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ORIGINAL PAPER

Regulation of shoot growth, root development and manganese allocation in wheat (*Triticum aestivum*) genotypes by light intensity

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Abstract The objective of this study was to assess effects of different light intensities on shoot growth, root development and allocation of root-borne solutes via the transpiration stream to various shoot parts of young wheat plants (*Triticum aestivum* L.). Hydroponic culture allowed direct access to the roots and shoots throughout the experiment. Under low light intensity (100 µmol photons m^{-2} s^{-1}), shoot growth was restricted, less (but larger) leaves were produced at the main shoot and only a few tillers became visible as compared to plants under high light intensity (380 µmol photons m^{-2} s^{-1}). The root system was indirectly also affected by the illumination of the aerial parts. A larger number of shorter roots were produced under high light leading to a denser root system, while only a small number of longer roots were present under low light. The distribution of ^{54}Mn (xylem-mobile, but essentially phloem-immobile in wheat) from the roots to the shoot lead to the conclusion that light regime strongly influences the distribution of root-borne solutes within the shoots. Labels introduced into the roots may allow a deeper insight into the transfer of solutes from the root system to the various shoot parts under different light regimes.

Keywords Light intensity · Manganese allocation · Root system · Tiller growth · *Triticum aestivum* · Wheat

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Introduction

Light and temperature are major environmental factors influencing the development of tillers in cereals (Friend 1965; Bos and Neuteboom 1998; Evers et al. 2006; Kim et al. 2010) and in perennial ryegrass (Bahmani et al. 2000). Low light intensity causes a reduced number of tillers, a reduced number of grains per spike and a reduced total grain weight in wheat (Fischer and Stockman 1980). Furthermore, low light intensity affects the time to ear emergence and the time to tillering in spring wheat cultivars (Evtushenko and Chekurov 2004). Tillers emerge from axillary buds of the main shoot as well as from the primary tillers themselves. Production of tillers is an important property in wheat because the number of tillers that reach the stage of grain filling influences grain yield. Nitrogen availability (Davies 1971) and plant population density (Darwinkel 1978) are two agronomically important factors having an effect on tillering in gramineous species. Shading after anthesis leads to a reduced starch yield in winter wheat (Li et al. 2010). Besides effects on shoot development, the light regime influences also root growth as reported by Vincent and Gregory (1989a, b) for winter wheat in the field and in the greenhouse. They found in their experiments that supplementary light increased root length and root dry matter.

Manganese is essential for higher plants (micronutrient) and is involved in the oxygen production in photosystem II and in a series of enzymatic processes (Marschner 1995; Welch 1995; Mukhopadhyay and Sharma 1991). Despite its importance, manganese can be detrimental for the plant when present in excess (El-Jaoual and Cox 1998). Manganese is absorbed by the plant mainly as divalent Mn^{2+} and moves easily in the xylem sap with the transpiration stream from the roots to the shoot (Mukhopadhyay and

Sharma 1991). This micronutrient is known for its poor mobility in the phloem of cereals (Herren and Feller 1994; Page and Feller 2005; Riesen and Feller 2005; Page et al. 2006a, b).

Light can strongly influence the development of tillers and below-ground plant parts in wheat and as a consequence long-distance translocation. Radiolabeled manganese (^{54}Mn) can be used to analyze the allocation of this rather phloem-immobile nutrient in the shoot (distribution of ions via the xylem). The radioisotope ^{54}Mn may therefore serve as an indicator for the fluxes of water and solutes in the xylem from the roots to transpiring shoot parts (e.g. individual leaves). The aim of this work was to compare the effects of the light intensity on shoot development, root growth and root-to-shoot transfer of manganese in wheat genotypes grown in hydroponic culture in a controlled environment allowing permanent access to the various plant parts.

