Nitrate uptake and N allocation in *Triticum aestivum* L. and *Triticum durum* Desf. seedlings

M. Trčková, Z. Stehno, I. Raimanová

Research Institute of Crop Production, Prague-Ruzyne, Czech Republic

ABSTRACT

Inter- and intra-species differences in nitrate uptake and N allocation were studied in wheat seedlings. Two collections of wheat cultivars *Triticum aestivum* and *Triticum durum* were grown at controlled conditions in hydroponics (773μM NO_3^-, i.e. 10.8 ppm N-NO_3^-). At the age of 3 weeks the net rate of nitrate uptake was measured in depletion experiments and it was expressed as μmol NO_3^- per g of root fresh weight per hour (μmol/g FW/h). Nitrate uptake capacity of the whole root system was expressed as μmol NO_3^- per plant per hour (μmol/plant/h). At the same time wheat plants were harvested and analyzed for nitrogen content. In contrast to the net rate of NO_3^- uptake (3.98–8.57 μmol/g FW/h) the net NO_3^- uptake capacity of *T. aestivum* roots (6.37–11.66 μmol/plant/h) significantly differed from *T. durum* roots (15.26–22.69 μmol/plant/h). Within *T. aestivum* collection cultivar Roxo exhibits the lowest value in both traits (3.98 μmol NO_3^-/g FW/h and 6.67 μmol NO_3^-/plant/h). By contrast Strela was characterized by relatively low NO_3^- uptake rate (5.47 μmol/g FW/h) and the highest NO_3^- uptake capacity (11.66 μmol/plant/h). Intra-species differences in *T. durum* group were not significant. In both species about 70% total nitrogen was found in shoot. Statistically significant differences in nitrogen content and its allocation were affected by growth rate in early stages of development.

Keywords: nitrate uptake rate; nitrate uptake capacity; nitrogen allocation; varietal differences; inter-species differences; wheat; *Triticum aestivum*; *Triticum durum*

Hexaploid bread wheat (*Triticum aestivum* L.) and tetraploid durum wheat (*Triticum durum* Desf.) differ in many characters and properties. Among them differences in grain protein quantity and quality are essential. Synthesis of protein can be limited by nitrogen availability. From this point of view, uptake of nitrogen and its following utilization is very important for grain yield and its quality.

Nitrogen, one of the most important macronutrients is consumed in the greatest quantity and most often limits plant growth. In arable well aerated soils, nitrate is the predominant form of nitrogen. Its concentration in soils of temperate zone is rather low due to leaching and microbial consumption and it exhibits great seasonal and spatial heterogeneity. Therefore plants have developed a very sensitive and selective uptake systems. The acquisition of nitrate from the ambient environment consists of the three successive steps. First, NO_3^- is actively transported from rhizosphere across plasma membrane into root cell. The intracellular nitrate can be metabolised (reduced by nitrate reductase), stored in the vacuole, or transported to leaves. In cereal (commonly monocotyledonous) roots the nitrate reduction is rather low; the main part of NO_3^- is translocated via xylem to the leaves for next metabolic use or vacuollar storage.

Plants grown in the environment without nitrates have very low ability for NO_3^- uptake. The exposure of plants to nitrate induces synthesis of carrier proteins and the rate of nitrate uptake continuously increases. It reaches maximum after several hours. Most information about net nitrate uptake was obtained by measurements of depletion of NO_3^- from surrounding medium. Net uptake of nitrate is the difference between influx and efflux of NO_3^- across plasma membrane. Short term studies with $^{13}NO_3^-$ or $^{15}NO_3^-$ provided appreciable details on the both.

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Uptake of nutrients starts on the root surface where the nutrients, including nitrates, are transported from surroundings into root cells. The transport goes against concentration gradient and requires energy available. Transport of nutrients is mediated by specific protein carriers localised in plasmalemma of root cells.

