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Temperature dependence of nitrate uptake kinetics in *Triticum aestivum* L. and *Triticum dicoccon* Schrank cultivars

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Abstract: Temperature is a key parameter that influences the uptake and subsequent utilization of nitrogen by plants. Both suboptimal and supraoptimal temperatures can impair nutrient uptake. The close relatives of bread wheat provide a possible source for breeders to increase stress tolerance. The effect of the increasing temperature (5, 10, 15, 20 and 30 °C) on nitrate uptake and metabolism in five modern spring cultivars of bread wheat (*Triticum aestivum* L.) and two cultivars of emmer wheat (*Triticum dicoccon* Schrank), was monitored. Wheat plants were grown under controlled conditions in hydroponics. The parameters of Michaelis-Menten kinetics, maximum uptake rate (V_{max}), the Michaelis constant (K_m) and selected characteristics of nitrate metabolism, the activity of nitrate reductase (NR) and contents of nitrate in leaves were observed. The effect of temperature was significant for all studied traits except K_m, while the cultivar factor was significant for V_{max}, K_m, NR and root/shoot ratio (R/S). Emmer wheat cultivar Rudico had significantly higher V_{max} at 5, 15, 20 and 30 °C than all bread wheat cultivars, on average 7.07, in comparison with 4.09–4.43 µmol NO_3^-/g FW/h in bread wheat cultivars. Emmer wheat Rudico and Tapiruz had significantly higher K_m (on average, 41.59 and 47.22 µM NO_3^-) than bread wheat cultivars (27.59–33.44 µM NO_3^-). Differences in the studied kinetic parameters of nitrate uptake offer the possibility of using *T. dicoccon* genotypes in breeding for better nitrogen use efficiency.

Keywords: emmer wheat; K_m; nitrate assimilation; nitrogen; V_{max}

Wheat is the most important food and economic cereal worldwide. *Triticum aestivum* L., the major wheat species grown throughout the world, accounts for about 95% of wheat production (Langridge et al. 2022). *Triticum aestivum* is a hexaploid species usually called "common" or "bread" wheat. *Triticum dicoccon*, emmer wheat, is an ancient two-rowed hulled wheat; unlike modern wheat, it is a tetraploid and contains 28 chromosomes instead of 42. Interest in this cereal species has increased, because it is tolerant to biotic and abiotic stress factors and is one of the sources for breeding into climate-smart crops (Zaharieva et al. 2010; Pour-Aboughadareh et al. 2021; Melese et al. 2022; Gupta & Bansal 2023). On the other hand, emmer wheat cultivars have a low harvest index and lower grain yield in comparison with common wheat (Konvalina et al. 2012).

Temperature is an important environmental factor that directly affects plant root and shoot development and is one of the main factors that limit crop yields (Ejaz et al. 2023). Global food security is threatened by increasing climate extremes caused by climate changes and rapidly rising financial and environmental costs of fertilizers, and pesticides (Langridge

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et al. 2022). Only 50% or less of applied nitrogen is used to produce aboveground biomass of cereals and other crops, leading to pollution of water sources and the release of gaseous forms into the atmosphere (Plett et al. 2018). Breeding varieties to improve nitrogen uptake is one of the ways to increase nitrogen use efficiency and reduce nitrogen losses to the environment.

The concentration of nitrates in the soil solution is usually significantly higher than the concentration of ammonium ions, and therefore nitrates are the predominant form of nitrogen in most arable soils (Andrews et al. 2013; Kabala et al. 2017). The uptake of nitrates from soil is mediated by 2 types of transport systems depending on their concentration. High-affinity transport systems (HATS) ensure active uptake at low external ion concentrations (< 0.5 mM) and show higher affinity for the substrate. At higher external concentrations (> 0.5 mM), low-affinity transport systems (LATS) are becoming applicable (Wang et al. 2012; Raigar et al. 2022). The rate of uptake increases linearly with increasing concentration in the surrounding environment. Under field conditions, nitrate concentrations vary considerably during vegetation, but conditions for LATS function usually occur only for a limited period (e.g., after fertilizer application or high mineralization in spring) (Bose & Srivastava 2001). Therefore, HATS is more important for uptake. At low external NO_3^- concentration, uptake kinetics are of the typical Michaelis-Menten type (Cornish-Bowden 2012), whereas at concentrations above 1 mM, the kinetics can be either saturable or linear. It is known that the maximum nitrate uptake rate is not constant and varies depending on plant species, genotype, plant development phase and external conditions (Lainé et al. 1993). The plants growing under natural field conditions do not express their full genetic potential of nitrogen utilization due to the limiting availability of N. Their full potential will be manifested under a non-limiting nitrogen supply, and therefore hydroponics cultures are used to determine uptake kinetics.

