THE EFFECT OF NITROGEN AND IRRADIANCE ON GROWTH PARAMETERS OF *TRITICUM AESTIVUM* L. AND *AEGILOPS TAUSCHII* SEEDLINGS*

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Seedlings of *Aegilops tauschii* and *Triticum aestivum* L. cv. Sparta were cultivated in nutrient solutions Hoagland 1 (LN – low nitrogen treatment) or Hoagland 3 (HN – high nitrogen treatment) with irradiance 50 μmol (Photosyntetically Active Radiation).m^{-2}.s^{-1} (LL – low light) or 300 μmol (PhAR).m^{-2}.s^{-1} (HL – high light) in growth chamber at day/night temperature 22 °C/18 °C. On 14, 21 and 28 days of cultivation, shoot and root dry mass and leaf area were determined on 3 samples, each consisting of 4 plants. Plants from the final sampling were used to determine the nitrogen content. The measured values were used to calculate plant dry mass and shoot/root ratio as well as leaf area ratio (LAR, mm^2 [leaf area] / mg [dry mass], relative growth rate (RGR, mg.mg^{-1}.day^{-1}) and net assimilation rate (NAR, g.m^{-2}.day^{-1}) and nitrogen use efficiency (NUE, mg [dry mass].mg^{-1} [N]). Shoot, root and plant dry mass was significantly modified by the nitrogen and radiation energy utilisation. It was shown that both dry mass and leaf area per plant considerably decreased under nitrogen limitation and especially radiant energy deficiency. In general, differences between *Aegilops* and *Triticum* were rather small and often statistically not significant. Shoot, root and plant dry mass was higher in *Triticum* than in *Aegilops*, although the values of relative growth rate were reversed. Differences in net assimilation rate were the same for *Aegilops* and *Triticum* for most of the experimental treatments. Hence, no considerable differences were found in the most measured parameters of the *Aegilops* and *Triticum* seedlings. It is deduced, that the presented data of the seedlings do not support the hypothesis first presented by E v a n s and D u n s t o n e (1970) about a systematic decrease in the rate of photosynthesis during the evolution of *Triticum*.

net assimilation rate; relative growth rate; leaf area ratio; evolution of *Triticum*

INTRODUCTION

Radiation energy affects photosynthesis and dry matter production in a decisive way during the whole vegetation period. Similarly nitrogen as a component of proteins is indispensable for plant growth that represents – in a slightly simplified way – accumulation of assimilate and nitrogen compounds. There is also a close functional relationship between energy and nitrogen supply (Nátr, 1997a). Photosynthetic machinery is built up of various protein structures and enzymes, especially ribulose-1,5-bisphospate carboxylase (rubisco) that is responsible for carboxylation. Hence, more nitrogen is available, more photosynthetic structure can be built up and more CO_2 fixed (Apel et al., 1985). In this way, the positive effect of nitrogen nutrition on dry matter production can be exemplified. On the other hand, nitrogen uptake, mainly in the form of nitrate, needs energy not only for the absorption but especially for the subsequent nitrate reduction and assimilation into amino acids (Lipavská, Nátr, 1992). Hence, more assimilate available, more nitrate may be taken up and more proteins synthesised (Garnier et al., 1995).

The effect of nitrogen and radiant energy on plant growth has been well documented (Lambers, 1987; Baker, McKiernan, 1988; Abbate et al., 1995). Most of the experiments were carried out with plants in later stages of their growth (Belford et al., 1987; Sinclair, Amir, 1992). But it has been shown that plants respond to nitrogen availability even during germination and seedling growth (Barthes et al., 1996). This is very important because an increase in dry matter production results in larger leaf area index after plant emergence and higher absorption of sun energy. This early stage events could be decisive for the whole subsequent growth rate (Nátr, 1997b). But there is another important phenomenon related to the effect of nitrogen on early plant growth. It has been demonstrated, that the presence or absence of nitrogen considerably modifies dry matter allocation between root and shoot. Such an effect of nitrogen can be observed during seed germination already (Tesařová, Nátr, 1986). It fully corresponds to the general effects on the shoot/root ratio as described by Brouwer (1962). He emphasised, that shortage of assimilate prefers the supply of assimilate into the shoot that can subsequently increase assimilate production. On the other hand, shortage of water or mineral nutrients induces preferential allocation of assimilate into the roots that are able to remove such a deficiency (Belford et al., 1987; Hirose, 1988).

