively, by the F-test

Means followed by different lowercase letters in the column, individually for N rate or genotype factors, differ from each other by the Student–Newman–Keuls’ test ($P < 0.05$) or Scott–Knott’s test ($P < 0.05$), respectively. Comparisons with significant interaction between the main effects have further interpretations in Fig. 3

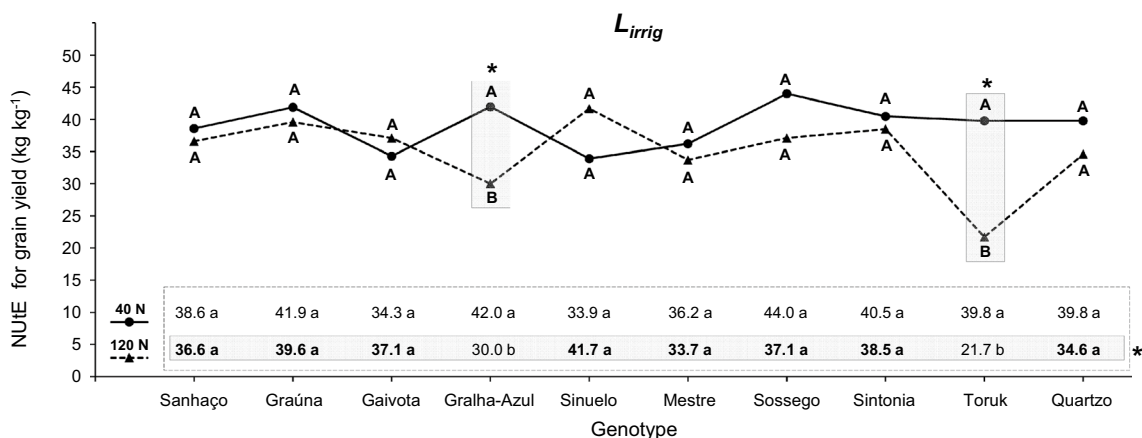


Fig. 3 Comparisons between treatment means when the two-way interaction between the main factors was significant, i.e. 'nitrogen (N) rate \times genotype' for N utilization efficiency (NUE) for grain yield in Londrina in irrigated (L_{irrig}) condition. Individually for each N rate (40 or 120 kg ha⁻¹, i.e. 40 N or 120 N), values within the box comparing genotypes (BRS Sanhaço, BRS Graúna, BRS Gaivota, BRS

Gralha-Azul, TBIO Sinuelo, TBIO Mestre, TBIO Sossego, TBIO Sintonia, TBIO Toruk, and Quartzo) followed by different lowercase letters differ (*) from each other by the Scott–Knott's test ($P < 0.05$). Individually for each genotype, symbols (black circle and black triangle) comparing N rates followed by different capital letters differ (*) from each other by the Student–Newman–Keuls' test ($P < 0.05$)

had temperatures a little milder, 54% higher accumulated rainfall, and a lower water deficit, which did not affect the wheat growth stages, despite having extended the crop growing cycle (159 days). Finally, in $PG_{rainfed}$, the crop growing cycle had 148 days, the mildest temperatures, intermediate rainfall, and the least water deficit. Therefore, as expected, the environmental conditions were the main determinants of wheat growth and yield, and N uptake and utilization by plants.

In Londrina, irrigation increased grain yield in a higher magnitude (in percentage terms) as compared to that of other wheat crop features (i.e. density of fertile spikes, plant lodging, NC_{SDM} , NA_{SDM} , and NUtE), and decreased only the shoot dry matter at anthesis. Therefore, in the environment with higher water availability (L_{irrig}), plants mobilized a higher proportion of the photosynthesized compounds for grain filling instead of for other shoot plant tissues. Source strength for photosynthesized is dictated by both net photosynthetic rate and the rate of photosynthesized remobilization from source tissues (Smith et al., 2018), which depends on water availability (Zheng et al., 2021). Thus, the source-sink relationship in the wheat crop was favoured by the improved water availability through irrigation that increased grain yield. The higher density of fertile spikes also contributed to increase grain yield in the irrigated environment, as the number of spike m⁻² is one of the main yield components of wheat crop (Zhang et al., 2020). The increased density of fertile spikes is mainly a result of higher plant tillering in conditions of better water availability (Shang et al., 2020). Thus, the increased water supply is conducive to increasing plant tillering and grain yield (Kaya-Altup et al., 2019). Moreover, the increase of plant NUtE by irrigation

