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REGULAR ARTICLE

# Magnesium applications to growth medium and foliage affect the starch distribution, increase the grain size and improve the seed germination in wheat

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**Abstract**
*Background and Aims* Magnesium (Mg) has diverse functions in plants and plays a critical role in carbohydrate partitioning between source and sink tissues. There is, however, limited information available about the effects of Mg deficiency on grain starch accumulation, yield formation and seed quality in terms of seed germination and seedling establishment in wheat.
*Methods* In a solution culture experiment, bread wheat (*Triticum aestivum*) was grown to maturity with low or adequate Mg under greenhouse conditions, and a post-anthesis foliar Mg application was tested on low-Mg plants. The effects of these Mg treatments on i) yield parameters, ii) distribution of starch among sink and source organs, iii) tissue concentrations of Mg and other minerals and iv) seed germination and seedling development were investigated.
*Results* Low Mg supply did not affect the vegetative biomass production; but substantially reduced the grain yield. Post-anthesis foliar Mg spray significantly minimized yield losses caused by Mg deficiency. Decreases in grain yield by Mg deficiency were due to decreases in individual seed weight rather than seed number per spike. Low Mg depressed the grain and root starch levels, while increasing the leaf starch. Foliar Mg spray largely reversed these effects of Mg deficiency. Seeds obtained from low-Mg plants exhibited severe impairments in germination and seedling establishment. These seed quality traits were also greatly improved by foliar Mg application to maternal plants.
*Conclusions* Magnesium deficiency reduces grain yield in wheat mainly by limiting the carbohydrate supply to developing seeds and thus by decreasing the seed weight. Since vegetative growth is far less affected than yield formation, Mg deficiency may remain latent until seed-filling. Therefore, foliar Mg application appears to be a promising tool to alleviate Mg deficiency during seed-filling and minimize its impact on yield and seed quality.

**Keywords** Foliar Spray · Grain Yield · Magnesium · Seed Germination · Starch · Wheat

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## Introduction

Magnesium (Mg) is an essential cationic macronutrient with structural and regulatory functions related to its interaction with nucleophilic ligands in plants (Shaul 2002; Cakmak and Kirkby 2008). It activates more enzymes than any other mineral nutrient (Epstein and Bloom 2005). As the central atom in the chlorophyll molecule and the activator of critical photosynthetic enzymes, Mg is a key element in photosynthesis (Wedding and Black 1988; Portis 1992; Marschner

2012). Magnesium is required for the synthesis and function of nucleic acids and adenosine triphosphate (ATP) (Sreedhara and Cowan 2002; Igamberdiev and Kleczkowski 2015). Up to 90 % of cytoplasmic ATP is complexed to $Mg^{2+}$ in Mg-sufficient plant cells (Yazaki et al. 1988).

Due to its large hydrated radius, $Mg^{2+}$ binds only weakly to negatively-charged soil particles, which makes it highly prone to leaching (Hermans et al. 2004; Cakmak and Kirkby 2008; Bose et al. 2011). Magnesium deficiency typically occurs in acidic and light-textured soils with low cation exchange capacities when Mg in the root zone is removed to deeper layers by leaching (Bose et al. 2011; Gransee and Fuhrs 2013). Another common cause of Mg deficiency in the field is ionic antagonism. Competing cations including $H^+$, $Al^{3+}$, $Ca^{2+}$, $K^+$ and $Na^+$ do not only displace $Mg^{2+}$ from the cation exchange sites and thus contribute to its leaching but also strongly inhibit its root uptake (Mengel and Kirkby 2001; Gransee and Fuhrs 2013). Also, the risk of Mg deficiency is increasing in intensive cropping systems where the Mg reserves in the root zone are being depleted as high-yielding varieties are grown continuously with heavy applications of nitrogen (N), phosphorus (P) and K fertilizers (Hermans et al. 2005; Cakmak and Yazici 2010).

Magnesium is critically involved in the phloem loading of sucrose and thus carbohydrate partitioning between source and sink tissues (Cakmak et al. 1994a, 1994b; Hermans et al. 2005). The proton-motive force generated by an $H^+$-pumping ATPase energizes $H^+$-sucrose symporters loading sucrose into sieve tube cells (Bush 1989; Hermans et al. 2005). About 2 mM $Mg^{2+}$ is needed for maximizing the activity of the $H^+$-pumping ATPase (Williams and Hall 1987). In Mg-deficient plants, carbohydrates start accumulating in source leaves before other physiological processes such as photosynthesis are affected by Mg deficiency (Laing et al. 2000; Hermans et al. 2004; Hermans and Verbruggen 2005). While excessive accumulation of carbohydrates enhance the production of reactive oxygen species (ROS) in chloroplasts of source tissues and limit photosynthesis by negative feedback effect, the sink organs including roots, seeds and tubers are deprived of carbohydrates (Cakmak and Kirkby 2008). Depending on the species and experimental conditions, impairments in carbohydrate partitioning within plants result in altered root-to-shoot ratios under Mg deficiency (Cakmak et al. 1994a, 1994b; McDonald et al. 1996; Hermans et al. 2005; Ding and Xu 2011; Mengutay et al. 2013).