Wheat represents the most important crop in the world food production. To meet future demand it will be needed to considerably increase its productivity. To achieve such a goal, more knowledge must be available about mechanisms of yield formation (Evans, 1996). It is generally accepted, that new high productive varieties and a more rational use of mineral fertilisers represent two potential sources for the future yield increase (Apel et al., 1985; Lambers, 1987). In 1970 already, Evans and Dunstone (1970) have published surprising results indicating that the rate of photosynthesis decreases during the evolution of the genus *Triticum*. Their results were partly confirmed by Khan and Tsunoda (1970). However, in general this surprising phenomenon has not been studied very often. As far as we are aware, no experiments have been carried out on seedlings. On the other hand, a thorough confirmation of the results of Evans and Dunstone (1970) and elucidation of the underlying mechanisms could provide breeders with new source of valuable genes.

The evolution of wheat (Breiman, Graur, 1995) could be well represented by the following species: There is a general agreement among scientists (Morris, Sears, 1967 and others) that soft hexaploid wheat *Triticum aestivum* (genome ABD) originated as an allopolyploid from three diploid ancestors. In the first step wild einkorn, most likely *T. urartu* (genome A; Dvořák et al., 1993), crossed with *Aegilops*, section Sitopsis resulting in tetraploid wheat. The origin of the Sitopsis *Aegilops* is not clear however, the most of evidence refer for a species close to *Ae. speltoides* (genome S, homoeologous to A of wheat, Dvořák, Zhang, 1990). In the second step the tetraploid wheat hybridized with *Aegilops tauschii* (genome D). Such hybridization must have occurred before 8700 B.C., before the first findings of naked wheat kernels (Wilcox, 1997).

For our experiments these more or less hypothetical progenitors were chosen as an evolution row from early progenitors to primitive cultivars and modern wheat. The D genome parent *Aegilops tauschii* is classified in two subspecies (Hammer, 1980) of which ssp. *strangulata* Eig. (Tzvel.) is considered to be ancestral for wheat. That is why the choice of material was directed to the accession 01C2105174, which belongs to this subspecies. The check cultivar Sparta is a recent widely grown soft wheat in the Czech Republic.

MATERIAL AND METHODS

For the experiment *Aegilops tauschii* (5174) from the collection of the Gene Bank Praha-Ruzyně were chosen. The recent soft winter wheat (*Triticum aestivum*) cultivar Sparta was used as a control. To remove single kernels, whole spikelets of *Aegilops* were immersed in distilled water and kept overnight at 8 °C. After removal the kernels were placed on wet filter paper in Petri dishes and kept for 3 days at 20 °C. The kernels of *T. aestivum*

cv. Sparta were germinated four days in distilled water in Petri dishes at 20 °C. Germinated seedlings were then placed partly into Hoagland 3 nutrient solution containing 5mM $Ca(NO_3)_2$, 5 mM KNO_3, 1 mM KH_2PO_4, 0.99 mM $MgSO_4$, 19 μM Fe-citrate and microelements (high N treatment – HN) and partly into Hoagland 1 nutrient solution containing 0.5mM $Ca(NO_3)_2$, 5mM K_2SO_4, 0.5mM $Ca(H_2PO_4)_2$, 2mM $CaSO_4$, 0.99mM $MgSO_4$, 19 μM Fe-citrate and microelements (low N treatment – LN). There were three replicates in two 3 litre vessels each consisting of 20 plants. The plants were cultivated in a growth chamber at 18 ± 1 °C (16 h photoperiod) and 12 ± 1 °C (night) temperatures and illuminated partly with 300 μmol.m^{-2}.s^{-1} (high light treatment – HL) and partly with 50 μmol.m^{-2}.s^{-1} photosynthetically active radiation (low light treatment – LL) provided by sodium high pressure lamps.

