THE EFFECT OF NITROGEN ON DRY MATTER ALLOCATION IN YOUNG SPRING BARLEY PLANTS (*HORDEUM VULGARE* L.)

L. Nátr

Department of Plant Physiology, Charles University, Prague, Czech Republic

Spring barley plants (*Hordeum vulgare* L., cv. Korál) were cultivated in nutrient solutions Hoagland 2 and Hoagland 3 containing 5 mM and 15 mM concentrations of nitrate, respectively. In the two to three day intervals, samples consisting of 4 replicates, each containing 4 plants, were taken. Dry mass of the leaf blades, remaining parts of the shoot, and of the roots were measured. Shoot and total plant dry matter was calculated. Values of the dry mass time course were fitted to an exponential function (except for leaf blades). Although the differences in the initial values and differences in the relative growth rate were rather small, the time course of the dry mass shoot/root ratio differed considerably between the two treatments. It can be concluded that the dry mass shoot/root ratio is an efficient measure not only to determine individual nutrient deficiency but also to detect differences in the nitrogen supply in the region of its general sufficiency.

spring barley; nutrient solution; nitrogen; relative growth rate (RGR); shoot/root ratio; nitrogen deficiency determination

INTRODUCTION

Nitrogen and dry matter allocation represent the most important factors determining the rate of plant growth. Nitrogen is of both "theoretical" and "practical" importance. The former may be seen in its quantitative superiority among all the mineral elements contained in plant dry matter as well as in its role as a constituent of proteins (Hikosaka, Terashima, 1996). The latter may be expressed in the fact that a farmer is able to efficiently modulate the time course of canopy productivity by timing various amounts of nitrogen fertilizers (Bockman et al., 1990).

Dry matter allocation plays a dominant role in yield formation. It also considerably regulates most of the processes connected with dry matter production and distribution. Brouwer (1962) in his classical paper emphasized the role and the "responsibility" of both shoot and root in the acquisition of energy and nutrients from both the atmosphere and the soil. The shoot is responsible for providing enough carbohydrates while the roots look after supply of water and mineral nutrients. Both shortage and excess of any of these three substances negatively affect plant growth. Hence, a functional equilibrium between the availability of carbohydrates, water, and mineral nutrients is of prime importance. A plant has certain possibilities to modulate the absorption of radiant energy, water and nutrients. However, the main and long-lasting regulation of equilibrium may be achieved by preferential growth of those organs that are able to supply the deficient substrate. Carbohydrate deficiency therefore induces an increase in the allocation of dry matter into the shoot while nutrient or water deficiency promotes the translocation of assimilates into the roots. Differences in dry matter allocation are best seen in changes of the dry matter shoot/root ratio (Baker, Milburn, 1989).

Studying mineral nutrient deficiencies most often involves treatments with deficient and sufficient amounts of the appropriate substance (Repka, 1990). In such a case, pronounced symptoms of nutrient deficiency are compared with those of complete sufficiency. In this paper, the results of a study on the effects of a good and increased nitrigen supply to young barley plants cultivated in nutrient solutions are reported. They are evaluated by growth analysis.

MATERIAL AND METHODS

Spring barley plants (*Hordeum vulgare* L., cv. Korál) were germinated for 3 days at 22 °C in darkness and then transferred to nutrient solutions Hoagland 2 (H2) or Hoagland 3 (H3) containing 5 mmol N per liter or 15 mmol N per liter, respectively (Laštůvka, Minář, 1967). Plants were cultivated at 16 hour photoperiod under irradiance of 320 $\mu mol.m^{-2}.s^{-1}$ (photosynthetically active radiation). The day/night temperature was 23/18 °C with fluctuations ±2 °C.

In the time interval of 2 to 3 days 4 replicates, each containing 4 plants, were sampled, oven dried and the dry mass of the leaf blades, roots and remaining parts of the plants was measured. The experiment terminated when the plants were 31 days old.

