Effect of the potassium and magnesium nutrition on potato (*Solanum tuberosum* L.) tuber quality and plant development

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Mirjam Thekla Koch
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1. Referentin: Prof. Dr. Elke Pawelzik

2. Referent: Prof. Dr. Klaus Dittert

3. Referent: Prof. Dr. Johannes Isselstein

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„Das letzte Ziel aller wissenschaftlichen Erkenntnis besteht darin, das größtmögliche Tatsachengebiet aus der kleinstmöglichen Anzahl von Axiomen und Hypothesen zu erhellen.“

Albert Einstein

Contents

Abbreviations

ADP, adenosine diphosphate

Al, aluminum

ANOVA, analyses of variances

ATP, adenosine triphosphate

Bp, base pairs

C, carbon

Ca, calcium

Ct, cycle threshold

Ctr, control

DAP, days after planting

DM, dry matter

DS, dry substance

DW, dry weight

E, primer efficiency

F, fertilization treatment

f, foliar application

FW, fresh weight

G6P-DH, glucose-6-phosphate dehydrogenase

HATS, high affinity transport system

HEPES, hydroxyethylpiperazine-ethanesulfonic acid

HK, hexokinase

HPLC, high-performance liquid chromatography

ICP-OES, inductively coupled plasma optical emission spectrometry

INV, invertase

IPNI, International Plant Nutrition Institute

IW, the initial weight

K, potassium

LAI, leaf area index

LATS, low affinity transport system

Mg, magnesium

Mn, manganese

N, nitrogen

NADP, nicotinamide adenine dinucleotide phosphate

NH_4^+, ammonium

NO_3^-, nitrate

Ns, not significant

OD, optical density

P, phosphorus

PGI, phosphoglucose isomerase

PPO, polyphenol oxidases

qRT-PCR, quantitative real-time polymerase chain reaction

rpm, rotations per minute

RuBP, ribulose-1,5-bisphosphate

RuBisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase

S, sulphur

SM, supplemental material

St, *Solanum tuberosum*

SUT, sucrose transporter

Chapter 1

General introduction

General introduction

Origin and history of potato

Potatoes were first cultivated by the Inca people in the Andes mountains in ancient time (Lee 2006). They are supposed to have been introduced from their origin South-America to Europe in the 1570s. The first records can be assigned to Spain from where it was disseminated to Italy, England and finally to Germany in 1600 (Brown 1993). The nowadays cultivated potato is classified as *Solanum tuberosum* L. consisting of seven subspecies of which the subspecies ssp. *tuberosum* has been introduced to Europe (Hawkes 1956; Hawkes 1990). However, there are high controversies about the number of existing subspecies (Huamán and Spooner 2002). Besides, there are still around 200 wild species distributed from the southwestern Unites States to Argentina and Chile (Hawkes 1990; Spooner and Hijmans 2001), comprising further desirable traits and a high potential for progress in breeding, especially with respect to resistances against pests or diseases (Spooner and Salas 2006). The potato belongs to the nightshade family (*Solanaceae)*, which are known to have poisonous properties, why they were regarded in Europe a quit long time with great suspicion. People awarded it a potential to cause leprosy or to have narcotic properties (Brown 1993; Lee 2006). Hence, the potential of potato as food crop was underestimated and unexploited for years and it was more considered as a botanic novelty (Brown 1993). The potential of potato as a food crop was first discovered in Europe in Ireland at the end of the 17th century. Probably a suitable climate and appropriate soils on the one hand and societal and economic reasons based on an immense growth of the Irish population on the other hand led to an increase of the importance of potato as a food crop (Bradshaw and Ramsay 2009). Today potatoes are grown in more than 100 countries and it is propagated from latitudes 65° N to 50° S and at altitudes from sea level to 4000m (Hijmans 2001).