In one to two day intervals, the length of 10 individual leaves was measured as the distance from the kernel to the tip of stretched leaf blades. The data were used to calculate both the rate of leaf growth during its linear phase as a regression coefficient of leaf length on time and the phyllochron expressed as the time interval when two successive leaves attained the length of 100 mm. After 14 and 21 days of cultivation, three samples of four plants each were taken and the blade area of all leaves was measured. After 28 days, three replicates with four plants each were harvested and the leaf blade area of all leaves as well as shoot and root dry mass determined. Leaf area was measured by scanning the leaves and measuring its area by a computer program developed by J a n á č e k (personal communication). In the plant dry matter total nitrogen was determined photocolorimetrically after mineralisation with H_2SO_4 and Se by using the system Scallar, Type San$^+$. From these data nitrogen use efficiency (NUE) was calculated as the ratio of dry mass and plant nitrogen content. All the primary (measured) data were statistically evaluated by analysis of variance. The leaf area ratio (LAR) was computed as the total leaf area L(t) divided by the plant dry mass W(t). The relative growth rate (RGR) is defined as absolute growth rate divided by the existing plant dry mass. Supposing RGR does not depend on time (that holds for the exponential period of plant growth) we get the dry mass W(t) to be exponentially dependent on time, i.e.

$$W(t) = W_0 \, e^{(RGR)t}$$

RGR was then estimated as the slope of regression line describing the dependency of dry mass natural logarithm on the time.

The net assimilation rate (NAR) is equal to the net gain in dry mass per unit of leaf area. If plant dry mass and the leaf area depend exponentially on time, then NAR is an exponential function of time, too. NAR was then computed from estimated dependencies of plant dry mass W(t) and leaf area L(t) on time.
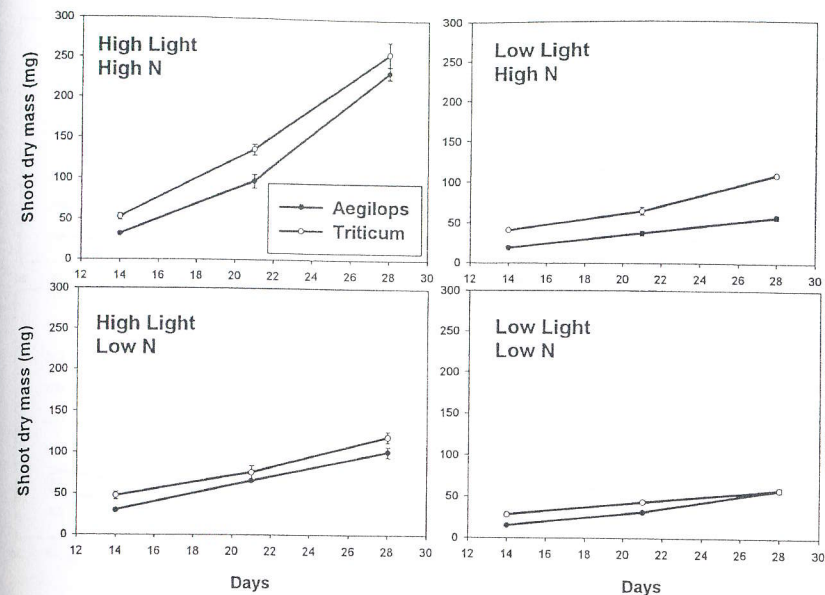
1. The effect of nitrogen (LN: low nitrogen: 1 mM [NO_3], HN: high nitrogen: 15 mM) and irradiance (HL: high light: 300 μmol [PhAR].m^{-2}.s^{-1}, LL: low light: 50 μmol [PhAR].m^{-2}.s^{-1}) on shoot dry mass (mg) per plant of *Aegilops tauschii* and *Triticum aestivum* 14, 21 and 28 days after sowing. The vertical bars indicate standard errors