also improved grain yield in Londrina, because wheat plants were more effective in producing grains per unit of N taken up. In fact, plant NUE decreases under water deficit conditions, which reduces wheat grain yield (Ehsanzadeh et al., 2021; Plaut et al., 2004). The greater water availability in L_{irrig} favoured the N uptake by plants, based on the higher value of NA_{SDM} as compared to that of $L_{rainfed}$. Considering that N improves wheat plant tillering (Yousaf et al., 2014), the better availability of N promoted by irrigation in L_{irrig} also favoured grain yield in this environment. Finally, plant lodging increased due to additional water supply in L_{irrig} as compared to $L_{rainfed}$, because higher water availability increases N uptake, density of plants per area, plant height, and grain load per plant that are factors that predispose plants to lodging (Khan et al., 2020; Ma et al., 2016; Peake et al., 2020).

Comparing the three rainfed environments, the milder temperature and higher water availability (among other edaphoclimatic factors) in $C_{rainfed}$ and $PG_{rainfed}$ increased the density of fertile spikes, grain yield, NC_{SDM} , NA_{SDM} and NUtE, and decreased plant lodging as compared to those of $L_{rainfed}$. In general, the magnitudes (in percentage terms) of these environmental effects were greater than that of irrigation (in L_{irrig}), considering $L_{rainfed}$ as a reference for all comparisons. For instance, whereas the accumulated irrigation of 125 mm increased grain yield by 43% in L_{irrig} , the additional rainfall of 252.3 mm (i.e. 717.6 mm/ $C_{rainfed}$ minus 465.3 mm/ $L_{rainfed}$) allowed the increase of grain yield by 79% in $C_{rainfed}$, both compared with that of $L_{rainfed}$. Thus, water availability played a preponderant role in these results, since it influences most aspects of plant growth and nutrition, as commented before. In $PG_{rainfed}$, despite grain yield

was on average 69% higher, the shoot dry matter at anthesis was 14.7% lower as compared to those of $L_{rainfed}$. Thus, among other factors, the lower temperature and reduced water deficit in $PG_{rainfed}$ favoured wheat plants to mobilize a higher proportion of the photosynthesized compounds for grain-filling instead of for shoot biomass production. Finally, there was no plant lodging in $PG_{rainfed}$, while it averaged 7.3% in $C_{rainfed}$ and 44.2% in $L_{rainfed}$. Thus, there was a direct relationship between temperature and plant lodging, considering that $PG_{rainfed}$ was the mildest and $L_{rainfed}$ the warmest environment. However, the factor 'temperature' cannot explain by itself the occurrence of plant lodging. Weng et al. (2017) reported that low temperature, and overcast and rainy weather reduced the lodging resistance of rice (*Oryza sativa* L.) plants when they occurred during the reproductive growth stage (i.e. from panicle initiation to the heading stage), which is the key period for internode development. During this period, weather conditions have a great influence on culm strength. For instance, low light incidence promotes internode elongation and reduces culm wall thickness, which results in fragile supporting tissue and low culm strength, aggravating plant lodging (Weng et al., 2017).