Afterward, the nitrate is taken up by the roots, it is reduced to nitrite by nitrate reductase (NR), which is the first step in the NO_3^- assimilation pathway. NR usually represents the rate-limiting step of the nitrogen assimilation pathway in higher plants (Chow 2012; Cormier et al. 2016). Its activity is one of the characteristics of nitrogen metabolism in plants. Studying nitrogen uptake and assimilation in wheat varieties in relation to temperature, a key parameter of nitrate uptake and utilization, is important for selecting genotypes with the potential for more efficient nitrogen utilization (Krapp 2015; Pan et al. 2020). Lowering the temperature at the roots leads to a significant decrease in the uptake rate.

There has been little attention paid to the issue of uptake and efficiency of nitrogen use in emmer wheat in comparison with modern bread wheat. This study aimed to find out the inter-species and intra-species differences of wheat plants in nitrate uptake and utilization under different temperature conditions.

MATERIAL AND METHODS

The experiments were part of a larger project aimed at evaluating selected commercial cultivars for future breeding. Five commercial cultivars of *T. aestivum* (Alicia, Astrid, Libertina, Odeta and Pexeso) and two cultivars of *T. dicoccon* Schrank (Rudico and Tapiruz) for nitrate uptake experiment (Table 1) were chosen.

The varieties of emmer wheat, Rudico and Tapiruz, come from the Crop Research Institute in Prague (VÚRV). Cultivar Tapiruz was bred from a population of Tapioszele (*Triticum turgidum* L. subsp. *dicoccon* Schrank), (GRIN Czech – CRI 1960). Rudico (*Triticum diccocon* Schrank, botanical variety rufum SCHUEBL) has been selected from emmer genetic resources in the Czech Gene Bank (GRIN Czech – CRI 2005). It is resistant to most fungal diseases and the grain yield is high in comparison with the other emmer genotypes (Stehno 2007).

Plant cultivation. For the first three weeks, the plants of the selected cultivars were grown hydroponically under standard conditions (photoperiod 16/8 h day/night, temperature regime 22/16 °C) in a cultivation room in 200-L containers (corresponding to 2 L per plant). Continuously aerated nutrient solution contained 158 μM $Ca(NO_3)_2$, 70.8 μM KNO_3, 52.5 μM KH_2PO_4, 41.3 μM $MgSO_4$, 47.5 μM KCl, 2.5 μM H_3BO_3, 2 μM Fe-EDTA, 0.2 μM $ZnSO_4$, 0.2 μM $MnSO_4$, 0.05 μM $CuSO_4$, and 0.01 μM $(NH_4)_6Mo_7O_{24}$. The nutrient solution was changed three times a week. At the age of 21 days, the plants were placed in smaller containers (8 L per 6 plants of one cultivar) in a culture box with a set temperature regime according to the temperature variant (5, 10, 15, 20 and 30 °C) (Table 2). The range of temperature corresponds to meteorological conditions during the growth of spring wheat, from March to July in the Czech Republic (CHMI 2024).

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Table 1. Characterisation of wheat and emmer cultivars used in the experiment

Description	Plant species and cultivars						
	Triticum aestivum L.					*Triticum dicoccon* Schrank	
	Alicia	Astrid	Libertina	Odeta	Pexeso	Rudico	Tapiruz
Country of origin	CR	CR	CR	CR	CR	CR	CR
Baking quality[1]	E	E	A	B	A	–	–
Tillering	high	medium	medium	high	medium	high	high
Plant height[2]	medium	medium	medium	medium	medium	high	high
Awns	no	no	no	no	no	yes	yes
Inclination to lodging	medium	medium	low	low	medium	low	medium
Resistance to fungal diseases	medium to high	medium to high	high	high	high	high	high

CR – Czech Republic; [1]E – elite class; A – quality class; B – bread class; [2]high: > 90 cm; medium: 85–90 cm; low: < 80 cm

Measurement of the nitrate uptake rate. At the age of four weeks (BBCH 21–22, 4 leaves unfolded, 1–2 tillers), the net nitrate uptake rate was measured in depletion experiments and expressed as μmol NO_3 per g of root fresh weight per hour. The plants were transferred to a nutrient medium without nitrogen 24 h before the measurement. 30 min before measurements, plants were left in a solution with the same nitrate concentration as the experimental solution (300 μM). For the depletion experiment, the plants were placed individually in 300 mL containers and the decrease of nitrates from the solution was monitored. The kinetic parameters of the Michaelis-Menten (V_{max} and K_m) were determined by non-linear regression using the Enzfitter program (Biosoft UK). The formula is given by the Michaelis-Menten equation, where V_{max} represents the maximum uptake rate approached by the system, and constant K_m is defined as the substrate concentration at which the uptake rate is half of V_{max}.