The statistical evaluation of the experimental data included the standard errors (SE) of the samples that are given in the figures. The time course of dry mass of the individual plant parts was fitted to the exponential function of the general form:

$$(\text{Dry Mass at day } D) = a \ . \ e^{R.D},$$

where R indicates the relative growth rate (RGR) in $mg.mg^{-1}day^{-1}$. Only the time course of leaf blade dry mass was fitted to linear regression:

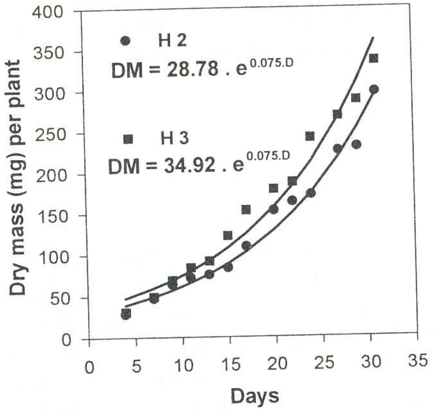
$$(\text{Dry mass at day D}) = a + b \ . \ D.$$

RESULTS AND DISCUSSION

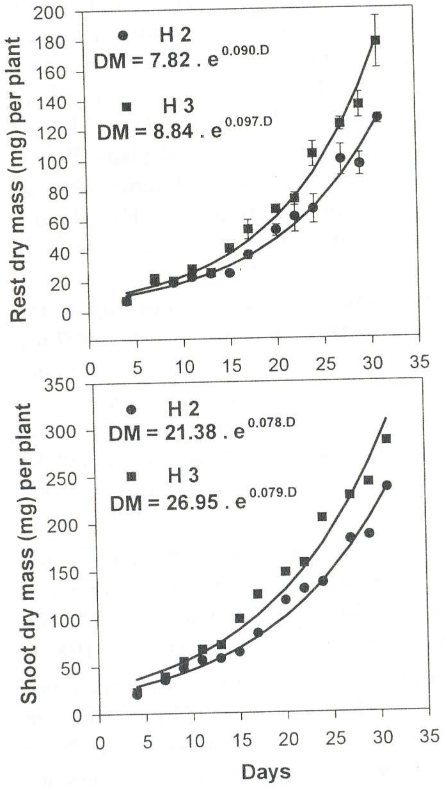
Nitrogen availability influences barley growth from the very beginning. In experiments with dark germinated and grown barley plants nitrogen deficiency affected the rate of respiration and the shoot/root ratio when plants were only 5 days old (Nátr, 1988, 1993). However, many experiments studying the effects of nutrient supply use the concentrations of ions that range from its absence from the solution to very high concentrations. In the experiments reported here, the differences between nitrogen availability were low and corresponded to sufficient N supply. The standard Hoagland 2 solution contains 5 mmol N per liter solution in the form of NO_3^- while Hoagland 3 15 mmol N per liter in the same chemical form. Even the lower concentration corresponding to the solution of Hoagland 2 should supply the plants with sufficient amounts of nitrogen (Laštůvka, Minář, 1967). The obtained results prove this assumption because in total dry mass of plant (Fig. 1) a relatively very small difference was between the two treatments. Strange enough, the RGR values were identical for plants cultivated in Hoagland 2 and Hoagland 3, i.e. 0.075 $mg.mg^{-1}.d^{-1}$ indicating that the daily increase in dry mass corresponded to 7.5 per cent. The difference between the two treatments seems to start from the very beginning of growth. According to the fitted function, the calculated value for Day = 0 equals 28.8 mg and 34.9 mg per plant for the H2 and H3 treatment, respectively. The experimental values for the 1st sampling, i.e. Day = 4 equal 27.9 mg and 30.9 mg for the H2 and H3 treatment. It confirms our previous results, that even during the first days of grain germination, the coleoptile, leaf and root growth was modified by the presence or absence of nitrogen from the ambient solution (Nátr, 1988, 1993).

The data also confirm the assumption, that during this short-term experiment, the plant growth expressed as dry matter increase was exponential (Lambers et al., 1990). It was therefore fully justified to calculate the average RGR by fitting the data to the exponential function (Hunt, 1982).