In rainfed conditions, the N uptake by plants was positively influenced by water availability throughout the period from wheat sowing to shoot biomass sampling for N analysis (i.e. 319, 424, and 425 mm of rainfall in $L_{rainfed}$, $C_{rainfed}$, and $PG_{rainfed}$, respectively), as well as by the extension of this period (96, 105, and 106 days in $L_{rainfed}$, $C_{rainfed}$, and $PG_{rainfed}$). In this context, in $C_{rainfed}$ and $PG_{rainfed}$, the plants had more time to uptake and accumulate N in the SDM (compared to $L_{rainfed}$) but the $C_{rainfed}$ environment was benefited by a higher water availability after the topdressing N application (70 mm of rainfall during 11 days), while in $PG_{rainfed}$ there were 20 days without rainfall after this N fertilizing, which reduced the N fertilizer solubilisation. Therefore, the NA_{SDM} was higher in $C_{rainfed}$ compared to that of $PG_{rainfed}$ and $L_{rainfed}$, since there were better conditions for N uptake from the native N (derived from the soil-mulch system) and from the N supplied by the topdressing fertilizing. It is known that the transport of nitrate (NO_3^-) and ammonium (NH_4^+) in the soil occurs mainly by the mass flow process that depends on the movement of water to the roots, which is influenced by the soil water content and plant evapotranspiration (McMurtrie & Näsholm, 2018; Srivastava et al., 2020). Thus, the uptake of NO_3^- and NH_4^+ by plants is gradually reduced by increasing soil water deficit. Considering that N concentration and N accumulation in the plant biomass have a direct relationship with photosynthetic activity (Zhong et al., 2018), higher grain yields were achieved in the environments with greater water availability (i.e. $C_{rainfed}$ and $PG_{rainfed}$). As a result of these outcomes, the NUtE increased in the wetter environments, showing that the plants used efficient physiological mechanisms to convert

into grains the highest N taken up in $C_{rainfed}$ and $PG_{rainfed}$ as compared to that of $L_{rainfed}$.

Nitrogen Fertilizing Effects on Wheat Growth and Yield, and N Uptake and Utilization by Plants

Increasing N rate from 40 to 120 kg ha⁻¹ provided the most consistent outcomes for NC_{SDM} , NA_{SDM} , plant lodging, and grain yield, whereas the shoot dry matter at the anthesis was not influenced by the additional N supply. However, it was expected higher magnitude of responses to N fertilizing, because the N rates were based on technical indications for wheat crops in the state of Paraná, Brazil. Thus, one can infer that the native N (derived from the soil-mulch system) and the N supplied by the base fertilizing (i.e. 20 kg ha⁻¹ N as formulated fertilizer 08–28–16) were almost enough for wheat crop to achieve its attainable tillering, shoot biomass production, fertile spikes per area, and grain yield, mainly in $C_{rainfed}$. This finding is an indication that the environmental conditions favoured the microbial activity on the decomposition of soybean straw and mineralization of soil organic matter, which released additional mineral N (NO_3^- and NH_4^+) to the soil. In fact, the soil-mulch system is capable to supply a significant amount of N for winter crops in Brazilian subtropical conditions (Fontoura et al., 2017), mainly in environments with higher temperature and rainfall, as it was the case of $C_{rainfed}$.

There was a wide genotype × environment interaction (except in $L_{rainfed}$) for N rate effect on grain yield. In general, SAN was the genotype more responsive to N rate increase, whereas GRAL, SINT and QUA did not yield more with an additional amount of N fertilizer. Thus, wheat farmers can use this genetic variability for specific indication of genotype by environment, aiming to improve the benefit–cost ratio in terms of N fertilizer use. Moreover, excessive N fertilizing in intensive agricultural areas has resulted in serious environmental problems concerning to atmospheric, soil, and water enrichment with several forms of N (Ju et al., 2009). Thus, an improved N balance can be achieved reducing environmental risk by adopting optimum N fertilizing management, such as using a suitable N rate for each wheat genotype according to regional weather and soil conditions.

Plant lodging increased as a result of increasing N rate (except in $PG_{rainfed}$), without any interaction with genotype. However, this effect of N fertilizing on lodging was of a lower magnitude (in percentage terms) as compared to increased water availability, as aforementioned. A challenge when determining optimum N rates for wheat crops is that high amounts of N fertilizer can increase plant lodging, particularly when combined with abundant and frequent rainfall after the anthesis stage (Peake et al., 2016). The main factors that make plants prone to lodging are genetic susceptibility, greater plant height, higher water and N availabilities, high

speed of winds with/after rainfall, weak culm structure, and high grain load per plant (Berry et al., 2004; Khan et al., 2020; Ma et al., 2016; Peake et al., 2020). Therefore, as the combination of several factors dictates the intensity of plant lodging, these outcomes show the complexity of managing this damage.