At the same time, wheat plants were harvested, the dry matter was determined and selected characteristics of nitrate metabolism (activity of nitrate reductase and contents of nitrate) in leaves were observed.

Measurement of *in vitro* nitrate reductase activity. Leaf samples (0.6 g of fresh weight) were homogenized in liquid nitrogen and extracted in 3 mL of 50 mM Tris-HCl buffer, pH 8.0, containing 3% bovine serum albumin at 4 °C for 30 min. Insoluble material was removed via centrifugation (12 000 RPM, 30 min). The NR activity was determined by measuring the conversion of nitrate to nitrite according to Gaudinová (1990) and expressed as nmol NO_2^-/g/min.

Determination of nitrate content. The leaf nitrate content was determined spectrophotometrically after homogenization and subsequent extraction with hot deionized water (for 30 min at 90 °C) on an automatic Skalar San Plus System analyzer (Breda, The Netherlands).

Statistical analysis. Statistical analysis was carried out using Statistica 13 (TIBCO Software Inc., Palo Alto, USA, 2018). For the statistical data processing and evaluation, we applied exploratory data analysis of variance (ANOVA); two-way ANOVA was used to evaluate the effects of temperature and cultivar, and one-way ANOVA for cultivar effect at the specific temperature level. The differences among means were tested with the Tukey test (HSD test) ($P \leq 0.05$; $n = 4$).

RESULTS AND DISCUSSION

The experiment focused on differences in the nitrate uptake parameters among bread wheat and emmer wheat cultivars, as well as the effect of increasing temperatures on these parameters.

Table 2. Temperature variants

Variant (°C)	5	10	15	20	30
Day/night temperature (°C)	5/4	10/8	15/12	20/15	30/22

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The selected uptake kinetic parameters (V_{max} and K_m) serve as reliable indicators of plants' ability to take up nitrates from the root zone and transport them to the site of utilization.

***V_{max}* and *K_m*.** Significant differences were found between the cultivars or species for both kinetic parameters. The effect of temperature was only significant for V_{max}. The emmer wheat cultivar Rudico had significantly higher V_{max} at 5, 15, 20 and 30 °C compared to all bread wheat cultivars, on average 7.07 µmol NO_3^-/g FW/h, in comparison with 4.09 to 4.43 µmol NO_3^-/g FW/h in bread wheat cultivars (Figure 1). The average V_{max} of the second emmer wheat cultivar, Tapiruz (4.91 µmol NO_3^-/g FW/h) was also higher than that of bread wheat cultivars although the differences were not statistically significant (Table 3).

The lowest V_{max} was observed at 5 °C; in Rudico showed a slight increase in V_{max} at 10 °C than at 5 °C. In bread wheat cultivars, the average V_{max} value mea-