In cereals, the yield components are the number of ears per plant, the number of grains per ear and the grain weight (Araus et al. 2008; Grzebisz 2013). With respect to yield formation, the life cycle of a crop plant grown for its fruits or seeds can be divided into 3 parts: foundation, construction and yield-formation (Sylvester-Bradley et al. 2002). After the vegetative establishment of a wheat plant is completed in the foundation period, the reproductive development starts in the construction period. The spikes are formed, and the potential number of grains per spike is set during this period, which ends at anthesis (Grzebisz 2013). The yield-formation period, also called the grain-filling period for cereals, is characterized by the development of caryopses from fertilized ovaries (Yang and Zhang 2006). The final grain weight of wheat is determined by the rate of assimilate transport during this period and the duration of grain-filling (Yang and Zhang 2006). Both the direct translocation of current assimilates and the redistribution of the reserve pool of assimilates contribute to grain-filling (Schnyder 1993; Gebbing et al. 1999). Starch is the most abundant component of cereals grains, and reduced starch content implies reduced grain weight (Hucl 1996; Wang et al. 2012). So, impairment of carbohydrate translocation to grains under Mg deficiency may affect the grain weight and thus both the grain yield and quality of wheat.

Magnesium is also an essential mineral for human health (de Baaij et al. 2015). In the second half of the 20th century, the Mg concentrations of conventionally grown fruits and vegetables decreased by 20–30 % on average (Worthington 2001). The Mg concentrations of cereal grains also declined significantly over the past decades while the grain yields increased (Cakmak 2013). According to Rosanoff (2013), up to two third of the population is possibly affected from low dietary intake of Mg, especially in well-developed countries. Enrichment of food crops with Mg to contribute to dietary Mg intake and well-being of human populations represents an important research topic and challenge in human nutrition (Cakmak 2015).

In the literature, there is very limited information about the impacts of Mg deficiency on carbohydrate translocation into seeds from source organs and on seed quality in terms of seed Mg and starch concentrations and seed vitality in wheat. It is also unknown how foliar Mg applications to maternal plants with suboptimal Mg levels affects i) grain concentrations of starch and Mg, and ii) seed germination capacity and seedling development in wheat. These issues were the main topics of the present study.

## Materials and methods

### Plant growth conditions and experimental procedure

The experiment was conducted in a computer-controlled, Venlo-type greenhouse with supplemental lighting at Sabanci University, Istanbul, Turkey (40°53′25″ N, 29°22′47″ E). During the experiment, the heating and evaporative cooling systems of the greenhouse kept the temperature at 24 ± 3 °C in the daytime and at 18 ± 3 °C at night.

Seeds of *Triticum aestivum* cv. Adana 99 were soaked in a saturated $CaSO_4$ solution for 30 min and then sown in perlite moistened with deionized water ($dH_2O$). After germinating for 6 days under greenhouse conditions, the seedlings were ready to be transferred to hydroponic pots. In each 5-L hydroponic pot made of black plastic, 4 wheat seedlings were placed. Throughout the experiment, the solutions in the pots were refreshed 3 times a week and constantly aerated. The nutrient solution was composed of the following components: 2 mM $Ca(NO_3)_2\ 4H_2O$, 0.2 mM $KH_2PO_4$, 0.85 mM $K_2SO_4$, 0.1 mM KCl, 100 μM Fe-EDTA, 1 μM $ZnSO_4\ 7H_2O$, 1 μM $MnSO_4\ H_2O$, 1 μM $H_3BO_3$, 0.2 μM $CuSO_4\ 5H_2O$ and 0.1 μM $(NH_4)_6Mo_7O_{24}\ 4H_2O$. As Mg source, $MgSO_4\ 7H_2O$ was added to the nutrient solution at two different levels: 50 μM for the low Mg treatment and 500 μM for the adequate Mg treatment. In addition to the low Mg and adequate Mg treatments, there was a low + foliar Mg treatment. For this treatment, plants were supplied with low Mg (50 μM) from the solution throughout the experiment, and starting at the end of anthesis (BBCH stage 69; 82 days after sowing), they were sprayed with 4 % (*w*/*v*) $MgSO_4.7H_2O$ mixed with 0.01 % Tween20 as surfactant once a week for 3 times. For each treatment, there were 5 replicate pots.