Materials and methods

Plant material and growth conditions

Grains of spring wheat (*Triticum aestivum* L. cv. CH Rubli, cv. Fiorina and cv. Greina) and winter wheat (*Triticum aestivum* L. cv. Arina) were separately germinated and grown in the dark for 3 days on wet paper in covered plastic bowls (experiment 1 with the four cultivars) or in the dark on wet gravel in covered plastic bowls (experiments 2 and 3 with only CH Rubli and Arina). The paper and the gravel were kept moist with de-ionized water. The temperature in the growth chamber was 18 °C during the night and 24 °C during the day. After day 3, the plants were exposed to light (100 µmol photons m^{-2} s^{-1}). The photoperiod was 14 h light and 10 h night. Half of the light tubes were warm white light tubes (Lumilux, Osram FQ 39 W/830 HO), the other half were cool white light tubes (Lumilux, Osram FQ 39 W/840 HO). The different light tubes were arranged in alternation. The maximum air temperature under low light intensity during the light period was 24.5 °C and under high light intensity 27.5 °C.

For experiment 1, six plants of the same cultivar were placed at day 5 on 1 l hydroponic brown plastic pots. The nutrient solution contained 5.8 mM KH_2PO_4, 3 mM $MgSO_4$, 1.3 mM $Ca(NO_3)_2$, 0.88 mM KNO_3, 64 µM Fe-EDDHA, 0.98 µM $MnCl_2$, 4.93 µM H_3BO_3, 0.17 µM $ZnSO_4$, 0.2 µM Na_2MoO_4, 0.05 µM $Ni(NO_3)_2$, 0.11 µM $CuSO_4$. The same nutrient solution was used for all experiments. All the pots were placed under low light intensity (100 µmol photons m^{-2} s^{-1}, measured on the top of the hydroponic pot with a Quantum Meter, Spectrum technologies, Inc.) for 1 day. The next day, one pot per cultivar was placed under the four different light intensities: 100, 200, 300 and 380 µmol photons m^{-2} s^{-1}. The nutrient solution was exchanged once per week.

For experiments 2 and 3, 4-day-old plants (CH Rubli and Arina) were transferred from the gravel to plastic cups (five plants per cup). The roots were washed with de-ionized water. These five plants in each plastic cup were then fed with 15 ml of radiolabeled nutrient solution for 24 h under low light intensity (100 µmol photons m^{-2} s^{-1}). The plants were labeled with the radionuclide ^{54}Mn (2.2 kBq, added to 260 ml nutrient solution). After 24 h the roots were washed three times using de-ionized water. The plants were placed on hydroponic brown plastic pots containing nutrient solution (1,000 ml per pot). One pot always contained only four plants of the same cultivar. Half of the pots containing the plants fed with the radionuclide were exposed to low light intensity (100 µmol photons m^{-2} s^{-1}), the other half to high light intensity (380 µmol photons m^{-2} s^{-1}). The nutrient solution was exchanged once per week. During the development of the plants the main shoot and the first tillers were labeled with thread in different colours.

Analyses

The plant height, the number of leaves on the main shoot and the number of tillers per plant were recorded once per week (for experiment 2 and 3) and after 3 weeks of growth in hydroponic pots (for experiment 1). The plant height was measured right from the top of the cover of the pot to the tip of the longest leaf. The values were averaged and the standard error was calculated ($n = 6$ for experiment 1, $n = 4$ for experiments 2 and 3).

The chlorophyll content was measured with a minolta chlorophyll meter, SPAD-502 (Minolta Camera CO., Ltd. Japan). The SPAD value served as an indicator for the amount of chlorophyll present in a particular leaf. Three measurements per leaf were taken to compare the chlorophyll content in the second leaf over a specific period. Then the averages of these three values were calculated. The values per leaf and treatment were averaged again and the standard error was calculated. The measurement was always taken in the middle of the leaves, with the window of the chlorophyll meter on the adaxial epidermis.

For the estimation of the transpiration under high and low light intensity, the remaining nutrient solution was measured weekly of all pots when the nutrient solution was changed as well as of the pots containing the plants that were dissected on the corresponding day.