At least, three types of transport systems were identified for plants (Crawford and Glass 1998). Higher plants grown in the environment without nitrates have constitutive high affinity transport system (cHATS) with low K_m (6–20μM) and V_{max} (0.3–0.82 μmol NO_3^-/g of fresh root/h). When NO_3^- are presented in the cultivation media for some hours or days, transport system with higher parameters K_m (20–100μM or more) and V_{max} (3–8 μmol NO_3^-/g of root/h) indicated as iHATS is induced. In the environment with high nitrate concentration (over 500μM corresponding 7 ppm N-NO_3^-) low affinity transport system (LATS) is responsible for additional acceleration of nitrate uptake. Up to now there were identified two groups of genes responsible for transport of nitrates – NRT1 and NRT2. Group NRT2 includes high affinity transport systems. Group NRT1 is not so specific and includes largely low affinity systems induced and constitutive ones as well.

In wheat plants the net rate of nitrate uptake quickly increases from germination to the end of tillering. The intensive growth of the root system during stem elongation is responsible for the subsequent increase of nitrate uptake capacity. It reaches maximum just before anthesis, and subsequently decreases (Oscarson et al. 1995, Trčková and Kamínek 2000). It is known, that about 80% of the total N content accumulates at anthesis and it accounts for 50–100% of the total N content of the wheat grain (Gebbing and Schnyder 1999). During the development there were no major changes in the affinity for nitrate, i.e. in K_m. When uptake capacity was put in relation to the need of the plant in order to maintain growth rate and nitrogen tissue concentration, it was found that wheat plants had a substantial overcapacity for net nitrate uptake at all times (Oscarson et al. 1995).

The main aim of this work was to find inter-species and intra-species differences in nitrate uptake among *T. aestivum* and *T. durum* cultivars.

MATERIAL AND METHODS

For the laboratory tests there were selected 10 cultivars per species (Table 1) of spring *T. aestivum* and *T. durum*. Seed samples were obtained from the Czech gene bank and selected with the aim to include representatives of different botanical varieties. Differences in protein and gluten contents and sedimentation by Zeleny were used as further selection criteria.

Wheat plants were grown in hydroponics under photoperiod 16 h illumination (a photon density 320 μmol/m^2/s) and 8 h darkness at temperatures 22°C and 15°C, respectively. Nutrient solution [316μM $Ca(NO_3)_2$, 141μM KNO_3, 105μM KH_2PO_4, 82.5μM $MgSO_4$, 95μM KCl, 2.5μM H_3BO_3, 0.8μM FeEDTA, 0.2μM $MnSO_4$, 0.2μM $ZnSO_4$, 0.05μM $CuSO_4$] was continuously aerated and replaced two – three times a week.

At the age of 21 days (*T. aestivum*) or 22 days (*T. durum*) the net rate of NO_3^- uptake was measured. At the same age plants were harvested, divided into shoot and root to determine their dry weight and total nitrogen content.

Table 1. List of *Triticum aestivum* L. and *Triticum durum* Desf. cultivars used for measurement of nitrate uptake

	Cultivar	Variety	Origin
Triticum aestivum	Broma	*aestivum*	POL
	Buck Yapeyu	*aestivum*	ARG
	Sandra	*aestivum*	CSK
	Saratovskaya 46	*aureum*	RUS
	AC Reed	*graecum*	CAN
	Roxo	*graecum*	PRT
	Kommissar	*lutescens*	AUT
	Munk	*lutescens*	DEU
	Pacific	*lutescens*	CAN
	Strela	*milturum*	RUS
Triticum durum	Kharkovskaya 21	*hordeiforme*	UKR
	Lyudmila	*hordeiforme*	RUS
	Marmilla	*leucomelan*	ITA
	Saadi	*leucomelan*	FRA
	Zenit	*leucomelan*	ITA
	Auroc	*leucurum*	FRA
	Kievlanka	*leucurum*	FRA
	Olinto	*leucurum*	ITA
	Valbelice	*leucurum*	ITA
	Mojo 2	*melanopus*	MEX

Bold types = cultivars with higher content of grain protein

The net rate of nitrate uptake was estimated by short-term depletion experiment. Intact wheat plants were transferred into well aerated fresh nutrient solution with 250μM NO_3^- (3.5 ppm N-NO_3^-). Each treatment was repeated three times. After 30 min lag period, NO_3^- concentration of the nutrient uptake solution was determined in 3h interval. The net rate of nitrate uptake was calculated from NO_3^- depletion and it was expressed as μmol NO_3^- per 1 g of root fresh weight per hour (μmol NO_3^-/g FW/h). Nitrate uptake capacity of the whole root system was expressed as μmol NO_3^- per plant per hour (μmol NO_3^-/plant/h).