RESULTS AND DISCUSSION

During the experiment, wheat produced more dry mass of both the shoot (Fig. 1) and root (Fig. 2) than *Aegilops*. This difference was very pronounced under high nitrogen of both high and low light for shoot and under high light of both high and low nitrogen for the roots. As to the plant total dry mass (Fig. 3), the differences between *Aegilops* and *Triticum* were apparent under high light and high nitrogen. On the other hand, the differences were small under cultivation conditions where both nitrogen and light (LN LL) were deficient. Following the shoot/root ratio (Fig. 4) *Aegilops* allocated relatively more dry matter into the shoot in all treatments.
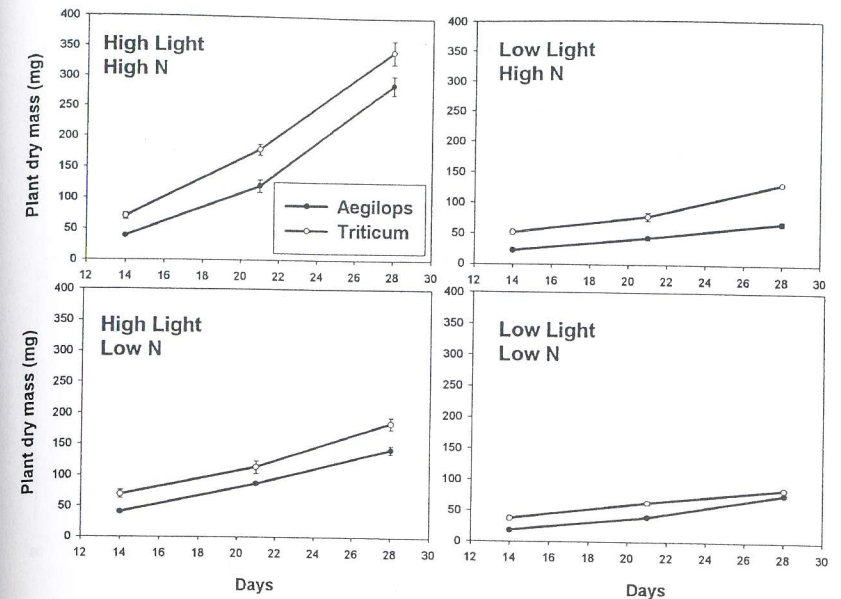
Statistical analysis was performed separately for the three samplings, i. e. for the data obtained 14, 21 and 28 days after sowing. The effect of irradiance, nitrogen and genotype was shown to be statistically significant for all samplings.
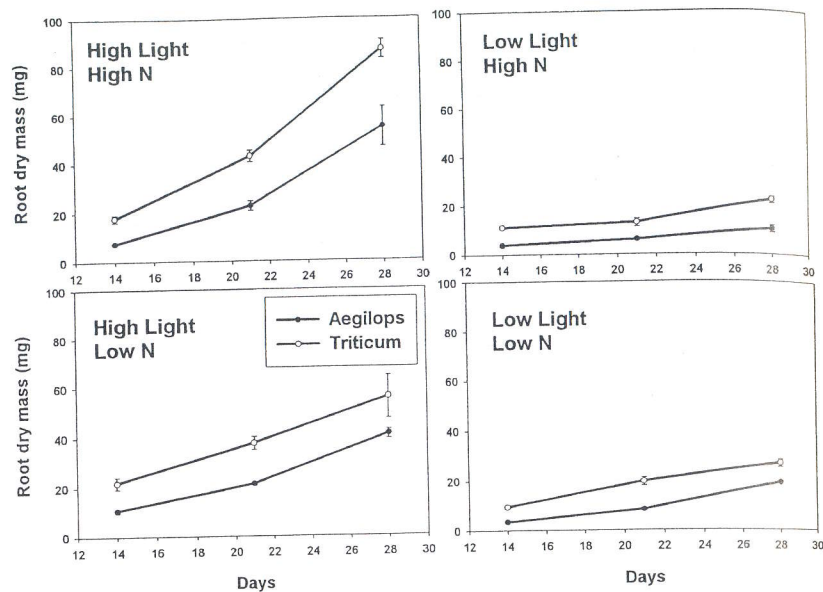
2. The effect of nitrogen and irradiance on root dry mass (mg) per plant. See description of Fig. 1 for details