On day 2, 7, 14 and 21 after labeling with the radionuclide (7, 12, 19 and 26 days after germination) four plants per cultivar and treatment were dissected into roots, scutellum, grain, coleoptile and oldest to youngest leaf of

the main shoot. All tillers were separated from the main shoot and counted together. All plant parts were air-dried in small plastic tubes and the radionuclide content was measured in the automatic gamma counter (1480 WizardTM 3'', Wallac Oy, Turku, Finland) during 10 min per plant part and expressed in % of total ^{54}Mn content in the plant. Pictures of the plants were taken just before the dissection.

The dry weight of all parts of the dissected plants was measured for day 7, 12 and 19 after the germination, to compare the differences between the high and low light treatments. The dry weight values for the different plant parts are shown for one set of plants (experiment 3, plants labeled with ^{54}Mn). These values were very similar to the other sets (experiment 2, data not shown). Comparing the dry matter and the radionuclide content of plant parts allows to distinguish the absence of ^{54}Mn because an organ was not yet present and the absence of ^{54}Mn because it was not transported into an existing organ.

Statistical analyses

For experiment 1, within each cultivar, the different light intensities were compared using a Tukey honest significant difference test (on a 95 % level) in R 2.10.1 (R Development Core Team 2009). For experiment 2 and 3, the data were analysed for significant differences between the two light intensity treatments by Student's *t* test.

Results

Wheat cultivars in hydroponic culture were exposed to 4 different light intensities (100, 200, 300 and 380 µmol photons m^{-2} s^{-1}). Arina, Greina and CH Rubli plants grown under the lowest light intensity were significantly higher than the plants grown under the three other light intensities (Fig. 1). Fiorina plants grown under 100 µmol photons m^{-2} s^{-1} were only significantly higher than the plants grown under the highest light intensity (380 µmol photons m^{-2} s^{-1}). Leaf number increased with increasing light intensity. The retardation of leaf production at the lowest light intensity was most pronounced for Fiorina. Taking together the responses of plant height and leaf expansion, Fiorina was affected in a different manner than the other varieties. The number of tillers increased with increasing light intensity, but this effect was less pronounced in Fiorina than in the other varieties. The strongest response of tiller formation to light intensity was detected in Arina and Greina.

Arina (winter wheat) and CH Rubli (spring wheat) were exposed to the lowest (100 µmol photons m^{-2} s^{-1}) and the highest light intensity (380 µmol photons m^{-2} s^{-1}) for more detailed studies including time courses. A significant difference in the plant height was observed already 13 days after germination (8 days after exposition to the different light treatments). For older plants (20 or 27 days after germination), these differences became more pronounced (Fig. 2a). The transpiration per plant was in both genotypes strongly affected by light intensity (Fig. 2c). The differences for the units of SPAD (indicator for chlorophyll