Nitrate concentration in experimental uptake solution was determined spectrophotometrically using a San Plus SKALAR System analyzer. The samples were passed through a column of granulated copper – cadmium to reduce the nitrate to nitrite. The nitrite was measured as azo dye at 540 nm.

Dried ground samples of plant tissues were mineralised with sulphuric acid and selenium as catalyst. Total nitrogen content was determined spectrophotometrically using San Plus SKALAR System analyzer and Bertholet reaction.

Statistically significant differences were determined by ANOVA *F*-test completed with Tukey honest significant difference (HSD) test at P = 0.95 level.

RESULTS AND DISCUSSION

Net rate of nitrate uptake

The net rate of nitrate uptake was estimated as consumption of NO_3^- per 1g of fresh root matter per hour. In *T. aestivum* the average net rate of nitrate uptake was 5.96 μmol NO_3^-/g FW/h (Table 2). It varied from 3.98 (Roxo) to 7.05 μmol/g FW/h (Sandra – registered cultivar in CR). High values 6.96 μmol have been determined also in Munk (registered cultivar) and Broma. Cultivar Roxo differed significantly from Sandra, Munk, Broma, Pacific and AC Reed with net rate of nitrate uptake over 5.9 μmol/g FW/h (Table 2).

The collection of *T. durum* cultivars was characterized by higher net NO_3^- rate uptake (the average 6.87 μmol/g FW/h). Intra-species variability analogous to *T. aestivum* was not statistically significant because of higher intra – varietal variability (Table 3).

Differences in the net rate of nitrate uptake between species were slightly under significant level at P = 0.95.

As mentioned in introduction, nitrate uptake by root cells is a key step of nitrogen metabolism. This process has been intensively studied at the physiological level and more recently at molecular level (Glass et al. 2004). Two classes of genes, NRT1 and NRT2, can be involved in the low and high affinity transport systems. Moreover, both NRT1 and NRT2 are represented by multigene families. Plant cultivation and all depletion experiments were realized in nutrient solutions with nitrate concentration below 1mM and 0.5mM (14 and 7 ppm N-NO_3^-), respectively. It means, the rate of net nitrate uptake probably correspond to the activity of inducible high affinity transport system (iHATS). In recent years inducible components of the HATS were identified and cloned from roots of several higher plant species – *Arabidopsis thaliana* (Filleur and Daniel-Vedele 1999), *Nicotiana*

Table 2. Net rate of nitrate uptake expressed as μmol NO_3^- per g root fresh weight per hour

	Cultivar	μmol NO_3^-/g FW/h	
Triticum aestivum	Roxo	3.98*	a
	Strela	5.47	ab
	Kommisar	5.64	ab
	Buck Yapeyu	5.74	ab
	Saratovskaya 46	5.87	ab
	AC Reed	5.95	b
	Pacific	5.97	b
	Broma	6.96	b
	Munk	6.96	b
	Sandra	7.05	b
	average	5.96	
Triticum durum	Kievlanka	5.67	a
	Olinto	5.67	a
	Saadi	6.33	a
	Mojo 2	6.69	a
	Lyudmila	6.78	a
	Kharkovskaya 21	6.86	a
	Marmilla	7.13	a
	Valbelice	7.30	a
	Auroc	7.74	a
	Zenit	8.57	a
	average	6.87	

Difference between species closely nonsignificant at P = 0.95
*μmol NO_3^- = 0.014 mg N-NO_3^-

Table 3. Capacity of nitrate uptake expressed as μmol NO_3^- per plant per hour

	Cultivar	mol NO_3^-/plant/h	
Triticum aestivum	Roxo	6.37	a
	Kommisar	7.13	ab
	AC Reed	7.71	ab
	Buck Yapeyu	7.89	ab
	Pacific	8.48	abc
	Saratovskaya 46	9.11	abc
	Broma	9.25	abc
	Sandra	9.41	abc
	Munk	10.12	bc
	Strela	11.66	c
	average	8.71	
Triticum durum	Kievlanka	15.26	a
	Saadi	15.28	a
	Kharkovskaya 21	16.10	a
	Olinto	16.62	a
	Lyudmila	16.67	a
	Mojo 2	17.64	a
	Valbelice	18.97	a
	Auroc	20.00	a
	Marmilla	20.70	a
	Zenit	22.69	a
	average	17.99	