As expected, the NA_{SDM} increased due to the additional supply of $80 \text{ kg ha}^{-1} \text{ N}$ (i.e. from 40 to $120 \text{ kg ha}^{-1} \text{ N}$), particularly in L_{irrig} and $PG_{rainfed}$. Based on Eq. (1), this increase of NA_{SDM} derived from the higher NC_{SDM} , because the shoot dry matter at anthesis was not influenced by N rates. As the increase of NA_{SDM} was on average $20 \text{ kg ha}^{-1} \text{ N}$ in L_{irrig} and $PG_{rainfed}$ while the N rate increased by $80 \text{ kg ha}^{-1} \text{ N}$, it is evident the lower effectiveness of N fertilizing in increasing the uptake of N by wheat plants. Thus, N losses due to NO_3^- and NH_4^+ leaching likely contributed to reduce the uptake of N from N fertilizer in the environments with abundant water availability. In fact, N losses by leaching are of higher magnitude in environments with high amount of rainfall or where irrigation is managed with a high water surpluses (Sun et al., 2021). Furthermore, we can infer that N losses by NH_3 volatilization were of low intensity because in more acidic soils [such as those used in our experiment (Table S1)] NH_3 volatilization is reduced (Liu et al., 2018a). Finally, the uptake of N (indirectly evaluated by NA_{SDM}) was increased more due to higher water availability (from rainfall or irrigation) than increasing N rate, particularly in Cascavel ($C_{rainfed}$) and Londrina ($L_{rainfed}$ and L_{irrig}) edaphoclimatic sites.

The N rate effects on NUtE were of low magnitude (except for GRAL and TOR genotypes in L_{irrig}). This finding shows that the N taken up and accumulated by wheat plant was proportionally converted into grain yield in the four environments. Tan et al. (2021) found that reducing N fertilizer rates increased the wheat NUtE in arid areas in Northwestern China, but this outcome was achieved only when coupled with additional water supply through irrigation, showing an interactive effect between water and N availabilities on NUtE. Brasier et al. (2019) highlighted that breeders should evaluate wheat genotypes under at least three N rates when the objective is to identify high-NUE genetic materials, in addition to carry out the experiment in as many environments as available resources allow. Thus, as we used only two rates of N fertilizer in our experiment, likely more significant results could be achieved if we had increased the number of N rates.

Genotype Effects on Wheat Growth and Yield, and N Uptake and Utilization by Plants

The factor 'genotype' showed a wide diversity of effects on most of the studied wheat features, and the Scott–Knott's test assembled the genotypes in different groups in the four

environments. In general, there was no clustering pattern for genotypes among wheat features within each environment.

Overall, the genotypes SAN, MES, SOS and QUA showed the highest density of fertile spikes, whereas the TOR genotype had the lowest one. The amount of fertile spikes per area is derived from plant tillering capacity, and this trait has a genetic control (Tshikunde et al., 2019), despite being influenced by environmental conditions such as temperature, and water and N availabilities (Giunta et al., 2018; Kaya-Altup et al., 2019; Yousaf et al., 2014). The density of fertile spikes had a positive correlation with grain yield ($r=0.63^{***}$) considering a combined analysis of all environments (Supplementary Table S4). This outcome reinforces the frequent use of the number of productive tillers per plant in wheat genetic improvement programmes, since it is a key agronomic trait that influences biomass production and grain yield potential (Tausz-Posch et al., 2015). Thus, four out of the ten studied genotypes (i.e. SAN, MES, SOS and QUA) have potential to be included in regional breeding programmes focussing on improving the density of fertile spikes for grain yield increase.