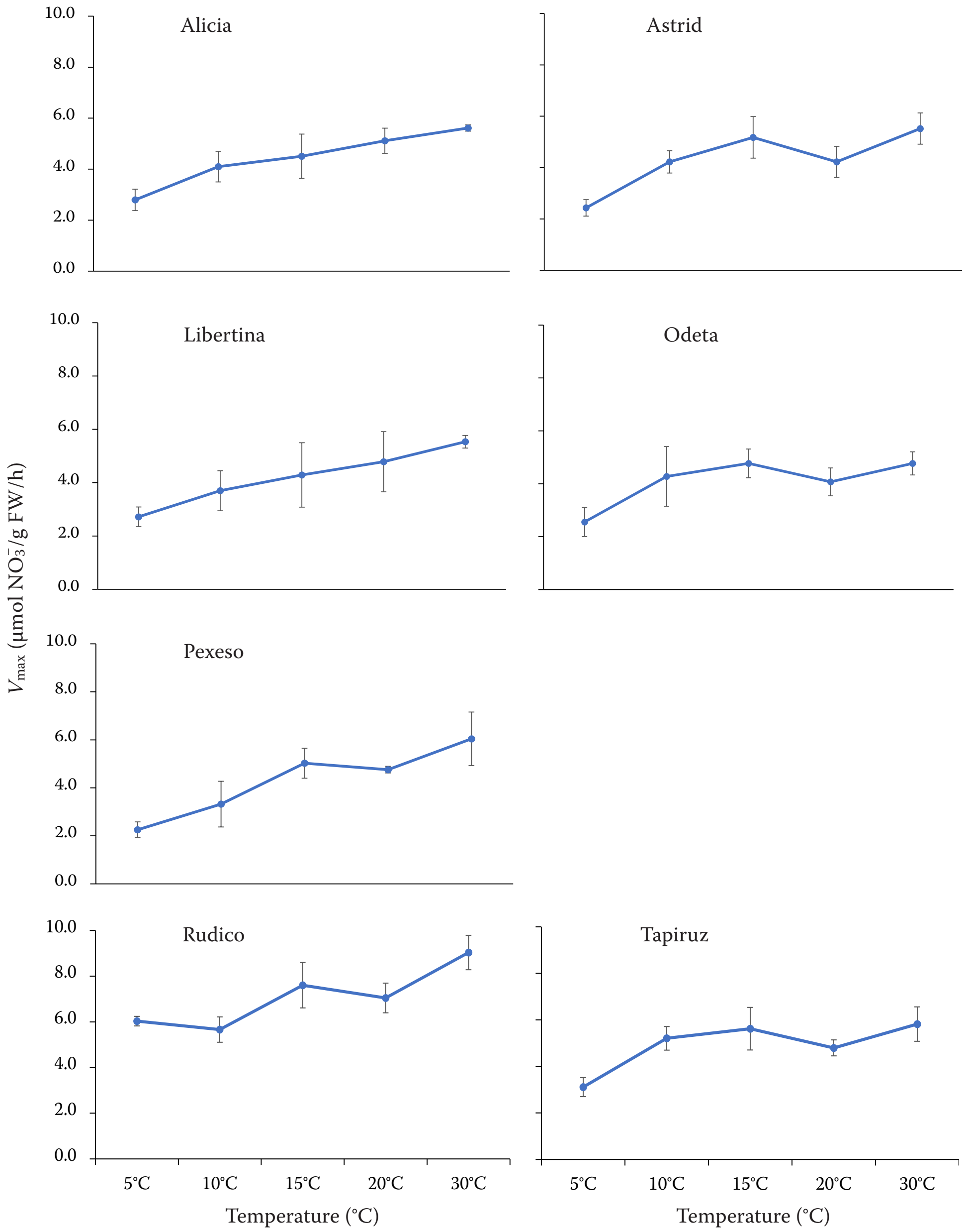

Figure 1. The effect of increasing temperatures on maximum rate of nitrate uptake (V_{max}) in bread and emmer wheat cultivars

Errors bars represent the standard deviation of means, n = 4

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sured at 5 °C was 2.55 μmol NO_3^-/g FW/h, with little variation observed between the cultivars (Figure 2). In both emmer wheat cultivars, a higher V_{max} value was observed, with Rudico reaching over twice the amount at 6.03 μmol NO_3^-/g FW/h. A pronounced increase in V_{max} value between 5 °C and 10 °C was noted in all examined bread wheat cultivars and in the emmer wheat variety Tapiruz. The observed increase ranged from 36% (Libertina) to nearly 74% (Astrid). Further increase was only moderate. The highest V_{max} value was recorded at 30 °C for all cultivars. In bread wheat, the V_{max} value was more than doubled on average (2.55 to 5.50 μmol NO_3^-/g FW/h), while in emmer wheat cultivars, the overall increase was lower (1.5× for Rudico and 1.87× for Tapiruz).

The Michaelis constant (K_m), which indicates the affinity to nitrate, is defined as the concentration of nitrate corresponding to 1/2 of the V_{max}. In our experiments, only the cultivar factor showed significance in K_m. The effect of temperature was not statistically significant. Both cultivars of emmer wheat had higher K_m values compared to cultivars of bread

Table 3. The statistical analysis (ANOVA) of the effect of temperature and cultivar on selected parameters

Source of variation										
Factor	ANOVA (P)	Temperature (°C)	ANOVA (P)	Alicia	Astrid	Libertina	Odeta	Pexeso	Rudico	Tapiruz
V_{max}		5	< 0.001	b	b	b	b	b	a	b
Temperature	< 0.001	10	< 0.01	abc	abc	bc	abc	c	a	ab
Cultivar	< 0.001	15	< 0.001	b	b	b	b	b	a	b
		20	< 0.001	b	b	b	b	b	a	b
		30	< 0.001	b	b	b	b	b	a	b
		average		b	b	b	b	b	a	b
K_m		5	ns							
Temperature	0.40700	10	ns							
Cultivar	< 0.001	15	< 0.01	b	b	b	b	b	b	a
		20	ns							
		30	ns							
		average		c	bc	bc	abc	c	ab	a
NR activity		5	< 0.01	ab	bc	a	bc	c	abc	bc
		10	ns							
Temperature	< 0.001	15	ns							
Cultivar	0.013	20	ns							
		30	ns							
		average		bc	c	a	bc	c	bc	bc
Nitrate content		5	< 0.001	b	b	a	b	bc	c	a
		10	ns							
Temperature	0.001	15	ns							
Cultivar	0.160	20	ns							
		30	< 0.001	b	b	b	b	b	b	a
		average		a	a	a	a	a	a	a
R/S ratio		5	< 0.001	bc	bc	c	bc	b	a	d
		10	< 0.01	a	ab	ab	ab	ab	b	b
Temperature	< 0.001	15	< 0.05	ab	ab	ab	a	ab	ab	b
Cultivar	< 0.001	20	< 0.001	a	a	ab	a	a	ab	b
		30	< 0.001	a	a	a	a	a	a	b
		average		abc	abc	c	ab	ab	abc	d