Difference between species highly significant at $P = 0.95$

plumbaginifolia (Fraisier et al. 2003), *Zea mays* (Quaggiotti et al. 2003) and *Hordeum vulgare* (Truelman et al. 1996, Tong et al. 2005). The measured rate of NO_3^- uptake was relatively high – about 5.96 μmol at *T. aestivum* and 6.87 μmol NO_3^-/g FW/h at *T. durum*. This values approach to V_{max}. In used concentration range of depletion experiments the rate of nitrate uptake exhibited features of saturable kinetics.

Net nitrate uptake capacity of the whole root system

The net rate of NO_3^- uptake per plant root system ranged in *T. aestivum* (Table 3) from 6.37 (Roxo) to 11.66 μmol NO_3^-/plant/h (Strela). Roxo was significantly different from Strela and Munk (10.12 μmol NO_3^-). Whole nitrate uptake capacity is highly modified by root development. From this point of view Strela was a very interesting cultivar. In spite of the relatively low rate of nitrate uptake (5.47 μmol NO_3^-/g FW/h) Strela reached the highest net uptake capacity (11.66 μmol NO_3^-/plant/h).

The enhanced development of root system in *T. durum* was responsible for considerably higher net uptake capacity ranging from 15.26 to 22.69 μmol NO_3^-/plant/h (Table 3). Similarly as in rate of nitrate uptake also the differences among cultivars in uptake capacity were not significant. Nevertheless, in both cases Kievlanka showed the lowest values (5.67 μmol NO_3^-/g FW/h and 15.26 μmol NO_3^-/plant/h) and Zenith the highest ones (8.57 μmol NO_3^-/g FW/h and 22.69 μmol NO_3^-/plant/h).

Differences in nitrogen uptake capacity between *T. aestivum* (8.71 μmol NO_3^-/plant/h) and *T. durum* (17.99 μmol NO_3^-/plant/h) species were highly significant.

According to certain authors, NO_3^- uptake rate is not identical in roots different in age or ontogeny. High uptake rate at root tip of barley (0–1 cm) temporarily decreases in prolongation zone (1–2 cm from tip) and again rises with root maturation. Older root parts with fully differentiated xylem were most active in nitrate uptake but nitrate reductase activity was very low; bulk of nitrate was translocated to the shoot (Jiao et al. 2000). In *T. aestivum* cultivar Munk the rate of NO_3^- uptake reached its maximum at the end of tillering, the increase of net uptake capacity at the later stages of development was caused mainly by enlargement of root system (Trčková and Kamínek 2000). Moreover, it is known that nitrate uptake undergoes to feedback regulation mainly by glutamine or ammonium (Gojon at al. 1998). Probably, N-status or N-demand of the plants is the main controlling factor in regulation of nitrate uptake (Tischner 2000).

Growth and partition of dry matter

Two groups of cultivars (*T. aestivum* and *T. durum*, respectively) were developing in different growth rate. Differences in growth of *T. aestivum* and *T. durum* plants measured by dry matter weight after 22 days of growing in nutrient solution were significantly different; average dry matter of *T. durum* group was about 1.8 times higher (0.455 g) than that of *T. aestivum* (0.254 g).