When all plants fully senesced 148 days after sowing, they were harvested in 5 fractions: roots, spikes, flag leaves, other leaves (all leaves except flag leaves) and stems. Roots were washed first in $dH_2O$, then in 1 mM $CaCl_2$, then 1 mM EDTA and finally again in $dH_2O$. All plant samples were put in paper bags, dried at 60 °C for 3 days, and then weighed at room temperature. The harvested spikes were threshed, and grains and husks were bagged separately.

### Mineral nutrient and starch determination

Dried plant samples were ground to fine powders by using an agate vibrating cup mill (Pulverisette 9; Fritsch GmbH; Germany).

For mineral determination, approximately 0.2 g from each ground sample was acid-digested with 2 ml of 30 % $H_2O_2$ and 5 ml of 65 % $HNO_3$ in a closed-vessel microwave system (MarsExpress; CEM Corp., Matthews, NC, USA). After the digestion, the total volume was brought to 20 ml with double-deionized water ($ddH_2O$) and the digests were filtered through ashless quantitative filter papers. The concentrations of Mg, P, K, Fe and Zn in these digests were determined by using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Vista-Pro Axial, Varian Pty Ltd., Mulgrave, Australia). To each set of 40 samples, 1 blank sample was added to check for contamination and 1 certified standard reference material obtained from the National Institute of Standards and Technology (Gaithersburg, MD, USA) was added to check for accuracy.

Grain N concentrations were measured with a LECO TruSpec C/N analyzer (LECO Corp., St. Joseph, MI, USA). The starch concentrations of ground grain, leaf, stem and root samples were measured by using a starch assay kit (Total Starch HK Assay Kit, Megazyme International, Ireland).

### Germination tests

Germination tests were conducted under greenhouse conditions in 3 different media: filter paper, perlite and soil. Seeds produced by the experimental plants grown with varying Mg supply as described above were used in the germination tests.

For the filter paper test, seeds were soaked in saturated $CaSO_4$ solution for half an hour and then placed between sheets of wet filter paper. This was a 3-replicate test, and 25 seeds were used for each replicate. The shoot lengths of all seedlings were measured when the seedlings were 5 days old, and the test was terminated.

For the test in perlite, seeds were soaked in saturated $CaSO_4$ solution for half an hour as in the case of the filter paper test, and then sown in moistened perlite.

There were 3 replicate containers for each type of seed and 150 seeds in each container. The shoot lengths of 30 random seedlings per container were measured when the seedlings were 8 days old, and the test was terminated.

For the soil test, seeds were germinated in soil that was transported from Ordu, Turkey. This sandy loam had the following properties: 0.52 % $CaCO_3$, pH 4.9 in $dH_2O$, 6.2 % organic matter. The $NH_4Ac$-extractable Mg concentration was 39 mg/kg. In this test with 5 pot replicates per treatment, 10 seeds were sown in each pot filled with 400 g soil fertilized with 100 mg/kg N in the form of $Ca(NO_3)_2.4H_2O$ and 100 mg/kg P in the form of $KH_2PO_4$. The shoot lengths of all seedlings were measured when the seedlings were 6 days old, and the test was terminated.

### Definitions and calculations

In this manuscript, the term "husk" refers to all vegetative tissues of the spike, the term "shoot" refers to all above-ground parts of the plant including the grains, and the term "straw" refers to all vegetative tissues (stems, leaves and husk) of the shoot. Mineral contents of vegetative tissues were calculated by multiplying their mineral concentrations with their dry weights. Grain mineral and grain starch yields per plant were calculated by multiplying grain mineral and grain starch concentrations with grain yield per plant. Starch content per grain equals grain starch concentration times thousand grain weight (TGW) divided by 1000.

### Statistical analysis

Statistical analysis of the data was conducted by using JMP (12.0.1) (SAS Institute Inc., Cary, NC, USA). The significance of treatment effects was evaluated by analysis of variance (ANOVA). Then, Tukey's honestly significant difference (HSD) test ($p < 0.05$) was used as a post-hoc test to determine significant differences between means.

## Results

Low Mg application resulted in severely chlorotic wheat plants (Fig. 1). When compared to wheat plants grown with adequate Mg, these Mg-deficient plants senesced earlier. Post-anthesis foliar Mg application largely corrected these deficiency symptoms and resulted in about 50 % increase in the leaf SPAD values of low-Mg plants but it could not fully substitute for adequate Mg supply from the nutrient solution under given experimental conditions (data not shown). Notably, varied Mg applications to plants did not have any effect on the size of wheat plants (Fig. 1).

In parallel with visual observations, Mg applications had mostly negligible effects of the dry weights of vegetative tissues at maturity (Table 1). While Mg applications did not affect the husk, stem and total straw dry weights of mature plants, increasing Mg supply significantly reduced the dry weights of leaves. Roots exhibited a statistically non-significant decrease in biomass upon increasing Mg supply.