V_{max} – maximum uptake rate; K_m – the Michaelis constant; NR – nitrate reductase; R/S – root/shoot ratio; the cultivars with different letter differ significantly in the trait at the specific temperature ($P < 0.05$)

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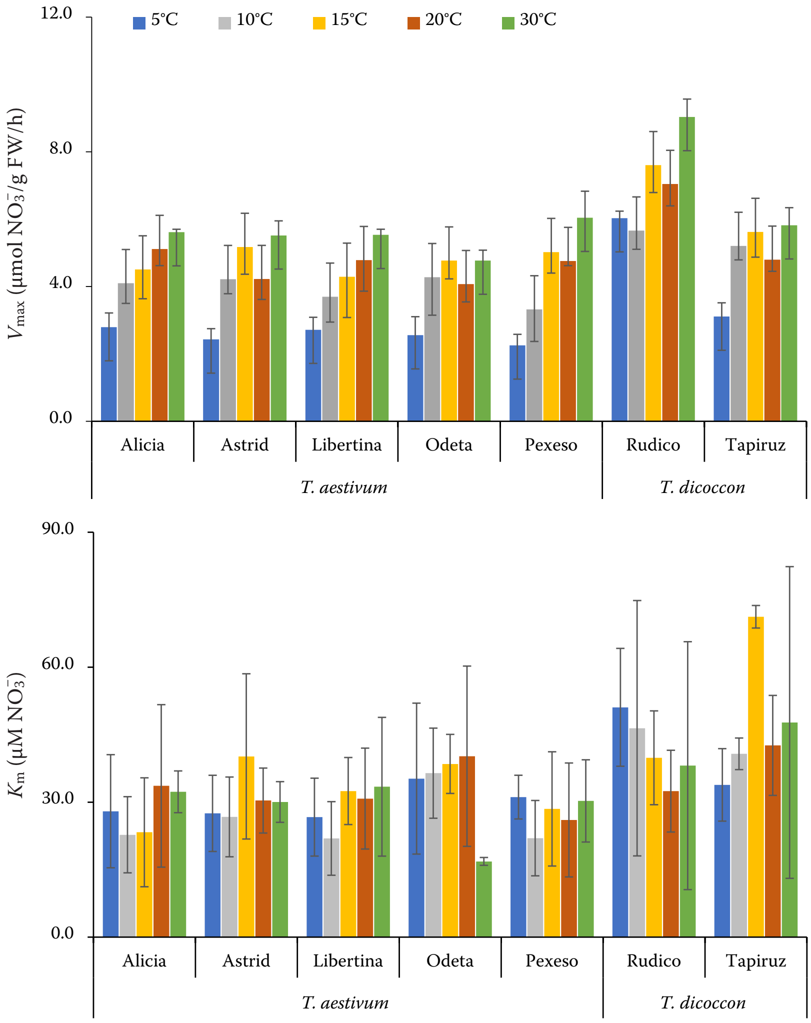

Figure 2. The comparison of the maximum uptake rate (V_{max}) and the Michaelis constant (K_m) in bread and emmer wheat cultivars under different temperatures
Errors bars represent the standard deviation of means, n = 4

wheat. On average, this difference was significant only for Tapiruz, with a K_m 47.2 µM NO_3^- (compared to 41.6 µM NO_3^- for Rudico), whereas K_m values for bread wheat cultivars ranged from 27.6 to 33.4 µM NO_3^- (Figure 2). For both values, the significant differences between species (bread × emmer wheat) were found in all temperatures (Figure 3). The average V_{max} and K_m of *T. dicoccon* cultivars were greater than of *T. aestivum* ones at all temperatures.

The maximum rate of nitrate uptake is not constant and varies depending on plant species, genotype, and growth conditions. Consequently, comparing nitrate uptake rates with data from the literature can be challenging. For example, Kuzyakov and Xu (2013) reported average + SE (median) values of V_{max} and K_m for a wide range of species, including grasses, shrubs and forest 37 ± 7.5 (8.2) µmol NO_3^-/g DW/h and 79 ± 11 (48) µM NO_3^-, respectively.