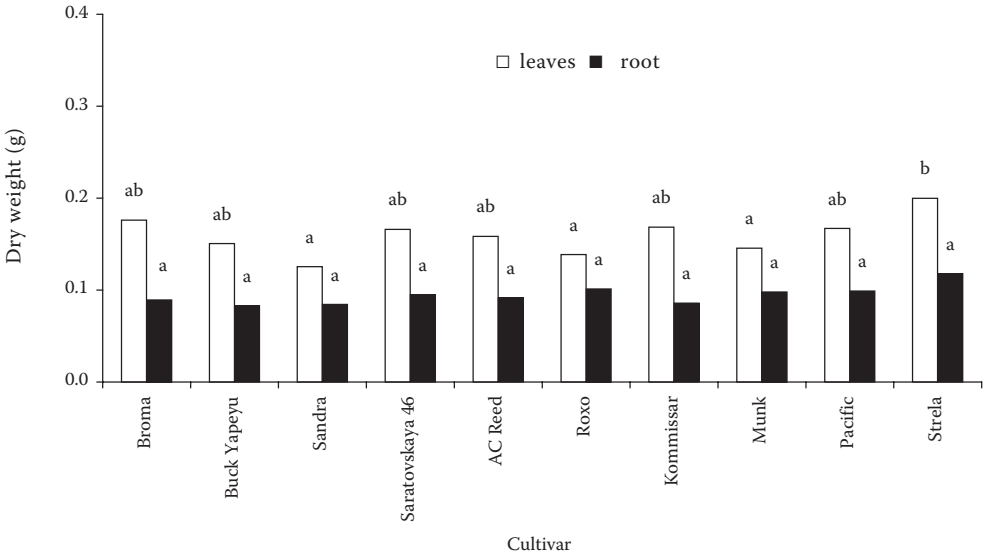

Figure 1. Dry weight of *Triticum aestivum* cultivars grown for 21 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

Seedlings of *T. aestivum* cultivars did not differ much and the significant difference was found only between Strela and Sandra. Within the group of *T. durum* cultivars Zenit with dry matter 0.329 g differed significantly from more intensively growing Khakovskaya, Marmilla, Mojo 2, and Lyudmila.

Partitioning of dry matter between shoot and root for *T. aestivum* is shown in Figure 1. Strela as a *T. aestivum* cultivar with highest net nitrate uptake capacity produced highest amount of root dry matter (0.118 g). On the other hand second cultivar in root dry matter weight Roxo (0.101 g) showed the lowest nitrogen uptake. Within the group of *T. durum* cultivars (Figure 2) the significant differences were determined. Zenit with dry matter of roots 0.101 g differed significantly from Lyudmila, Marmilla, Valbelice, Mojo 2 and Kievlanka that produced over 0.153 g root dry matter.

Similarly like in roots, cultivars of different species differentiated also significantly in dry matter of leaves (shoot). Average leaves dry matter (Figures 1 and 2) of *T. durum* group was nearly two times higher (0.307 g) than that of *T. aestivum* (0.160 g).

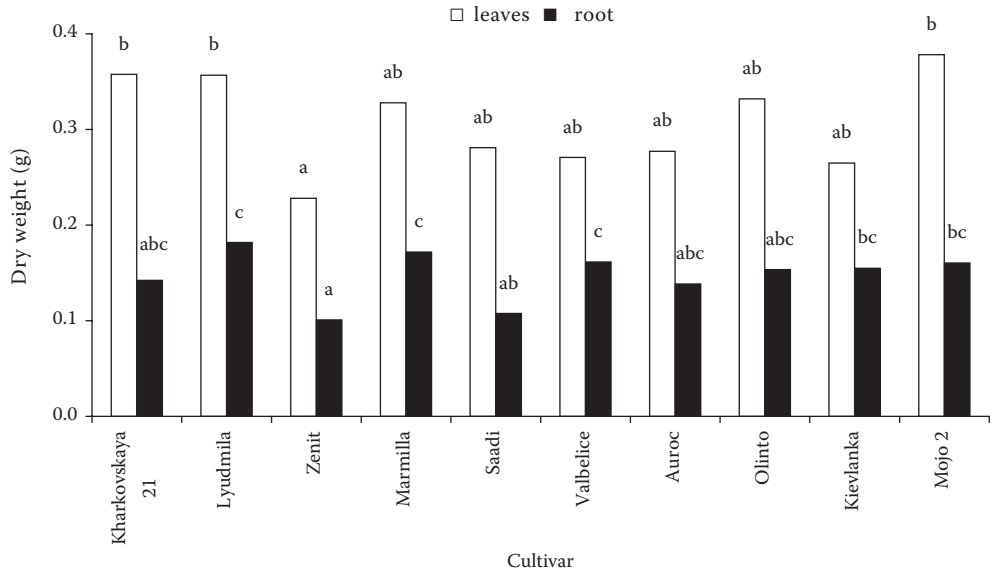

Figure 2. Dry weight of *Triticum durum* cultivars grown for 22 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