In contrast to vegetative biomass, the grain yield was significantly enhanced by Mg applications (Table 2). When compared to low Mg, foliar Mg increased the grain yield by 50 % and adequate Mg by nearly 100 %. Foliar Mg application did not result in a significant increase in the total shoot (straw + grain) dry weight of the low-Mg plants while adequate Mg supply significantly improved the shoot dry weight. The number of spikes per plant and the number of grains per spike were not significantly affected by Mg treatments (Table 2). The low Mg treatment was, however, associated with a sharp decline in the thousand grain weight (TGW). With foliar Mg application, the TGW of low-Mg plants almost reached the TGW of adequate-Mg plants.

In agreement with the TGW data, grains obtained from the low-Mg plants appeared distinctly smaller, thin and deformed (Fig. 2). Foliar Mg application clearly improved the grain size and minimized shriveling. The largest grains with the best shapes were produced by plants supplied with adequate Mg from the growth medium.

Mature wheat plants grown with low Mg had explicitly lower Mg concentrations and contents in all their vegetative tissues when compared to those grown with adequate Mg (Table 3). At adequate Mg supply, leaves had by far the highest Mg concentration and content among all the vegetative tissues. Leaf Mg concentrations of wheat plants at maturity declined by nearly 90 % when plants were cultivated with low Mg.

Under low-Mg conditions, the grain Mg concentration fell below 50 % of the concentration obtained under adequate-Mg conditions (Table 4A). A significant improvement in the grain Mg concentration was achieved by foliar Mg application. The N and P concentrations of

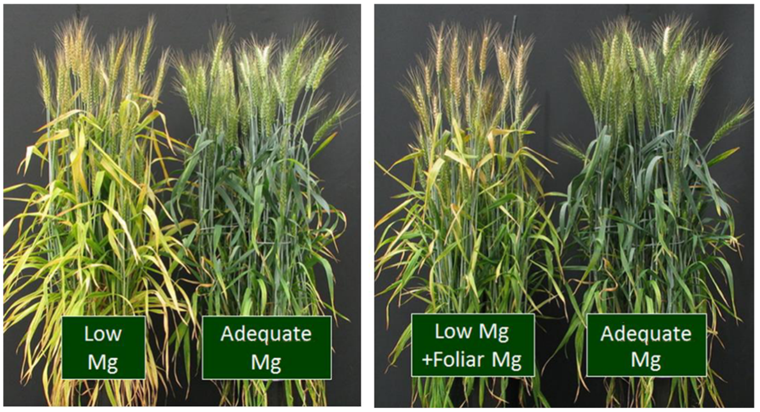


**Fig. 1** 115-day-old bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low Mg supply (50 μM $MgSO_4$•$7H_2O$), low Mg supply + foliar Mg spray (4 % MgSO4•$7H_2O$) or adequate Mg supply (500 μM $MgSO_4$•$7H_2O$) under greenhouse conditions

grains did not show a clear response to Mg applications (Table 4A). Low Mg supply without foliar Mg supplementation was associated with enhanced grain K concentrations.

The starch concentrations measured in the flag and other leaves were highest for low Mg, lower for low + foliar Mg and lowest for adequate Mg (Table 5A). Also, the leaf starch contents decreased significantly when Mg supply increased (Table 5B). In contrast, the root starch concentrations and contents were lowest for the low-Mg plants not treated with foliar Mg. (Table 5). The starch concentration and content of stem tissue was unaffected by the Mg treatments.

Compared to low Mg, adequate Mg enhanced the grain starch concentration by 10 %, the average starch content per grain by 85 % and the grain starch yield per plant by over 100 % (Table 6). Foliar Mg application to low-Mg plants provided the same significant improvements of grain starch concentration and content but was significantly less effective than adequate Mg in enhancing the grain starch yield per plant.

When seeds produced by the experimental plants were germinated in different media including filter paper, perlite and soil, it was observed that seed germination and seedling vigor were markedly affected by the Mg applications to maternal plants (Fig. 3). Compared to germinating seeds of the low + foliar-Mg plants and adequate-Mg plants, seeds of the low-Mg plants showed impaired shoot and root growth (Fig. 3 & Table 7). In all germination environments, the highest shoot lengths of seedlings were recorded for the seeds of the adequate-Mg plants (Table 7).