Similar conclusion may be drawn from the data on shoot dry mass per plant (Fig. 2) calculated as the sum of leaf blade dry mass (Fig. 3) and the remaining parts of the plant (Fig. 2). Again, the shoot dry mass differs from the values of the fitted function for the Day = 0 while the RGR values are



1. Experimental data (individual points) and fitted curves of exponential function of the time course of dry mass (mg) per plant of young barley plants cultivated 31 days in Hoagland 2 (●) or Hoagland 3 (■) nutrient solutions containing 5 mM and 15 mM nitrate, respectively



2. Experimental data (individual points) and fitted curves of exponential function of the time course of dry mass (mg) per plant of young barley plants cultivated 31 days in Hoagland 2 (●) or Hoagland 3 (■) nutrient solutions containing 5 mM and 15 mM nitrate, respectively

BELOW: Shoot dry mass consisting of leaf blades and leaf sheaths
ABOVE: Shoot plant parts with leaf blade dry mass excluded. Vertical bars indicate the ± standard error

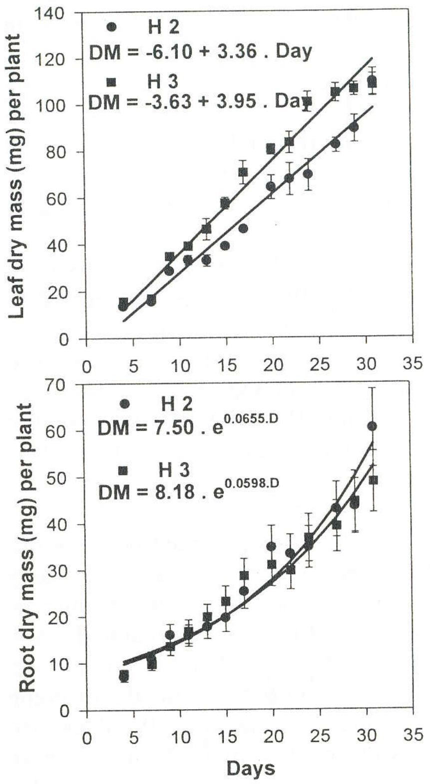
practically identical reaching 0.08 mg.mg^{-1}.day^{-1}, i.e. 8 per cent increase in dry mass per day.

The changes of the dry mass of the remaining parts of the plant consisting mainly of leaf sheaths yielded differences in RGR reaching some 10 per cent (relative value). The daily dry mass increase corresponds to 9.0 per cent and 9.7 per cent for the H2 and H3 treatments, respectively. The fitted curve (Fig. 2) indicates similar values at the beginning of the experiment with considerable divergence by its end.

The only values where the exponential fit yielded inadequate results were those for leaf blade mass per plant (Fig. 3). The linear regression seemed to produce the best fit indicating the constant dry mass increase of 3.36 mg and 3.95 mg per plant and day for the H2 and H3 treatment, respectively. Because of the relatively small values of standard errors of the leaf dry mass (see Fig. 3), the difference is statistically significant. The difference between the treatments reached some 15 per cent and clearly indicates the positive effect of higher nitrogen concentration in plants cultivated in the H3 treatment on leaf area development (Saeki, 1961; Nátr, 1989).

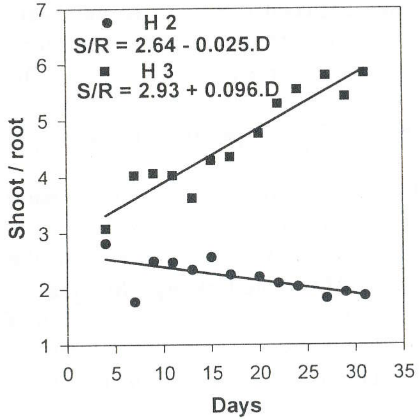
On the other hand, the differences in root dry mass per plant between the two experimental treatments are not statistically significant for all the samplings in the course of the experiment. The RGR values were lower compared with those for the shoot or rest dry mass (Fig. 2) and reached only 0.066 mg.mg^{-1}.day^{-1} and 0.060 mg.mg^{-1}.day^{-1} for the H2 and H3 treatment, respectively. Although the experimental values were not statistically different when their standard errors were compared, their calculated RGR values differed by some 10 per cent. This indicates clearly that more dry matter was allocated into the roots of plants supplied with lower nitrogen content in the course of the experiment. The time course of the two curves illustrating the RGR values also shows that the difference between the two treatments increases with the age of the plants. There were no differences at the beginning of the sampling period either between measured or calculated values. The calculated values for the Day = 0 were 7.50 mg and 8.18 mg while the measured values on Day = 4 were 7.0 mg and 7.6 mg per root dry mass per plant for H2 and H3, respectively.