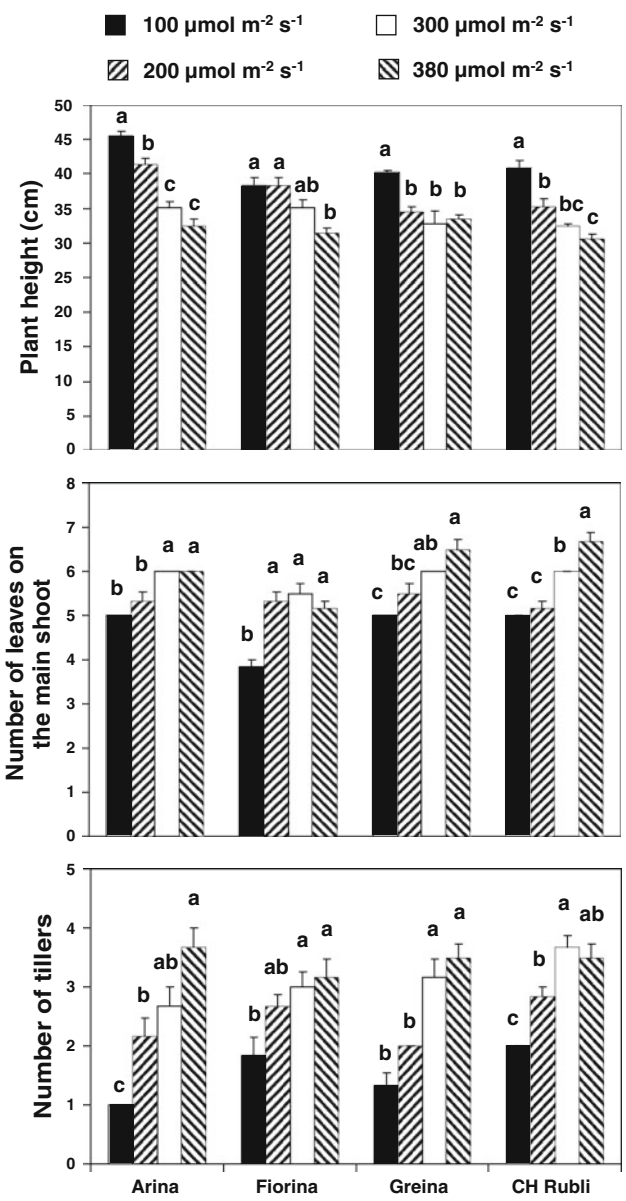

Fig. 1 Plant height, number of leaves on the main shoot and number of tillers per plant in winter wheat (Arina) and three spring wheat varieties (Fiorina, Greina and CH Rubli) exposed to different light intensities. The plants were measured after 3 weeks of hydroponic culture and they were 26 days old. Columns represent means + SE (n = 6). Different letters on the top of the *bars* indicate significant differences between various light intensities in the same variety at $P \leq 0.05$ level as determined by Tukey honest significant difference test

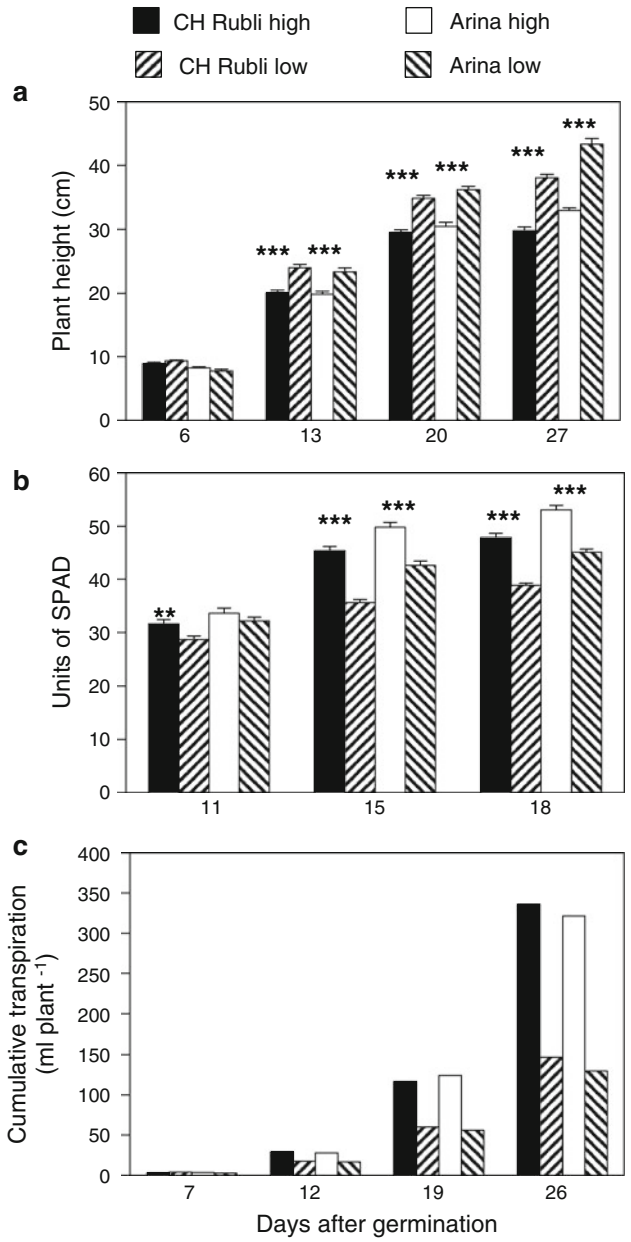

Fig. 2 Plant height (**a**), units of SPAD as an indicator for the chlorophyll content (**b**), and cumulative transpiration (**c**) for winter wheat Arina and spring wheat CH Rubli exposed to two different light intensities (high = 380 µmol photons m^{-2} s^{-1} and low = 100 µmol photons m^{-2} s^{-1}). Columns represent means + SE (n = 4). *Asterisks* indicate a statistically significant effect of the light intensity (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$)