## Discussion

In wheat, Mg deficiency typically results in light green beading along the veins of fully extended leaves, which progresses into interveinal chlorosis as deficiency becomes more severe (Scott and Robson 1991; Craighead and Martin 2001; Mengutay et al. 2013). Remobilization of Mg from mature leaves causes early

**Table 1** Dry weights of vegetative tissues of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4$·7H2O) or adequate (500 μM) Mg under greenhouse conditions

| Dry Weight (g.plant$^{-1}$) | | | | | | |
|---|---|---|---|---|---|---|
| Mg Supply | Husk | Flag Leaves | Other Leaves | Stem | Root | Straw |
| Low | 11.4 a | 2.4 a | 5.7 a | 16 a | 3.0 a | 36 a |
| Low + Foliar | 9.1 a | 2.1 b | 5.1 ab | 15 a | 2.7 a | 31 a |
| Adequate | 11.8 a | 2.1 b | 4.3 b | 17 a | 2.5 a | 34 a |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

**Table 2** Grain yield, shoot dry weight (DW) including all above-ground parts, thousand-grain weight (TGW), number of spikes per plant and number of grains per spike of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4 \cdot 7H2O$) or adequate (500 μM) Mg under greenhouse conditions

| Mg Supply | Grain Yield (g.plant$^{-1}$) | Shoot DW (g.plant$^{-1}$) | Number of Spikes (plant$^{-1}$) | Number of Grains (spike$^{-1}$) | TGW (g) |
|---|---|---|---|---|---|
| Low | 19 a | 55 a | 25 a | 31 a | 24 a |
| Low + Foliar | 28 b | 60 a | 21 a | 35 a | 39 b |
| Adequate | 36 c | 71 b | 23 a | 38 a | 41 b |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

senescence (Marschner 2012). In this study, low-Mg plants appeared senescent while adequate-Mg plants were still dark green (Fig. 1). The increase in the leaf chlorophyll concentration upon foliar Mg application to low-Mg plants indicates that foliar Mg was effective in increasing the longevity of leaves (Jezek et al. 2015).

The apparent size of the plants at grain-filling (Fig. 1) and the straw dry weight at maturity (Table 1) were unaffected by Mg supply, implying that even the low-Mg treatment in this study provided sufficient Mg to the plants to maintain vegetative growth. It is important to note that the plants in this study were not limited by any other nutrient deficiency as there was an ample supply of all mineral nutrients except Mg in the nutrient solution. In previous hydroponic pot studies on Mg deficiency in wheat, significant declines in vegetative biomass production were reported but in those studies, the Mg supply per plant was below the low-Mg level in this study (Scott and Robson 1991; Mengutay et al. 2013). Here, the purpose was to mimic a latent Mg deficiency which becomes more severe at later stages of the development as the Mg demand increases with increasing sink activity. It is important to note that the results presented in Table 1 are the dry weights of vegetative tissues after senescence. The significant decreases in leaf dry weights of senesced plants upon improved Mg supply suggest enhanced carbon remobilization from source to sink tissues (Table 1).

The yield responses to Mg supply were impressive (Table 2). Taken together, the dry weight and yield data in Tables 1 and 2 indicate that provided an optimum supply of other minerals including N and P, a low Mg supply which does not impair the vegetative growth of wheat at all may reduce its grain yield by 50 %. Moreover, here, the Mg supply from the solution was constant and not discontinued during grain-filling. In practice, wheat is widely grown as a rain-fed crop in Mediterranean-type or semi-arid climates, and the top soil dries out toward the end of the growing season (Elias and Manthey 2005; Distelfeld et al. 2007), which limits mass flow-driven uptake of minerals including Mg (Lambers et al. 2008). Under such conditions, the yield depression caused by a previously latent Mg deficiency may be even more dramatic. That post-anthesis

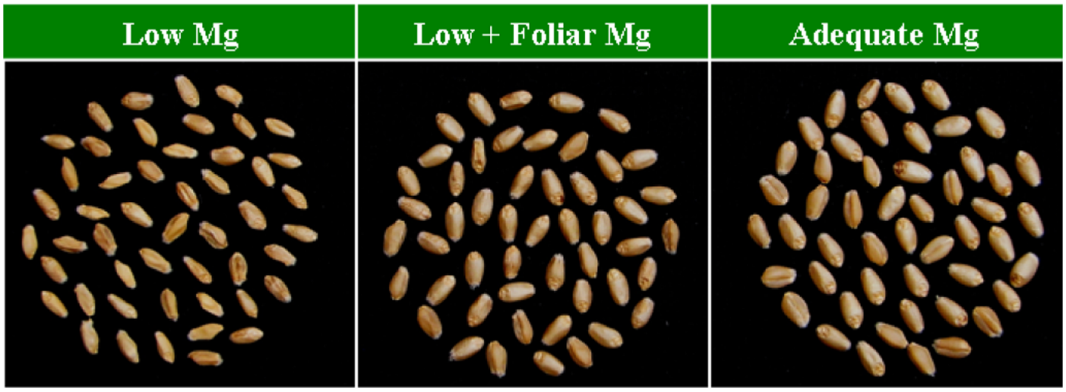


**Fig. 2** Mature seeds of bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with i) low Mg supply (50 μM $MgSO_4 \cdot 7H_2O$), ii) low Mg supply + foliar Mg spray (4 % $MgSO4 \cdot 7H_2O$) or iii) adequate Mg supply (500 μM $MgSO_4 \cdot 7H_2O$) under greenhouse conditions