To the best of our knowledge, except for one, no data on the kinetic parameters of emmer wheat have been published. Trčková et al. (2006) studied nitrate uptake among a set of modern cultivars of two wheat species (*T. aestivum* and *T. durum*). Similar to our experiments, differences in nitrate uptake rates were observed between these two species. Cultivars of bread wheat achieved lower V_{max} values (ranging from 3.98 to 7.05 µmol NO_3^-/g FW/h) compared to durum wheat cultivars (ranging from 5.67 to 8.57 µmol NO_3^-/g FW/h). This is an interesting finding considering that durum wheat is tetraploid, just like emmer wheat. Conversely, in the evaluation of groups of wheat cultivars *T. dicoccum*, *T. monococcum*, and *T. spelta*, the lowest V_{max} was found in emmer wheat (averaging 4.7 µmol NO_3^-/g FW/h) compared to the other two species (13.3 respectively 6.77 µmol NO_3^-/g FW/h). In the experiment, however, wild types of these species were also included in the evaluation (Trčková et al. 2005).

Many authors have also described the differences in nitrate uptake rate according to the developmental stage (Mattsson et al. 1992; Malagoli et al. 2004). This factor can complicate comparisons. Oscarson et al. (1995) did not find significant genotypic differences in either V_{max} or K_m of spring wheat cultivars. They reported that V_{max} increased until anthesis and subsequently decreased while, there were no major changes in the affinity for nitrate, i.e. K_m, during the development.

Nitrate uptake (therefore kinetic uptake parameters), as well as its utilization and accumulation in plants, are also affected by environmental factors, such as light, temperature and pH (Anjana & Iqbal 2007). Many studies have confirmed that nitrate uptake is temperature-dependent (MacDuff & Hopper 1986; Lainé et al. 1993; Malagoli et al. 2004; Liu et al. 2016). Both, suboptimal and supra-optimal temperatures can impair nutrient uptake. Average air temperatures at the beginning of spring wheat growth, in March and April, in agricultural areas of the Czech Republic range between 5–10 °C (CHMI 2024). Maximum uptake and depletion of soil nitrogen in the period contribute to the reduction of losses through nitrate leaching. However, Herrera et al. (2016) conclude the ability to minimize NO_3-N leaching by using spring wheat genotypes with higher fertilizer. N recovery was limited because maximum N leaching occurred in the early crop season. Regarding high temperatures, our results did not show a reduction in V_{max}. These extremes are more common in the late stages of development.

Finding crop genotypes that have better nitrogen use efficiency under low temperatures or ones that can grow and yield well under low N conditions, i.e., N-efficient genotypes, is an important challenge (Javed et al. 2022; Mălinaş et al. 2022; Li et al. 2024). Further, higher N uptake (thanks to fertilization) was proposed to alleviate the damage of frost to wheat plants (Li et al. 2022). Another aspect is the influence of nitrogen nutrition on the uptake of other macro and microelements (Guo et al. 2019; Rahman et al. 2020).

The V_{max} and K_m of nitrate uptake for 10 species of catch crop were determined (Lainé et al. 1993). Consistent with our findings, a decrease in temperature from 25 to 9 °C led to a significant reduction in V_{max} (up to 2/3), while the effect of temperature on the value of K_m was not observed. The higher V_{max} at lower temperatures in emmer wheat Rudico suggests a possible advantage during the early stages of development. On the opposite, the tendency (mostly insignificant) towards higher K_m values (lower affinity) in emmer wheats is rather disadvantageous for uptake at low NO_3^- concentrations.

Cultivar differences in the nitrate uptake rate are further influenced by the development of the root system and its ratio to the aboveground part of the plants. In the experiment, we observed a very similar R/S ratio (on average 0.43) among the cultivars. The only exception was the emmer wheat cultivar Tapiruz, which had an average R/S ratio of 0.30 (Figure 4). The low R/S ratio was attributed to the high tillering ability of the cultivar and thus higher aboveground biomass. This characteristic may provide Tapiruz with a competitive advantage, despite having the highest K_m value, by creating a stronger sink for absorbed nitrates in the aboveground part.

Old, landraces or wild ancestors of cereals are often expected to have a larger root system related to better nutrient and water uptake, and stress tolerance and thus be better adapted to growth at low nitrogen concentration (Woodend et al. 1986; Pourazari et al. 2015). However, the evidence for a greater affinity of the genotypes for nitrogen are not conclusive (Paschen et al. 2022).