3. The effect of nitrogen and irradiance on plant dry mass (mg) per plant. See description of Fig. 1 for details

It might be instructive to analyse the data obtained on the 3rd sampling in more detail. The mean plant dry weight of all the experimental treatments was 143.6 mg and 186.2 mg of *Aegilops* and *Triticum*, respectively. It indicates, that wheat produced by about one third more dry matter than *Aegilops* during the 28 days of their growth. Nitrogen effect on plant dry matter production was also very pronounced. All the treatments give a value of plant dry mass of 122.2 mg and 207.6 mg for low (LN) and high (HN) treatment, respectively. Hence an improved nitrogen supply induced an increase in dry matter production by some 70 per cent, that fully corresponds to the generally positive effects of this nutrient (A p e l, 1985). But the most pronounced effect was that of irradiance. Plant dry mass of all the treatments was 90.2 mg and 239.6 mg for low (LL) and high (HL) irradiance, respectively. This result indicates that for both wheat and *Aegilops*, light energy is the factor the most affecting seedling growth rate when expressed in dry matter accumulation. However, from the results no conclusion can be drawn about higher rate of assimilate production by the *Aegilops*.

Plant leaf area (Fig. 5) was practically not different between *Aegilops* and *Triticum*. Mean value of leaf area per plant on the 3rd sampling was 3588 mm^2 and 3759 mm^2 for *Aegilops* and *Triticum*, respectively. This difference was not statistically significant. If we now compare the effect of nitrogen nutrition by calculating mean leaf area of all the treatments in low nitrogen (LN) and high nitrogen (HN), we get the values of 2514 mm^2 and 5083 mm^2, respectively. This difference is statistically significant. Similar difference was found between all the treatments cultivated under low (LL) and high (HL) irradiance with values of 2702 mm^2 and 4895 mm^2, respectively.
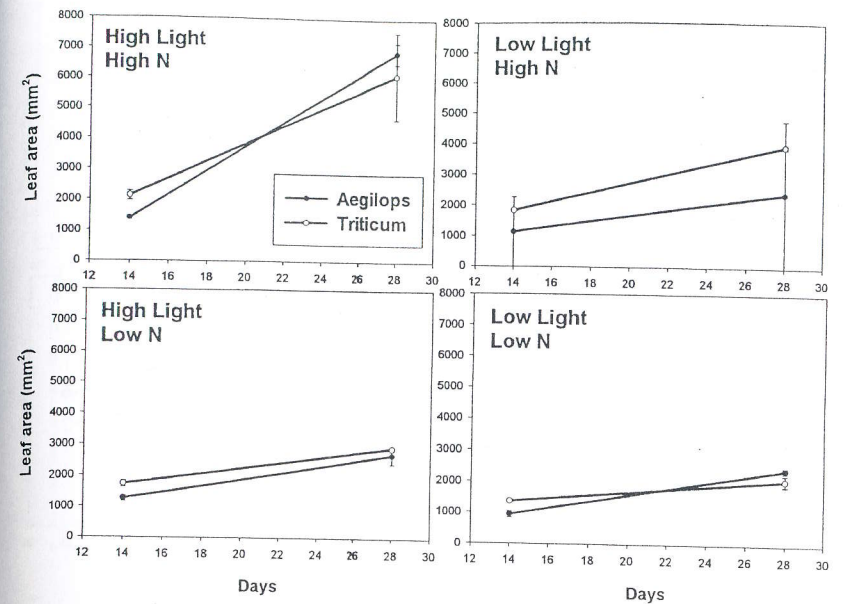
The data on leaf dry mass and area were used to calculate leaf area ratio (Fig. 6). Although *Aegilops* had higher values, they were statistically significantly different from *Triticum* only at low light (LL) of both nitrogen treatments on the 1st sampling. Hence, it is possible to deduce that Aegilops shows the tendency to produce thinner leaves as indicated by the higher values of LAR as compared with *Triticum*.
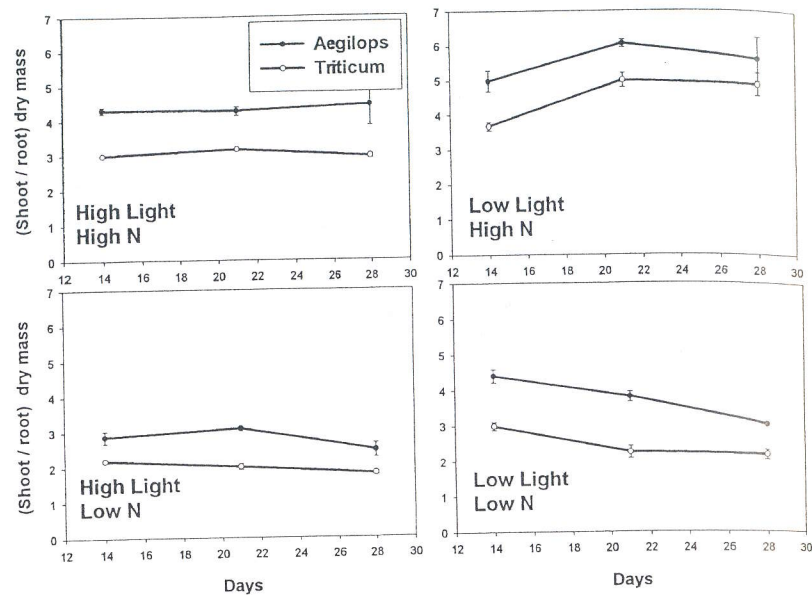
4. The effect of nitrogen and irradiance on shoot/root dry mass ratio. See description of Fig. 1 for details