**Table 3** (**A**) Mg concentrations and (**B**) Mg contents of vegetative tissues of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM) or adequate (500 μM) Mg under greenhouse conditions

| Mg Supply | Husk | Flag Leaves | Other Leaves | Stem | Root |
|---|---|---|---|---|---|
| (A) | Mg Concentration (mg.kg$^{-1}$) | | | | |
| Low | 226 a | 299 a | 336 a | 94 a | 231 a |
| Adequate | 647 b | 2308 b | 3212 b | 356 b | 391 b |
| (B) | Mg Content (mg.plant$^{-1}$) | | | | |
| Low | 2.59 a | 0.71 a | 1.9 a | 1.53 a | 0.69 a |
| Adequate | 7.63 b | 4.80 b | 13.8 b | 6.12 b | 0.98 a |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

Vegetative tissues of plants supplied with low + foliar Mg were not analyzed for Mg because of surface contamination

foliar Mg application could significantly reduce yield losses due to Mg deficiency (Table 2) is a very important finding of this study because minerals applied to soil at grain-filling stage may not be efficiently taken up when soil and environmental conditions are not favorable (Gooding and Davies 1992; Fageria et al. 2009; Jezek et al. 2015). Foliar Mg application was also shown to be effective in correcting Mg deficiency in other crops (Barlog and Grzebisz 2001; Vrataric et al. 2006; Neuhaus et al. 2014; Jezek et al. 2015).

Grain yield per plant can be largely expressed as the product of following factors: number of spikes per plant, number of grains per spike and single grain weight (TGW/1000) (Araus et al. 2008; Grzebisz 2013). Hydroponically-grown wheat plants typically produce a very high number of tillers under hydroponic conditions and have a very high yield potential (Kutman et al. 2012). It is noteworthy that each plant produced more than 20 spikes in this study, irrespective of Mg supply (Table 2). While the number of grains per spike tended to increase in response to higher Mg supply, suggesting a slight impairment of grain setting by Mg deficiency, it is evident that the impact of Mg supply on grain yield was mainly a result of its impact on TGW (Table 2; Fig. 2). In the literature, increases in TGW upon Mg fertilization were reported for barley (Beringer and Forster 1981) and wheat (Al'Shevskii and Derebon 1982). The TGW is a yield component that heavily depends on carbohydrate supply during grain filling (Grzebisz 2013). So, the effect of Mg supply on the TGW can be explained by the disruption of phloem loading and thus carbohydrate translocation from source

**Table 4** (**A**) Grain mineral concentrations and (**B**) grain mineral yields of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4 \cdot 7H2O$) or adequate (500 μM) Mg under greenhouse conditions

| Mg Supply | Mg (%) | N (%) | P (%) | K (%) |
|---|---|---|---|---|
| (A) | Grain Mineral Concentrations | | | |
| Low | 0.06 a | 2.98 a | 0.48 ab | 0.69 a |
| Low + Foliar | 0.08 b | 2.77 b | 0.46 a | 0.53 b |
| Adequate | 0.14 c | 2.93 ab | 0.51 b | 0.54 b |
| (B) | Grain Mineral Yields (mg.plant$^{-1}$) | | | |
| Low | 11 a | 560 a | 90 a | 129 a |
| Low + Foliar | 22 b | 783 b | 131 b | 149 a |
| Adequate | 51 c | 1038 c | 182 c | 191 b |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

**Table 5** (**A**) Starch concentrations and (**B**) starch contents of vegetative tissues of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4 \cdot 7H2O$) or adequate (500 μM) Mg under greenhouse conditions

| Mg Supply | Flag Leaves | Other Leaves | Stem | Root |
|---|---|---|---|---|
| (A) | Starch Concentration (mg.g$^{-1}$) | | | |
| Low | 3.3 a | 3.6 a | 1.2 a | 1.0 a |
| Low + Foliar | 2.8 ab | 2.5 b | 1.1 a | 1.7 b |
| Adequate | 2.1 b | 2.1 b | 1.2 a | 1.7 b |
| (B) | Starch Content (mg.plant$^{-1}$) | | | |
| Low | 8.0 a | 20.6 a | 19 a | 2.9 a |
| Low + Foliar | 5.8 b | 12.8 b | 16 a | 4.5 a |
| Adequate | 4.3 b | 9.3 b | 21 a | 4.1 a |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

**Table 6** Grain starch concentration, starch content and starch yield of mature (148-day-old) bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4 \cdot 7H2O$) or adequate (500 μM) Mg under greenhouse conditions

| Grain Starch | | | |
|---|---|---|---|
| Mg Supply | Concentration ($mg.g^{-1}$) | Content ($mg.grain^{-1}$) | Yield ($g.plant^{-1}$) |
| Low | 520 a | 12.6 a | 9.8 a |
| Low + Foliar | 575 b | 22.4 b | 16.3 b |
| Adequate | 575 b | 23.6 b | 20.4 c |