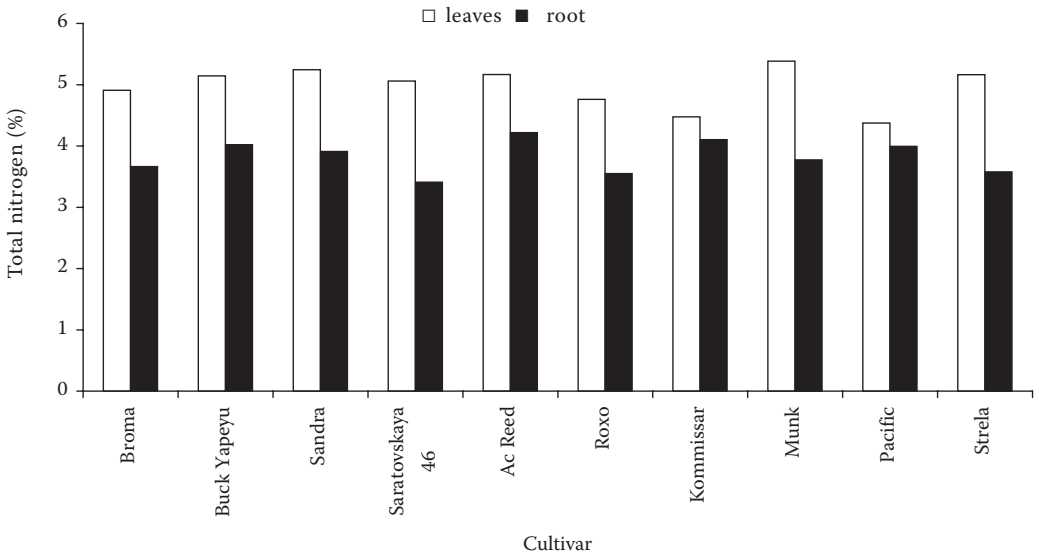

Figure 3. Nitrogen content (%) in dry matter of *Triticum aestivum* cultivars grown for 21 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

Within *T. aestivum* group, Strela produced the highest amount of leaf dry matter and Sandra the lowest one (0.125 g). The cultivars mentioned above were significantly different in this trait; Strela differed also from Roxo and Munk. Among *T. durum* cultivars, Zenit produced the lowest quantity of leaf dry matter and was statistically different from all other *T. durum* cultivars.

Nitrogen content and nitrogen allocation

Some intra-species differences in growth of *T. aestivum* and namely *T. durum* indicate different demand of shoot for N at both species. As expected, the main part of total nitrogen was accumulated in the shoot. Three weeks after sowing this part represents about 70% (65–72% at *T. aestivum* and 68–78% at *T. durum* cultivars) total N. This proportion is usual for good N supply during vegetative growth of wheat (Larsson et al. 1991).

Total nitrogen content (N concentration) in dry matter of wheat tissues is higher at *T. aestivum* than *T. durum* (Figures 3 and 4). In roots of *T. aestivum* group it varies from 3.41 to 4.22%, leaf N content is higher 4.37–5.24%. The same values for *T. durum* are 2.85–3.8% and 3.23–4.44%, respectively.