content) were after 15 days around 20 % between high and low light intensity for both varieties (Fig. 2b). From Figs. 1 and 2 it becomes evident that shoot development is rapidly and considerably influenced by light intensity. The effects are documented photographically for two separate experiments in Fig. 3. The longer leaves and the smaller number of tillers under low light intensity are obvious. Furthermore, these pictures allow the comparison of the root systems of differently illuminated plants. The plants exposed to low light intensity had longer but less branched roots than those growing under high light intensity.

The dry matter accumulation in the various organs served as an indicator for root and shoot development (Fig. 4). The grain, the coleoptile and leaf 1 (oldest leaf) were in both genotypes not significantly affected, while the dry weight of the scutellum was influenced. Apparently the grain reserves were mobilized similarly under low and high light intensity. Strongest effects of light intensity were detected for the dry matter of tillers, youngest leaves and roots. The light effects were in general more rapidly detectable and more pronounced in CH Rubli than in Arina.

The radionuclide ^{54}Mn applied to the root system of 4-day-old plants was allocated differently in plants exposed to high and low light intensities (Fig. 5). The ^{54}Mn level in the roots decreased within 3 weeks to very low levels and the label appeared in shoot parts. Under high light intensity a considerable portion of ^{54}Mn accumulated in the tillers, while older leaves at the main shoot were the main destinations under low light intensity. Similar effects were observed in Arina and in CH Rubli. These results indicate a different allocation of root-borne ions via the xylem in the various shoot parts.

Discussion

A significant difference of the plant height was in our experiments already observed after 8 days under the different light intensities. Throughout the experiment this difference became more pronounced. This light effect is consistent with the findings reported by Repková et al. (2009) indicating that the length of barley leaves exposed to shaded environment were longer than in an environment with full irradiation. The increased final size can be explained by an increased leaf expansion rate and a longer duration of leaf expansion (Repková et al. 2009).

Hydroponic culture allowed the inspection of the root system throughout the experiment. It became evident that under high light more, but shorter roots were produced than under low light. Since nutrients were directly available for the plants in the liquid medium, root growth did not contribute to accessing nutrients in other regions as this is the case in soil. Therefore the different root growth was not controlled by nutrient gradients in the rooting zone. The irradiation of the shoots influenced root growth (number and length of roots) via shoot-root interactions. Nagel et al. (2006) suggested that a higher rate of sucrose export from the leaves to the roots under high light intensity may regulate in tobacco the development of the root system.

Fig. 3 Spring wheat CH Rubli and winter wheat Arina grown under two different light intensities (high = 380 µmol photons m^{-2} s^{-1} and low = 100 µmol photons m^{-2} s^{-1}). The plants were aged 19 days (*left picture*: plants from experiment 3; 14 days after exposition to the different light treatments) and 26 days (*right picture*: plants from experiment 2; 21 days after exposition to the different light treatments)