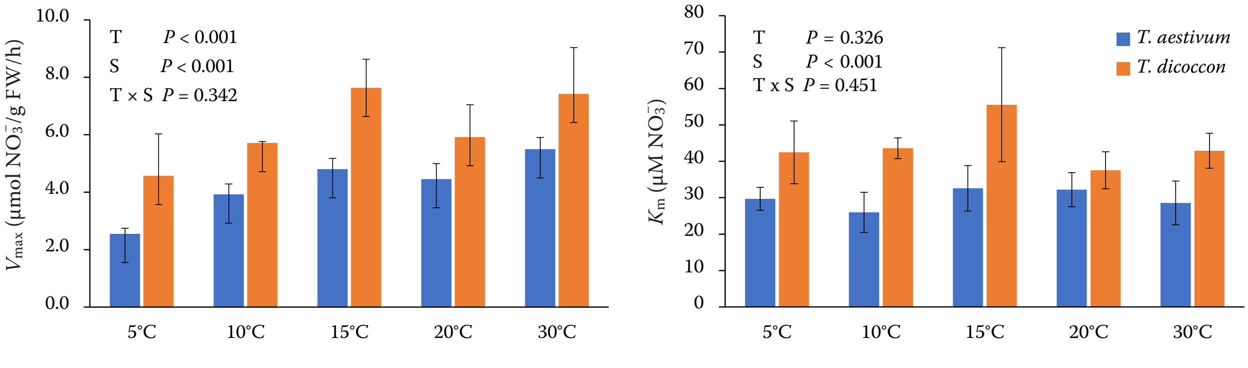

Figure 3. The comparison of the maximum uptake rate (V_{max}) and the Michaelis constant (K_m); average data of *T. aestivum* (n = 20) and *T. dicoccon* (n = 10) cultivars and the results of ANOVA; T – temperature; S – species

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Nitrate reductase activity and nitrate content. The absorbed nitrates are either immediately reduced within the plant, stored in vacuoles, or transported by the xylem to the aerial parts for further utilization (Tischner 2000). Nitrate reductase (NR) activity and the free nitrate content in leaves were chosen as indicators of subsequent metabolic utilization. NR activity alone indicates the leaves' ability to metabolize mineral nitrogen, simultaneously (in addition to nitrate content) it serves as an indirect indicator of nitrogen uptake from the soil (or its availability).

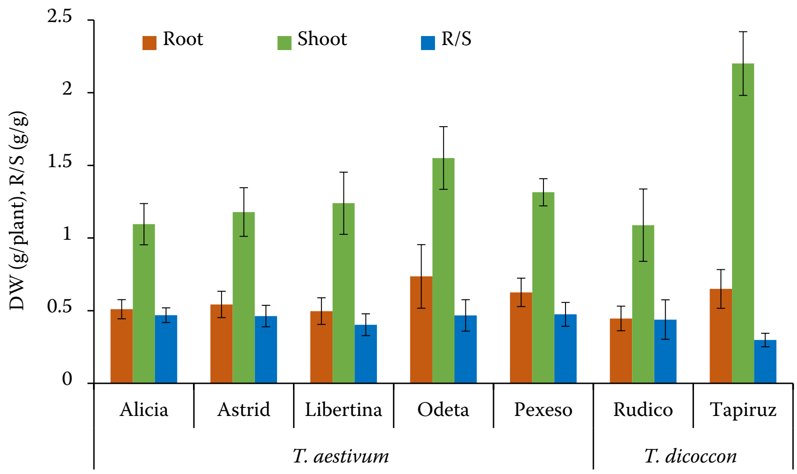
The analysis of variance confirmed a significant effect of temperature on NR activity and nitrate content but not the effect of cultivar. Differences among cultivars were observed only at 5 °C, as indicated in Table 3.

The highest NR activity was measured at lower temperatures (10 °C) in most cultivars (Figure 5), with an average of 192 nmol NO_2^-/g FW/min. At the highest monitored temperature (30 °C), NR activity decreased by more than 70%, with its value averaging around 50 nmol NO_2^-/g FW/min in most cultivars.

Similarly, the nitrate content of the leaves was highest on average at 10 °C, and at 30 °C, it decreased almost to zero (Figure 5). In a related finding, Yan et al. (2013) observed that higher temperatures in the root zone of cucumber reduced nitrate content and increased the rate of nitrate uptake. In contrast to our results, they also reported an increase in NR activity. However, in our experiments, we observed significant differences between cultivars, although their conclusiveness was somewhat reduced by high variability in replicates.

Das et al. (2006) compared wheat cultivars with high and low nitrate reductase activity and confirmed the different relationship between the K_m and V_{max} of these wheat cultivars. While the high NR activity cultivars had lower K_m (0.186 mM) and V_{max} (0.170 mmol/g FW/h), the low NR activity cultivars had both higher values (0.725 mM and 0.798 mmol/g FW/h, respectively).

In our experiment, the highest NR activity showed bread wheat Libertina (on average in all temperatures 167 nmol NO_2^-/g FW/min) with V_{max} about the average of bread wheat cultivars. Conversely, the NR activity of emmer wheat cultivar Rudico (with the highest V_{max}) moved around the average of bread wheat (116 nmol NO_2^-/g FW/min).