5. The effect of nitrogen and irradiance on leaf area (mm² per plant) 14 and 28 days after sowing. See description of Fig. 1 for details

Also the differences in nitrogen per dry matter were not very different between *Aegilops* and *Triticum* (Fig. 7). Taking all the treatments of the individual species together the nitrogen content (mg nitrogen per g dry mass) was 33.5 and 34.9 for *Triticum* and *Aegilops*, respectively. Similar data for all the treatments of low (LL) and high (HL) irradiance are 38.3 and 30.1 mg N per g dry mass, respectively. It indicates, that photosynthesis was inhibited by light to a higher degree than by nitrogen shortage. Of course, there is a large difference in the nitrogen content between low (LN) and high (HN) nitrogen treatment giving 25.2 and 43.3 mg N per g dry mass, respectively. In this case, nitrogen uptake was inhibited more than photosynthesis. If we express nitrogen content per plant (Fig. 7, left hand lower figure), the values of *Triticum* are higher than those of *Aegilops* because of the higher *Triticum* dry matter per plant. Finally, it is interesting to realise that nitrogen use efficiency was similar for *Triticum* and *Aegilops* cultivated under sufficient nitrogen supply (HN). But *Triticum* was more efficient in nitrogen use under conditions of low nitrogen (LN). This is again an unexpected result indicating that during the evolution and breeding of wheat the modern cultivars acquired

the ability to use nitrogen more efficiently. However, such a result must be confirmed in further experiments, because large differences in nitrogen use efficiency could be expected to exist among the modern cultivars.