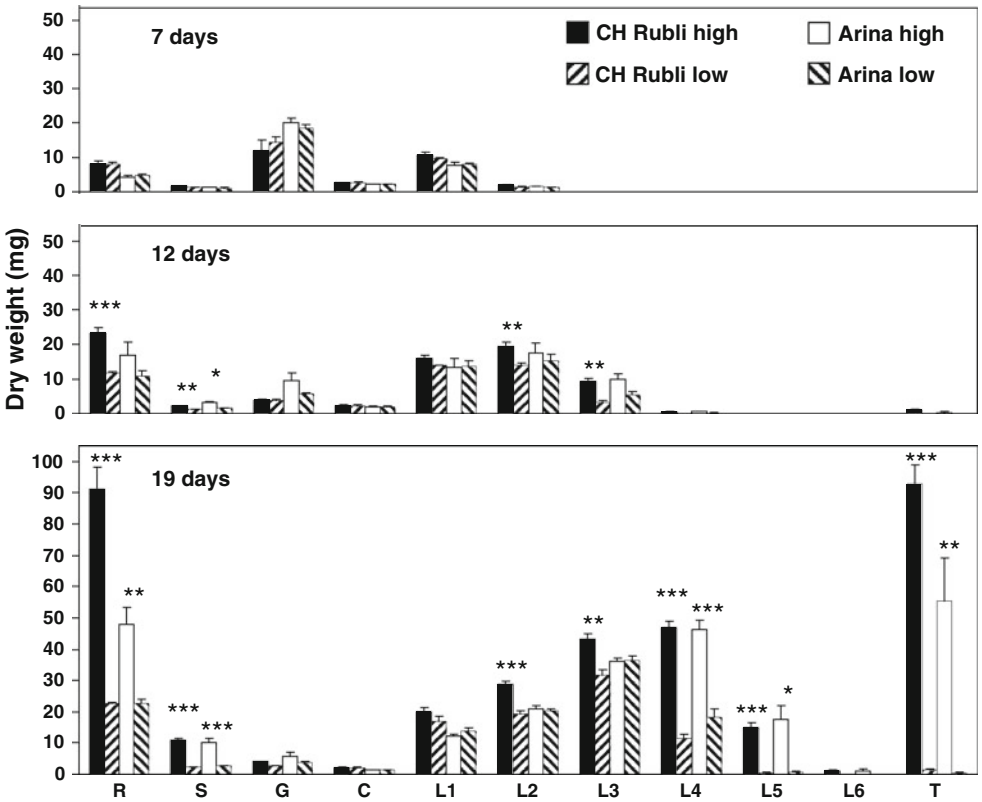

Fig. 4 Dry weight of plant parts of spring wheat CH Rubli and winter wheat Arina exposed to two different light intensities (high = 380 µmol photons m^{-2} s^{-1} and low = 100 µmol photons m^{-2} s^{-1}). The dry weight of plant parts is shown 7, 12 and 19 days after germination. The plants were dissected into roots (R), scutellum (S), grain (G), coleoptile (C), oldest leaf (L1) to youngest leaf (L6) of the main shoot and tillers (T). Columns represent means + SE (n = 4). *Asterisks* indicate a statistically significant effect of the light intensity (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$)