Values are means of five independent replicates. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

**Table 7** Shoot lengths of seedlings grown in different media (filter paper for 5 days; perlite for 8 days; soil for 6 days) from seeds of bread wheat (*Triticum aestivum* cv. Adana99) plants cultivated hydroponically with low (50 μM), low + foliar (50 μM + 4 % $MgSO_4 \cdot 7H2O$) or adequate (500 μM) Mg under greenhouse conditions

| Shoot Length of Seedlings (cm) | | | |
|---|---|---|---|
| Mg Supply* | Filter Paper | Perlite | Soil |
| Low | 0.61 a | 5.6 a | 3.8 a |
| Low + Foliar | 0.82 b | 6.8 b | 4.7 b |
| Adequate | 0.96 c | 7.0 b | 6.0 c |

Values are means of 3 replicates for filter paper, 3 replicates for perlite and 5 replicates for soil. Different letters indicate significant differences between means according to one-way ANOVA and Tukey's HSD test ($p \leq 0.05$)

*Mg supply to maternal plants

tissues to developing grains by Mg deficiency (Cakmak et al. 1994b; Hermans et al. 2005). The TGW is also considered an important technological quality parameter because the milling efficiency depends on the grain size (Greffeuille et al. 2006; Gerendás and Führs 2013).

The critical leaf concentration for Mg deficiency is about 1000–1100 mg/kg in wheat (Jones et al. 1991; Scott and Robson 1991; Reuter and Robinson 1997). In this study, the leaf Mg concentrations of the adequate-Mg plants were 2–3 times higher than this critical level whereas those of the low-Mg plants were only about 1/3 of it at maturity (Table 3). As Mg is remobilized from source tissues during senescence (White and Broadley 2008), it is safe to assume that the Mg concentrations of vegetative tissues were higher than those reported in Table 3 before senescence. Under both low- and adequate-Mg conditions, 60 % of the total shoot Mg was allocated to grains at maturity (Tables 2 and 3).

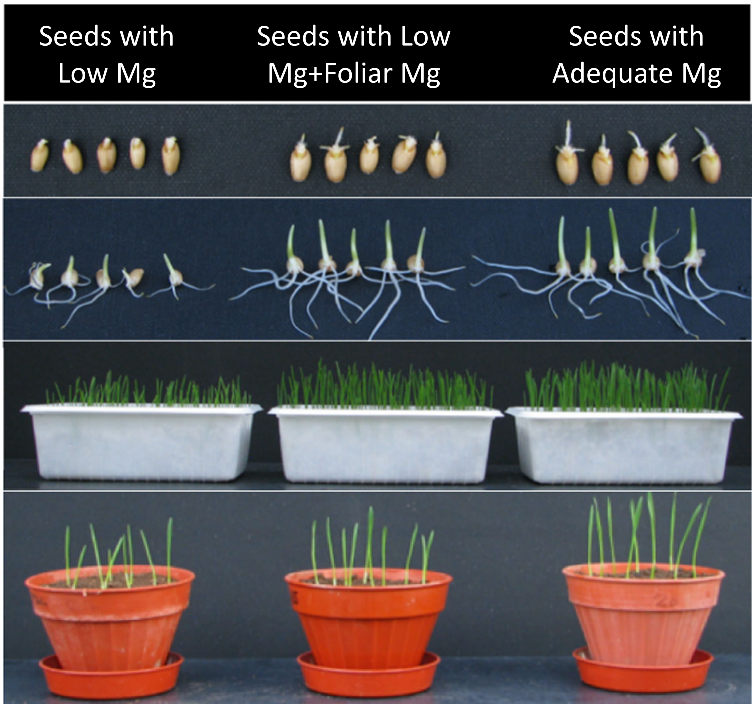


**Fig. 3** Seedlings obtained from seeds of bread wheat (*Triticum aestivum* cv. Adana99) plants grown hydroponically with i) low Mg supply (50 μM $MgSO_4 \bullet 7H_2O$), ii) low Mg supply + foliar Mg spray (4 % $MgSO4 \bullet 7H_2O$) or iii) adequate Mg supply (500 μM $MgSO_4 \bullet 7H_2O$) under greenhouse conditions. (**a**) 3-day-old seedlings grown in filter paper; (**b**) 5-day-old seedlings grown in filter paper; (**c**) 8-day-old seedlings grown in perlite; (**d**) 6-day-old seedlings grown in soil

Foliar Mg application to the low-Mg plants was not as effective as adequate Mg supply in enhancing the grain Mg concentration (Table 3), which is important for the nutritional quality of wheat grain and human nutrition.