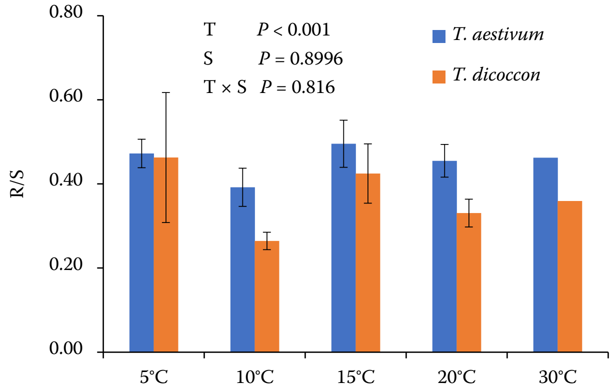


Figure 4. Average root and shoot dry mass (DW) and root/shoot ratio (R/S) in bread and emmer wheat cultivars (up); errors bars represent the standard deviation of temperature means (n = 20) and average R/S ratio of *T. aestivum* (n = 20) and *T. dicoccon* (n = 10) cultivars and the results of ANOVA (down)
T – temperature; S – species

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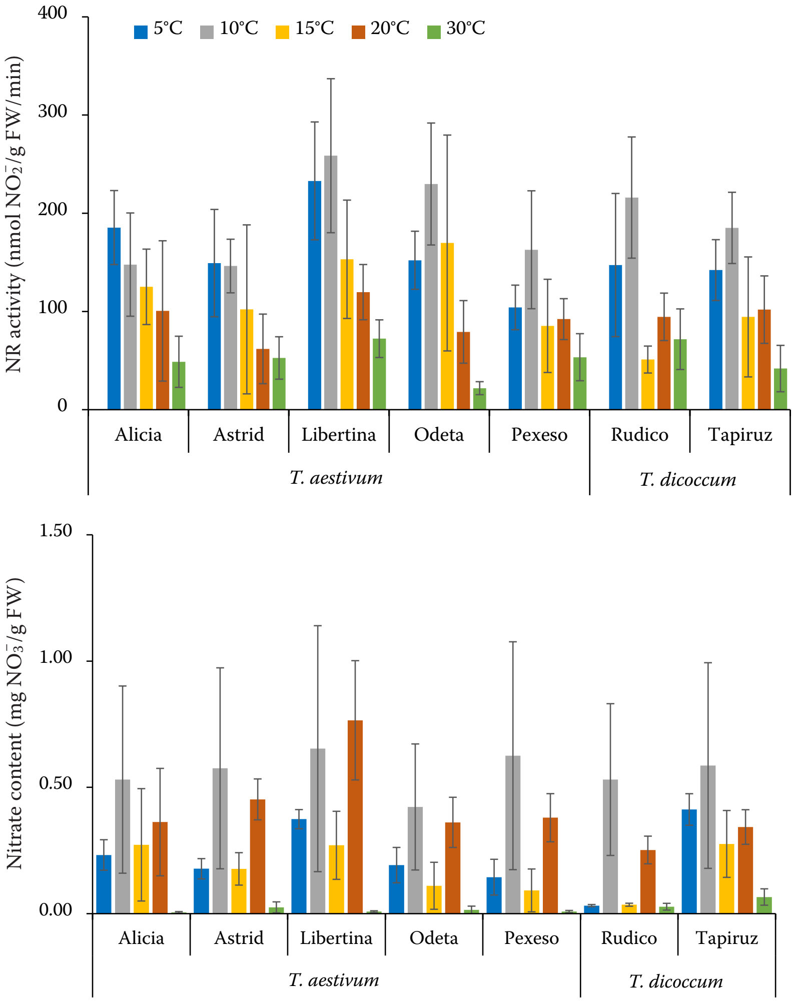

Figure 5. The comparison of nitrate reductase (NR) activity and nitrate content in bread and emmer wheat cultivars under different temperatures

Errors bars represent the standard deviation of means, $n = 4$

In the same set of bread and emmer wheat cultivars, as in our experiment, according to Platková et al. (2020), Libertina was the most resistant cultivar against aphid infestation, while Rudico was the most susceptible. Interestingly, Libertina consistently had the highest leaf nitrate content in most temperature regimes, while Rudico had the lowest (Figure 5).

CONCLUSION

The temperature played a crucial role in determining the rate of nitrate uptake and its utilization. The evaluation of varietal differences in terms of the ability to take up nitrate from the external environment based on the determination of kinetic parameters of uptake systems could be used as one of the criteria for the selection and evaluation of breeding material. The varieties of emmer wheat may have a better ability to absorb nitrates from the media compared to bread wheat cultivars. This could be significant for agricultural production systems with limited nitrogen fertilizer input. Selecting appropriate genotypes will require assessing various nitrogen use indices in both low and high-input environments.

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