The effect of nitrogen and irradiance on relative growth rate (Fig. 8) corresponds to what could be expected. The highest values were found for plants grown under higher irradiance and higher nitrogen supply. In all the treatments, *Triticum* has lower RGR values than *Aegilops*. This is somehow surprising, because *Triticum* produced more dry matter per plant (Fig. 3). It is difficult to explain this discrepancy. It may only be hypothetized that the difference could be attributed to the difference in kernel dry mass that was 19.8 mg and 40.3 mg for *Aegilops* and *Triticum*, respectively. Higher *Triticum* kernel dry mass could have contributed more to final plant dry matter compared to that of *Aegilops* (see also N á t r et al. 1999). Again, such a hypothesis is supposed to be verified or rejected by further experiments.
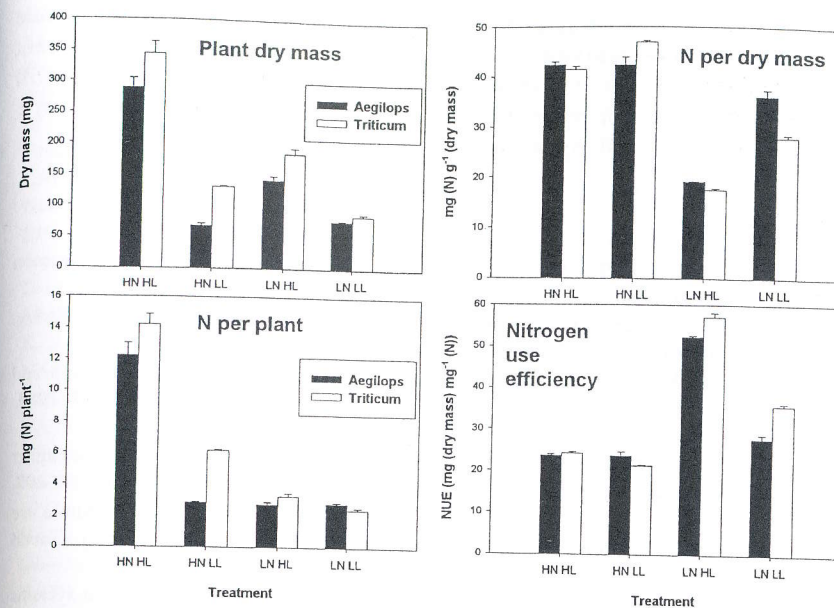
The efficiency of leaf area to produce assimilate and expressed in values of net assimilation rate seems to be the same for *Aegilops* and *Triticum* (Fig. 8). There was just one significant difference between *Triticum* and
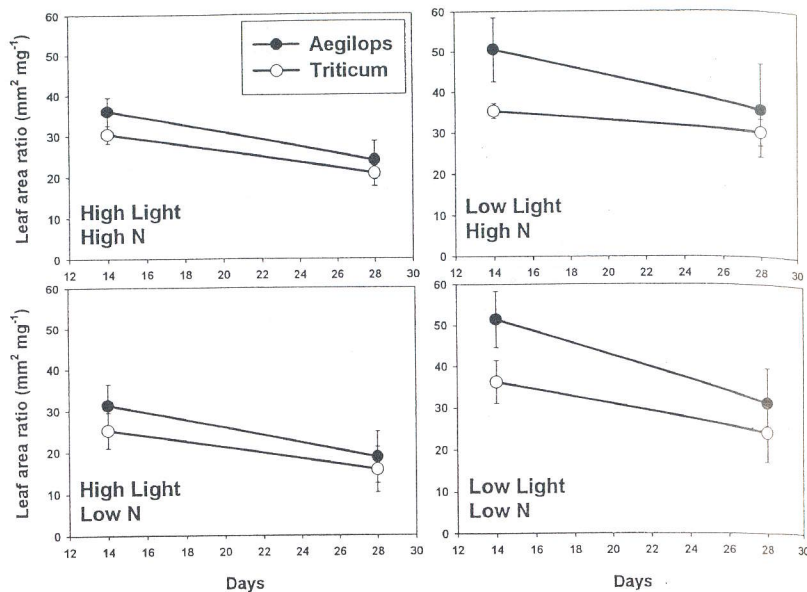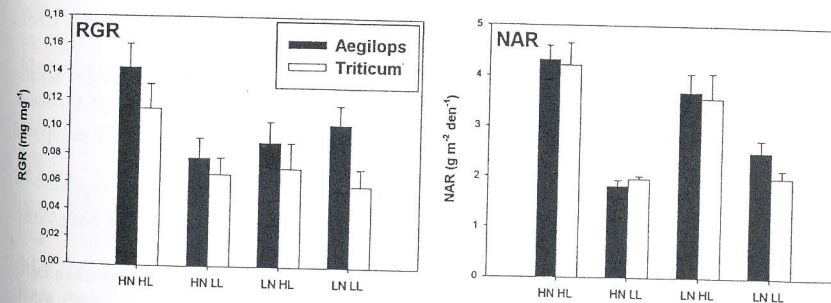
6. The effect of nitrogen and irradiance on leaf area ratio (LAR, mm^2.mg^{-1}) 14 and 28 days after sowing. See description of Fig. 1 for details

7. The effect of nitrogen on plant dry mass (mg per plant), nitrogen content (mg N per g dry mass), plant nitrogen content (mg N per plant dry mass) and nitrogen use efficiency (NUE, mg dry mass per mg nitrogen) 28 days after sowing. See description of Fig. 1 for details

8. The effect of nitrogen and irradiance on relative growth rate (RGR, mg increase in dry mass per mg dry mass) and net assimilation rate (NAR, g dry mass increase per m^2 leaf area per day). See description of Fig. 1 for details

Aegilops in plants cultivated under deficient light and nitrogen (LN LL). It indicates once more (see also Černohorská et al., 1999) that growth parameters of Aegilops seedlings are quantitatively characterized by values that are not superior to *Triticum*.