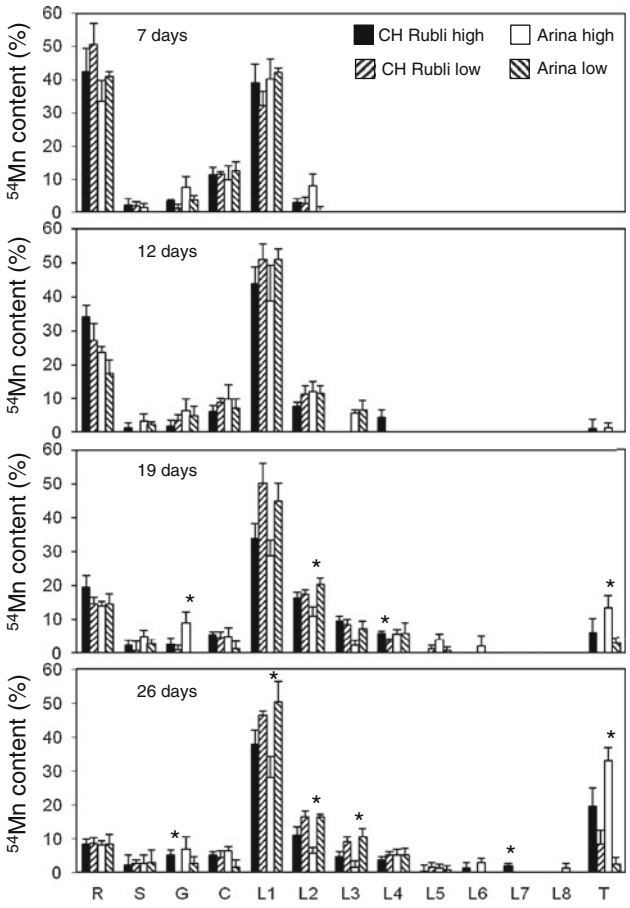

Fig. 5 Time course of ^{54}Mn in spring wheat CH Rubli and winter wheat Arina labeled at seedling stage (4 day-old plants). The plants were exposed to two different light intensities (high = 380 µmol photons m^{-2} s^{-1} and low = 100 µmol photons m^{-2} s^{-1}). They were collected 7, 12, 19 and 26 days after germination and dissected into roots (R), scutellum (S), grain (G), coleoptile (C), oldest leaf (L1) to youngest leaf (L8) of the main shoot and tillers (T). The ^{54}Mn content per plant part is shown in % of total ^{54}Mn content in the plant. Columns represent means + SE (n = 4). *Asterisks* indicate a statistically significant effect of the light intensity (*$P \leq 0.05$)

Besides the length of the main shoot, the number and the size of tillers were strongly influenced by light intensity in the two genotypes investigated in more detail. Although the number of tillers at low light intensity differed between varieties, more tillers were produced in all four genotypes at high light intensity. This effect was most pronounced in the winter wheat variety Arina. It must be borne in mind that besides the light quantity the spectral composition (Gautier et al. 1999; Evers et al. 2006) and the temperature regime may also affect the production of tillers (Friend 1965; Bos and Neuteboom 1998).

The allocation of the radionuclide ^{54}Mn via the xylem to the different shoot parts was comparable for the winter wheat Arina and the spring wheat CH Rubli. The content of this heavy metal decreased in the root system (labeled part of the plant) and increased initially in the first leaf indicating that this radionuclide was released from the roots into the xylem and moved via the transpiration stream into the photosynthetically active leaves. This is in agreement with the long-distance transport properties of ^{54}Mn in wheat reported previously (Page and Feller 2005; Riesen and Feller 2005). Between day 12 and day 26, the ^{54}Mn content in the roots decreased similarly under high and low light, but the distribution in the shoot was considerably different. Under low light, ^{54}Mn reached mainly older leaves of the main shoot. Under high light, ^{54}Mn was mainly directed to tillers and to some extent also to the uppermost leaves of the main shoot. A competition between the main shoot and the tillers for nutrients in barley was suggested by Kirby and Jones (1977). Since the release of ^{54}Mn from the roots was not or only slightly affected by the illumination and the transpiration rate of the whole shoot was increased after day 12 by more than 100 %, it became evident that the root-borne ^{54}Mn was distributed differently in the shoots. Although the roots were labeled with ^{54}Mn in an early phase when only the main shoot was visible, the allocation of this label was modified by newly emerging parts of the shoot under the higher light intensity.

The responses of winter wheat Arina and spring wheat CH Rubli to the two light treatments were similar. Although some responses were more pronounced in the winter wheat variety (number of tillers and allocation of Mn) and others in the spring wheat variety (dry matter accumulation in the various organs), a generalization of differences between winter and spring wheat varieties would be premature (only one winter and three spring wheat varieties considered). Indeed, there were some differences between the three spring wheat varieties Fiorina, Greina and CH Rubli with respect to some of the parameters checked.

In conclusion, light intensity strongly affects shoot development (especially tillering) and indirectly also the development of the root system (number and length of roots). As a consequence, root-borne solutes are distributed differently with the transpiration stream to the various shoot parts. Labeling with radioactive or stable isotopes may represent a suitable technique to identify the allocation of nutrients from the roots to the various shoot parts. A rather phloem-immobile label like ^{54}Mn allows the identification of the primary distribution with the transpiration stream in the shoots. A phloem-mobile label could allow in the future a deeper insight into light effects on nutrient redistribution within aerial parts depending on the source-sink network (Page and Feller 2005; Riesen and Feller 2005).

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