The genotype TOR was the more resistant and GRAL the more susceptible to plant lodging, with averages of 2.5% and 60%, respectively. Thus, the first could be an option as a genetic source of lodging resistance, considering that plant lodging has high genetic heredity and it has been a priority for several breeding programmes (Khobra et al., 2019; Muszynska et al., 2021). However, the TOR genotype showed the lowest density of fertile spikes and grain yield, restricting its use by wheat breeders. In the present paper, there was a negative correlation ($r=-0.34^{***}$) between plant lodging and grain yield, reinforcing the importance of this trait for wheat farmers and breeders. Plant lodging reduces crop yield as it limits the translocation of photoassimilates to grain development and increases the risks of foliar diseases and grain sprouting (Berry et al., 2004; Khobra et al., 2019; Nunes et al., 2016). Moreover, plant lodging can cause problems for harvest operations and usually decreases wheat grain milling and baking quality (Berry et al., 2004; Peake et al., 2016, 2020).

Grain yield showed a wide variability among wheat genotypes, which was intensified by interactions with N rates and environments. Wheat grain yield depends on several factors such as genetic, adaptability and stability to environmental conditions, water and nutrient use efficiencies etc. (Brasier et al., 2019; Liu et al., 2018b; Nazim-Ud-Dowla et al., 2018; Nouri et al., 2011). In this context, grain yield had positive correlations with NC_{SDM} ($r=0.48^{***}$), NA_{SDM} ($r=0.40^{***}$), and NUtE ($r=0.64^{***}$) considering a combined analysis of all environments (Table S4). Thus, these N nutrition traits can be better explored in wheat breeding programmes to achieve genotypes more productive and efficient in using N. For instance, the SINU genotype had higher

NC_{SDM} , NA_{SDM} , $NUtE$, and grain yield across most of the four environments, showing potential to be added in regional breeding programmes. On average, the NA_{SDM} ranged from 141 kg ha⁻¹ N for SINT genotype to 164 kg ha⁻¹ N for SINU genotype. These outcomes reflect the higher capacity of the SINU genotype to uptake N from the soil. The $NUtE$ is a function of root biomass, the morphological ability of the roots to explore regions of the soil with higher N availability, and the root physiological capacity for nutrient uptake (Glass, 2003). Finally, considering the average of all environments, the $NUtE$ ranged from 35.7 kg kg⁻¹ (for GAI genotype) to 42.5 kg kg⁻¹ (for QUA genotype), excluding the TOR genotype that had an outlier value, i.e. 25.0 kg kg⁻¹. Therefore, most wheat genotypes showed a similar capacity to convert into grains the N accumulated in the shoot biomass at anthesis. These outcomes evidence that Brazilian wheat breeders have an opportunity to improve wheat yield by increasing the $NUtE$.

Conclusions

The higher water availability (from rainfall and/or irrigation) has greater effects than N fertilizing rates on increasing the density of fertile spikes, plant lodging, grain yield, NC_{SDM} , NA_{SDM} , and $NUtE$. However, the combination of better water supply and N rate further improved grain yield, and N uptake and N utilization efficiencies, showing a synergistic interaction-effect of water and N availabilities. As the SINU genotype showed higher NC_{SDM} , NA_{SDM} , $NUtE$, and grain yield across most of the environments, it has potential to be added in wheat breeding programmes in southern Brazil aiming to increase grain yield at reduced N fertilizer requirement. Furthermore, as grain yield had positive correlations with NC_{SDM} , NA_{SDM} , and $NUtE$, these N nutrition traits can be better explored in breeding programmes to achieve new wheat genotypes more productive and efficient in N uptake and N utilization, considering a wide range of environmental conditions, including soil water and N availabilities.

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Author Contributions JdLM: investigation, analysis and interpretation, visualization, writing—original draft preparation. SRS: conceptualization, study design, methodology, data acquisition, analysis and interpretation, supervision, validation, writing—original draft preparation, and graphic design. ICdBF: statistical analysis, visualization, writing—review and editing. CZ: visualization, writing—review and editing.

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Data Availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflicts of interest The authors declare that the research was carried out in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Consent for publication All the authors have given their consent for the publication of this manuscript.

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