We are aware of the fact, that results presented in this paper were obtained by measuring just one *Aegilops tauschii* and one *Triticum aestivum* species. However, in our previous papers, we found no significant differences among various *Aegilops speltoides* (Černohorská et al., 1999) or *Aegilops tauschii* (Nátr et al., 1999) provenances. On the other hand, varietal differences of modern cereal genotypes have been shown to exist (Nátr, 1966; Barthes et al., 1996). To confirm general validity of the presented results, more experiments will have to be carried out. Relating the conclusion by Evans and Dunstone (1970) on the higher rate of photosynthesis in wild *Triticum* ancestors as compared with modern hexaploid wheat, our experiments with seedlings do not indicate such a difference. Although relative growth rate is a reasonable analogue of the rate of photosynthesis, its values are not identical because of the night respiration included into its measure-

ments. But Gloser et al. (1998) measured gas exchange and fluorescence parameters of some *Aegilops* and *Triticum* species without finding significant change during the evolution of wheat. Nevertheless, more measurements will be needed to extend or reject the conclusion by Evans and Dunstone (1970) also to the seedling stage.

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Vliv dusíku a ozářenosti na růstové parametry mladých rostlin *Triticum aestivum* L. a *Aegilops tauschii.*

Mladé rostliny *Aegilops tauschii* a *Triticum aestivum* cv. Sparta byly pěstovány v klimatizované komoře v živném roztoku Hoagland 1 (LN – nízký dusík) a Hoagland 3 (HN – vysoký dusík) a při intenzitě ozáření 50 μmol (fotosynteticky aktivní radiace).$m^{-2}.s^{-1}$ (LL – nízká ozářenost) a 300 μmol (FAR).$m^{-2}.s^{-1}$ (HL – vysoká

ozářenost). Tři opakování po čtyřech rostlinách byly odebrány po 14, 21 a 28 dne
kultivace. Měřena byla hmotnost sušiny nadzemní části a kořenů, velikost listo
plochy a celkový obsah dusíku (obsah N stanoven jen v rostlinách posledního odb
ru). Z naměřených hodnot byly vypočítány relativní růstové rychlosti (RGR), čis
výkon asimilace (NAR) a účinnost využití dusíku (NUE).

Ve všech pokusných variantách měla pšenice větší hmotnost sušiny nadzemní čá
i kořenů. U pšenice i *Aegilops* se velmi silně projevil nedostatek dusíku v živné
roztoku i deficit zářivé energie. Relativní růstová rychlost byla u pšenice nižší n
u *Aegilops*, i když v produkci celkové sušiny převládala pšenice. Je pravděpodobn
že se zde projevil vliv výrazně rozdílného množství zásobních látek v endosper
obilek (hmotnost obilek 19,8 mg u *Aegilops* a 40,3 mg u pšenice). Při celkové
hodnocení nelze vyvodit jednoznačnou převahu hodnot růstově-analytických pa
metrů u *Triticum* nebo *Aegilops*. Naměřené parametry včetně čistého výkonu asir
lace nelze ztotožňovat s hodnotami charakterizujícími rychlost fotosyntézy. Přesto
ukazuje jako nepravděpodobné, že by uvedené minimální a nejednoznačné rozd
v růstově-analytických parametrech mezi *Triticum* a *Aegilops* bylo možno uvést
souladu s představami o výrazně větší rychlosti fotosyntézy u rostlin *Aegilops*. N
předpokládáme proto, že teorie, kterou poprvé popsali E v a n s   a   D u n s t o
(1970), platí i pro mladé rostliny zástupců druhů charakterizujících evoluci pšeni

čistý výkon asimilace; relativní růstová rychlost; specifická listová plocha; evo
Triticum

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