Small differences in the dry matter allocation into the individual plant parts summed up and finally yielded considerable differences in the shoot/root ratio of plant dry mass (Fig. 4). During the whole duration of the experiment, the shoot/root ratio was steadily increasing in the H3-treated plants while that of the H2-treated plants was slowly decreasing. Hence, small differences found in the dry mass of the individual plant parts yielded considerable difference in the time course of the shoot/root ratio. This is the very conclusion of the whole experiment.



3. Experimental data (individual points) and fitted lines of exponential function (curve) of the time course of the root dry mass (mg) per plant or linear regression of leaf dry mass of young barley plants cultivated 31 days in Hoagland 2 (●) or Hoagland 3 (■) nutrient solutions containing 5 mM and 15 mM nitrate, respectively. Vertical bars indicate the ± standard error

BELOW: Root dry mass
ABOVE: Leaf blade dry mass



4. Values of the shoot/root dry mass ratio calculated from measured values (points) and fitted linear regression to these values (lines) of young barley plants cultivated 31 days in Hoagland 2 (●) or Hoagland 3 (■) nutrient solutions containing 5 mM and 15 mM nitrate, respectively

Brower (1962) was among the very first authors explaining the principles of dry matter allocation into the individual plant parts under conditions of nutrient, water or radiation energy deficiency. His idea about the preferential translocation of assimilates into the roots when either water or nutrients were deficient has been proved by many subsequent experiments (Lambers et al., 1990; Schenk, 1996). However, in most cases, sufficient supply of nutrients was most often compared with various degree of their deficiency. In our experiments, even the lower concentration of nitrate in the H2 treatment cannot be considered as a deficient one. Nevertheless, the H3 treatment supplied plants with a 3 times higher concentration of this nutrient. It was shown that the shoot/root ratio represents an extremely sensitive indicator of the nutrient availability (Nátr, 1988). It is able to clearly indicate not only nutrient deficiencies but also differences between those treatments that could be otherwise considered as fully sufficient, i.e. having adequate supply of the particular nutrient.

It may be that when the shoot/root ratio differences between treatments are quite small, the time course of this parameter may provide more information on the level of nutrient supply. Hence, the measurements and calculation of the time course of the shoot/root ratio may considerably increase its sensitivity and liability.

The importance of the dry matter allocation into the shoot and root has been confirmed even in an *in vitro* experiment. Lipavská and Nátr (1991, 1992) supplied the *in vitro* cultivated rape plants with various amounts of both carbohydrates and nitrogen. Under these conditions, roots became the source organ not only of nitrogen but also of carbon. Even under these experimental conditions the shoot/root ratio reflected the level of nitrogen availability.

There is an increasing body of evidence that dry matter allocation represents one of the most important processes regulating plant response to external conditions. However, not enough is known on mechanisms regulating this allocation (Ničiporovič, 1988; Turgeon, 1996). In other words, not enough is known on mechanisms determining the degree of preferences of the individual plant sinks under the given external conditions and at the given developmental stage of the plant.

On the other hand, the determination of the indicator consisting of the shoot/root value is difficult from the methodical point of view. It is relatively easy to measure root dry mass in plants cultivated in nutrient solution. However, considerable difficulties arise when field grown plants are to be analyzed (Haberle, Bláha, 1990; Haberle et al., 1996). If, this methodical handicap is overcome one day, the determination of the shoot/root ratio may become generally used even by the farmers.