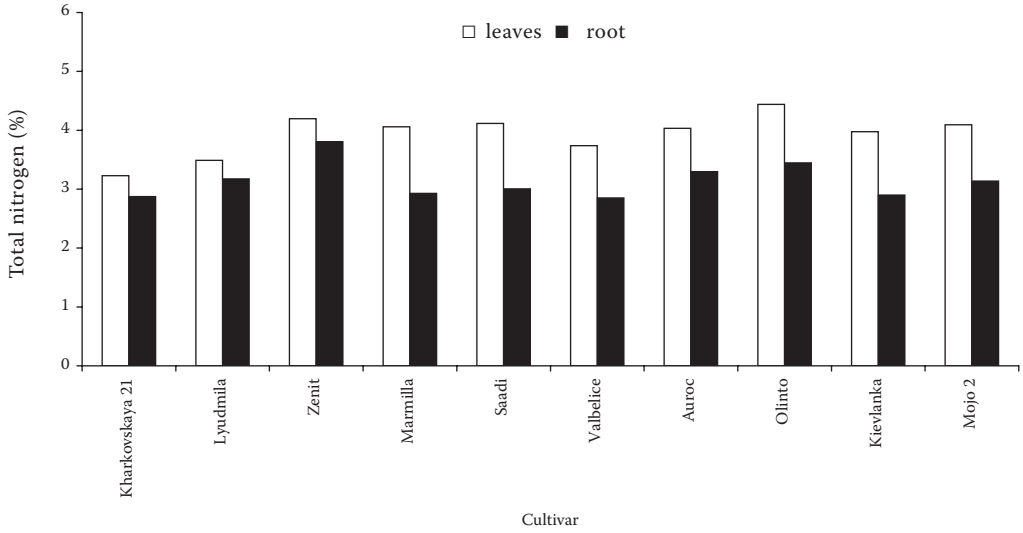

Figure 4. Nitrogen content (%) in dry matter of *Triticum durum* cultivars grown for 22 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

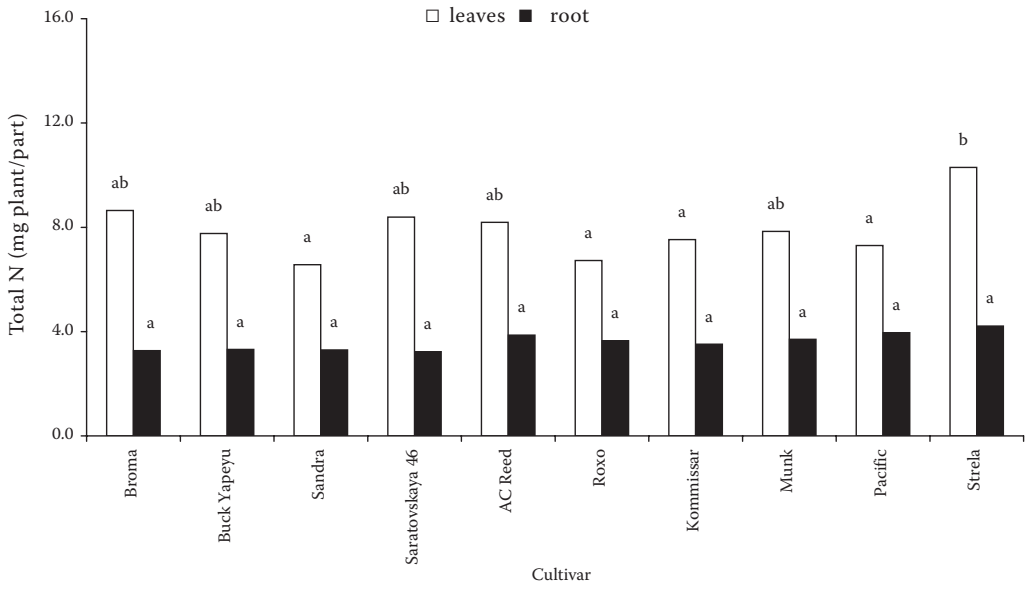

Figure 5. Nitrogen allocation (partition) in shoot and root of *Triticum aestivum* cultivars grown for 21 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

On the contrary, the nitrogen accumulation in root tissues was significantly lover in *T. aestivum* group (3.60 mg per plant) in comparison to *T. durum* group (4.59 mg). *T. aestivum* cultivars did not differ deeply (Figure 5) – no significant difference was found. Their nitrogen accumulation in roots ranged from 3.23 mg (Saratovskaya 46) to 4.21 mg (Strela).

The extent of nitrogen accumulation in roots of *T. durum* cultivars (Figure 6) varied from the same level as in *T. aestivum* (3.24 mg in Saadi) to 5.77 mg (Lyudmila). Saadi was significantly different from Lyudmila, Olinto, Mojo 2 and Marmilla.

Deep statistically significant difference was determined between the species in leaf nitrogen accumulation. Average nitrogen accumulation in *T. aestivum* leaves reached only 7.93 mg, whereas in faster developing *T. durum* group it was 12.05 mg per plant. *T. aestivum* cultivar Strela, likely as in roots, accumulated highest amount of nitrogen (10.30 mg) in leaves too. It overcame in this trait