Both the uptake and the assimilation of N are impaired under Mg-deficient conditions (Ding et al. 2006; Grzebisz 2013). Magnesium deficiency was also reported to depress the phloem export of amino acids (Cakmak et al. 1994b; Ruan et al. 2012). In this study, the lack of a clear response of the grain N concentration to Mg supply (Table 4A) may be attributed to dilution due to significant yield improvement by Mg. The grain N yield, on the other hand, shows clearly that higher Mg supply enhanced the N use (Table 4B). The well-documented antagonistic interaction between K and Mg (Zengin et al. 2008; Cai et al. 2012) was also observed in this experiment. Accordingly, the grain K concentration increased significantly at low Mg supply (Table 4A).

The typical starch concentration of whole grains of American and Canadian bread wheat varieties grown under field conditions ranges from 63 to 72 % (Lineback and Rasper 1988; Hucl 1996). In this solution culture study, the grain starch concentrations of the adequate-Mg plants were slightly lower than this range, which might be a varietal effect or caused by the experimental conditions (Table 6). Here, the important finding is that the grain starch concentration was depressed significantly by Mg deficiency and enhanced by post-anthesis foliar Mg treatment to the level measured at adequate Mg supply. The average starch content per grain and the starch yield per plant show the impact of Mg on grain starch accumulation even clearer. In agreement with impaired source-to-sink translocation of carbohydrates under Mg deficiency (Cakmak et al. 1994b; Hermans and Verbruggen 2005), the starch concentrations and contents of leaves increased whereas those of roots decreased significantly at low Mg supply (Table 5). By using the same wheat cultivar used in the present study, Mengutay et al. (2013) showed that the source leaves of Mg-deficient plants accumulated by about 4-fold more soluble carbohydrates than those of Mg-adequate plants whereas the sink leaves of Mg-deficient plants were poor in soluble carbohydrates. Accumulation of carbohydrates in source leaves under Mg deficiency was also reported for other crops (Cakmak et al. 1994b; Hermans et al. 2004; Hermans and Verbruggen 2005; Mengutay et al. 2013).

The importance of mineral nutrition and seed mineral reserves for the seed quality is well documented in the literature (Welch 1999; Cakmak 2008). Nutrient-rich seeds can improve crop growth and yield (Grewal and Graham 1997; Cakmak 2008; Kutman et al. 2013) whereas critical mineral deficiencies can have devastating effects on seed viability, germination and seedling vigor (Brown et al. 1987; Longnecker et al. 1996; Rerkasem et al. 1997). Most of these studies focused on micronutrients. The results presented here in Fig. 3 and Table 7 demonstrate that grains produced by Mg-deficient maternal plants have low seed quality as they show diminished vigor during germination and early seedling growth. To our knowledge, this is the first report demonstrating the specific effect of seed Mg on germination and seedling establishment. This critical finding may be explained by the adverse effects of Mg deficiency on the grain size (Fig. 2; Table 2) and starch content (Table 6). Germination and seedling emergence largely depend on seed reserves such as starch (Douglass et al. 1993; Wang et al. 2011), and accordingly, a clear correlation between seed size and seedling vigor was shown for durum wheat (*Triticum durum*) (Royo et al. 2006). Also, during germination, ATP must be rapidly synthesized and utilized (Perl 1986; Weitbrecht et al. 2011). In a previous study, a good correlation was found between ATP concentration and germination capacity of seeds (Siegenthaler and Douet-Orhant 1994). Since Mg is required for the synthesis and function of ATP (Boyer 1997; Marschner 2012; Igamberdiev and Kleczkowski 2015), inadequate levels of Mg in the seed may also impair germination by affecting the pool and physiological activity of ATP. Adequate levels of Mg might be also important in sugar transport in germinating seeds and developing seedlings. In germinating seeds, there is intensive sucrose transportation from scutellum into actively developing sink tissues of roots and shoots to maintain germination (Aoki et al. 2006; Scofield et al. 2007) and as in leaves, sufficient amount of Mg is likely required for the translocation of sugars into the sink tissues of germinating seeds.

From the results of this study, it can be concluded that Mg deficiency affects wheat yield mainly by limiting the carbohydrate supply to developing seed and thus by decreasing the seed size (weight) rather than the number of grains per spike. It was very obvious that Mg deficiency affects the yield formation of wheat more than its vegetative growth. The nutritional quality of wheat grain is also impaired by Mg deficiency as the grain Mg concentrations are reduced. In addition, the seed quality of wheat in terms of germination and seedling establishment is substantially impaired by Mg deficiency as the seeds produced by Mg-deficient maternal plants are associated with poor germination and seedling vigor. Since vegetative biomass production of wheat is far less affected than grain yield formation if at all, Mg deficiency may remain latent until grain-filling. Foliar Mg application is, therefore, a promising tool to alleviate Mg deficiency during seed-filling and minimize its impact on both yield and seed quality parameters.

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