Acknowledgement

The author wishes to thank Martin Ligr for his help in translating this paper into English.

References

BAKER, D. A. – MILBURN, J. A. (eds.): Transport of Photoassimilates. Harlow, Longman Scientific and Technical 1989.

BOCKMAN, O. C. – KAARSTAD, O. – LIE, O. H. – RICHARDS, I.: Agriculture and Fertilizers. Oslo, Agric. Group, Norsk Hydro a. s., 1990.

BROUWER, R.: Nutritive influences on the distribution of dry matter in the plant. Neth. J. Agric. Sci., *10*, 1962: 399–408.

COOPER, H. D. – CLARKSON, D. T.: Cycling of amino-nitrogen and other nutrients between shoots and roots in cereals. A possible mechanism integrating shoot and root in the regulation of nutrient uptake. J. Exp. Bot., *40*, 1989: 753–762.

HABERLE, J. – BLÁHA, L.: Kořenový systém zemědělských plodin – šlechtitelské a agrotechnické cíle (Root system of crops with respect to breeding and management targets.) Praha, ÚVTIZ 1990.

HABERLE, J. – SVOBODA, P. – RŮŽEK, P.: Root length of winter wheat and the content of mineral nitrogen in soil profile. Rostl. Výr., *42*, 1996: 193–197.

HIKOSAKA, K. – TERASHIMA, I: Nitrogen partitioning among photosynthetic components and its consequence in sun and shade plants. Funct. Ecol., *10*, 1996: 335–343.

HUNT, R.: Plant Growth Curves. London, Edward Arnold 1982.

LAMBERS, H. – FREIJSEN, N. – POORTER, H. – HIROSE, T. – van der WERF, A.: Analyses of growth based on net assimilation rate and nitrogen productivity. Their physiological background. In: LAMBERS, H. – CAMBRIDGE, M. L. – KONINGS, H. – PONS, T. L.: Causes and Consequences of Variation in Growth rate and Productivity of Higher Plants. The Hague, SPB Academic. Publ. bv. 1990.

LAŠTŮVKA, Z. – MINÁŘ, J.: Metoda vodních kultur vyšších rostlin.(Methods for cultivating of higher plants in nutrient solution). Folia Fac. Sci. Natur. Univ. Brno, B, *16*, 1967: 1–83.

LIPAVSKÁ, H. – NÁTR, L.: Changes in shoot/root ratio resulting from different sugar and nitrogen nutrition of rape seedlings grown *in vitro*. Acta Horticult., *289*, 1991: 127–128.

LIPAVSKÁ, H. – NÁTR, L.: The effect of exogenous sugar supply and nitrogen deficiency on dry matter allocation in rape seedlings grown *in vitro*. Biochem. Physiol. Pflanzen, *188*, 1992: 261–266.

NÁTR, L.: Shoot/root ratio during the early heterotrophic growth of barley as influenced by mineral nutrition. Plant and Soil, *111*, 1988: 237–240.

NÁTR, L.: Vliv dusíku na růst listů pšenice (The influence of nitrogen on wheat leaf growth). Rostl. Výr., *35*, 1989: 353–358.

NÁTR, L.: Negative correlation between the amount of respired substrate and the shoot/root ratio in dark grown barley seedlings. Rostl. Výr., *39*, 1993: 581–588.

NIČIPOROVIČ, A. A. (ed.): Fotosintez i produkcionnyj process. (Photosynthesis and production process). Moskva, Nauka 1988.

REPKA, J.: Funkcia minerálnych živín v regulácii fotosyntézy a rastu rastlín (The function of mineral nutrients in the regulation of plant photosynthesis and growth). Bratislava, Veda 1986.

SAEKI, T.: Leaf growth as influenced by dry matter production. Bot. Mag. (Tokyo), *74*, 1961: 70–78.

SCHENK, M. K.: Regulation of nitrogen uptake on the whole plant level. Plant and Soil, *181*, 1996: 131–137.