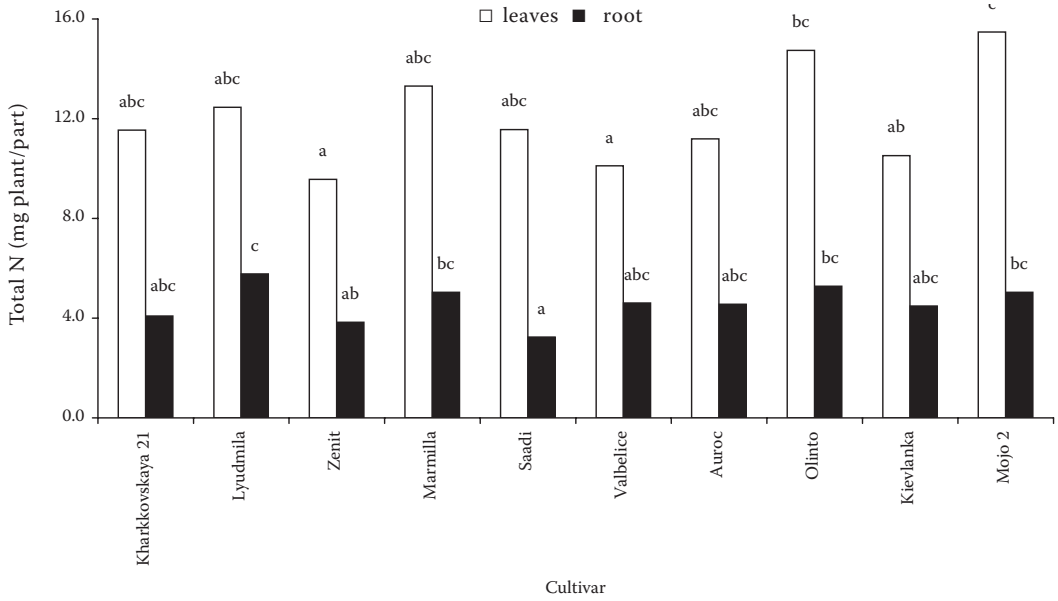

Figure 6. Nitrogen allocation (partition) in shoot and root of *Triticum durum* cultivars grown for 22 days in nutrient solution containing 773μM NO_3^- (10.8 ppm N-NO_3^-)

significantly in the group of cultivars Sandra, Roxo, Pacific and Kommisar. Nitrogen accumulation in *T. durum* leaves ranged from 9.57 mg (Zenit) to 15.48 mg (Mojo 2). Cultivars Zenit and Valbelice were significantly different from Mojo 2 and Olinto.

Nitrate uptake – plant growth relationship is manifested in nitrogen concentration. From this point of view it is possible to distinguish some types of cultivars. At *T. aestivum* the highest value was found at AC Reed, the low one at Roxo and Broma respectively. The registered cultivars Munk and Sandra with unregistered Strela and Saratovskaya are characterized by high leaf N concentration and average or low root concentration (Figure 3). In contrast Kommisar and Pacific have low leaf but high root N content. *T. durum* cultivars exhibit lower N concentration in both leaves and roots. The lowest values were estimated for Kharkovskaya and Lyudmila (hordeiforme) and in less extend for Valbelice. Relatively high N concentrations were found in tissues of Olinto, Zenit and Mojo. Cultivars Saadi, Marmilla and Kievlanka are characterized by higher leaf and lower root N concentration (Figure 4). It is possible to find similar intra- and inter-species differences in later stages of development (unpublished data) and, of course, in grain nitrogen content (Stehno et al. 1998).

Observed nitrate uptake and N allocation enable us to estimate the efficiency of N use by wheat seedlings. Nitrogen use efficiency is usually expressed as ratio between grain yield (weight) and total N content (Przulj and Momcilovic 2001, Presterl et al. 2002); in young plants or seedlings it can be expressed as ratio between dry matter formation and total N content. Analogous to other traits, at the age of 3 weeks this ratio at *T. durum* cultivars (27.3 mg dry weight per mg total N) exceeded the values found for *T. aestivum* (22.04 mg dry weight per mg total N). With regard to the intra-species differences the N use efficiency was usually negatively correlated with nitrogen concentration.

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Corresponding autor:

Ing. Marie Trčková, Výzkumný ústav rostlinné výroby, Drnovská 507, 161 06 Praha 6-Ruzyně, Česká republika
phone: + 420 233 022 474, fax: + 420 233 310 636, e-mail: trckova@vurv.cz