TURGEON, R.: Phloem loading and plasmodesmata. Trends in Plant Sci., *1*, 1996: 418–423.

Received for publication on April 11, 1997

NÁTR L. (Katedra fyziologie rostlin Univerzity Karlovy, Praha, Česká republika):

Vliv dusíku na alokaci živin u mladých rostlin jarního ječmene (*Hordeum vulgare* L.).

Scientia Agric. Bohem., *27*, 1997 (1): 7–16.

Rostliny jarního ječmene (*Hordeum vulgare* L., cv. Korál) byly pěstovány v živném roztoku Hoagland 2 obsahujícím 5 mM koncentraci nitrátů a v roztoku Hoagland 3 obsahujícím 15 mM koncentraci nitrátů. Kultivace probíhala v 16hodinovém dni při ozářenosti 320 µmol.m^{-2}.s^{-1} a teplotě den/noc odpovídající 22 °C/18 °C s kolísáním ±2 °C. V pravidelných dvou až třídenních intervalech byly odebírány 4krát 4 rostliny a stanovena hmotnost sušiny listových čepelí, kořenů a zbytku rostliny s tím, že byla dopočítána hmotnost sušiny celé nadzemní části a celé rostliny.

Časovým průběhem experimentálních hodnot byla proložena exponenciální funkce, jejíž exponent vyjadřuje hodnotu relativní rychlosti růstu, RGR (mg.mg^{-1}.den^{-1}). Pouze pro průběh hmotnosti sušiny listových čepelí se ukázala jako vhodnější lineární regrese.

RGR hmotnosti sušiny celé rostliny (obr. 1) byla identická a činila 0.075 mg.mg^{-1}.den^{-1}, což odpovídá dennímu přírůstku hmotnosti sušiny 7,5 %. Významné však byly rozdíly v počáteční hodnotě vypočtené pro nultý den, a to 28,78 mg pro rostliny H2 a 34,92 pro rostliny H3. Experimentálně naměřené hodnoty při 1. odběru, který proběhl 4. den od počátku nakličování, činily 27,78 mg pro H2 a 30,96 mg pro H3. Obdobné závěry byly vyvozeny z časového průběhu hmotnosti sušiny nadzemní části (obr. 2). Naproti tomu hmotnost sušiny zbylých částí rostlin vykázala při stejných počátečních hodnotách téměř 10% rozdíl v RGR (obr. 2).

Lineární regrese hmotnosti sušiny listů na stáří rostlin poskytla hodnoty denního přírůstku sušiny 3,36 mg na rostlinu pro H2 a 3,95 mg pro H3 (obr. 3). RGR hmotnosti sušiny kořenů se lišila mezi oběma variantami opět přibližně o 10 % a činila 6,55 mg.mg^{-1}.den^{-1} pro rostliny H2 a 5,98 mg.g^{-1}.den^{-1} pro H3.

Přes poměrně malé rozdíly v průběhu hmotnosti sušiny jednotlivých částí rostlin (obr. 1, 2 a 3) byly stanoveny podstatné rozdíly v hodnotách poměru hmotnosti sušiny nadzemní části/kořeny (obr. 4).

Pokusy prokázaly vysokou citlivost a vhodnost parametru hmotnost sušiny nadzemní části/kořeny pro detekci stavu zásobení rostlin minerálními živinami, především dusíkem. Tímto parametrem lze stanovit nejen výrazný deficit, ale i poměrně

malé rozdíly při celkově dobré zásobenosti rostlin dusíkem. Citlivost tohoto parametru lze zvýšit stanovením dynamického průběhu jeho hodnot při několika časově následných odběrech.

jarní ječmen; živný roztok; dusík; relativní růstová rychlost (RGR); poměr nadzemní část/kořeny; detekce deficitu dusíku

Contact Address:

Prof. RNDr. Lubomír Nátr, DrSc., Katedra fyziologie rostlin Univerzity Karlovy, Viničná 5, 128 44 Praha 2, Česká republika, tel.: 02/2195 3184, e-mail: natr@prf-dec.natur.cuni.cz