Potatoes in Germany – in the past and today

In Germany the potato mainly served as animal feed until an economical cultivation started in the 70s and 80s of the 18th century (Schick and Klinkowski 1962). In the following 100 years the potato production and consumption experienced first a progressing growth followed by a sudden decrease which is persistent until today (Burton 1983). Since the 18th century the potato yield recorded a steady increase what mainly can be referred to breeding progress, the introduction of certified seed use, inorganic fertilizers and plant protection agents (Evans and Fischer 1999; Walker et al. 1999). While the harvested amount of potatoes in Germany accounted 33 million tons in 1964, in 2014 it decreased more than twice to 11 million tons. Contrary to this, the yield accounted about 20 t/ha in 1964 and increased

more than twice to 47 t/ha until 2014 (FAO 2017). So while there was still an increase in the potato´s yield potential in the last 50-60 years, the demand and consumption of potato heavily decreased. There are assumptions about a distinct relation between the consumption of potatoes and the people´s income. While under low income levels the contribution of potatoes to the energy intake of the diet is much higher it severely drops down with rising income level (Burton 1983; Walker et al. 1999). Besides, in developed nations there has been a clear change in dietary habits. 50 years ago, people spent much more time on preparation of food and not every kind of food, for instance tropical fruits or vegetables, were available all year around. Today pre-cut vegetables or complete prepared meals are available everywhere (Regmi 2001). With respect to potatoes, the consumption of fresh potatoes has declined while the demand for processed potato products like chips has increased (Camire et al. 2009).

Nutritional aspects of potato

Nowadays, potatoes have sometimes a poor reputation as they have a high content of rapidly digestible starch why they can be classified as a high-glycemic-index food. Long-term and high consumption of food with an high glycemic index might increase the risk of diet related disorders such as cardiovascular disease and type-2 diabetes (Kakoschke et al. 2014). Furthermore, there has been a rising interest in low-carbohydrate diets with respect to the intention of weight loss in the last years (Last and Wilson 2006) what likely lowered the appeal of potato consumption (McGregor 2007). Besides, fried potatoes and potato chips might have a carcinogenic potential due to potentially high concentrations of acrylamide which can be found in starch-containing foods that have been processed under high temperatures (Pelucchi et al. 2003). Nonetheless, potatoes combine several advantageous nutritional properties. The tubers are rich in vitamin C and are a good source for several B vitamins and minerals like potassium, magnesium and iron (Andre et al. 2014; Camire et al. 2009). Moreover, tubers are low in fat and offer protein with an excellent biological value of 90-100 (Andre et al. 2014). Especially colored potato cultivars additionally contain a number of phytochemicals like phenolics, flavonoids, or carotenoids which are supposed to be health-promoting (Ezekiel et al. 2013). However, the health benefit of potato consumption may heavily depend on the preparation method (Tian et al. 2016).

Usages and quality determinants of potatoes

As indicated previously, there are various usages of potatoes. First, there is the fresh potato market (McGregor 2007), which, however, lost in importance in developed countries (Kirkman 2007). Besides, potatoes are processed to mainly

French fries or potato chips (Keijbets 2008) or they are used for starch production which is utilized in the food or textile industry (Grommers and van der Krogt 2009; Jobling et al. 2002). Finally, there is a seed potato market and an usage as animal feed - but today only to a very small extend (Lange and Kawchuk 2014). The majority of potato production in Germany can be assigned to potatoes for fresh consumption and processed potato products, although likewise in Germany there was a sharp decline for the consumption of fresh potatoes (Lange and Kawchuk 2014). Each usage has special quality requirements although there might be some conformability. For the fresh potato market especially the external experience is of central importance and mainly influences on the consumers purchase behavior (Fiers et al. 2010). Consumer preferences can differ between individual or origin, but generally tuber sizes of 150-200 g, tuber shapes without protuberances, recessed eyes or stolon attachments and without superficial blemishes such as tuber cracks are preferred (Burton 1974). But also for other intended usages than for fresh consumption the absence of superficial blemishes is of interest as injuries of the tuber skin might be entrance point for secondary infections (Hide and Lapwood 1992). The mineral status of tubers might be a further important quality trait, especially for tubers for fresh consumption. Potato tubers can be a good source for several minerals in diet (Andre et al. 2007; Subramanian et al. 2011). However, minerals can show distinct distribution patterns in the tubers (Subramanian et al. 2011; Johnston et al. 1968).

For the production of French fries as well as for chips the dry matter (DM) content is a central quality parameter. High DM contents are desired to achieve a high yield of product but low oil content (Lulai and Orr 1979; Sayre et al. 1975). Furthermore, the texture of chips produced with tubers of high DM content is supposed to be harder and more desirable compared to chips produced with tubers of low DM content which are supposed to have a more greasy or sticky texture (Kita 2002). Likewise for the starch production a high DM content is aspired (Haase 2003) as starch is the most important component of DM (Poberezny and Wszelaczynska 2011). For the seed tuber market the most important quality requirements are the absence of diseases and pests, a sufficient growth vigor of the seed and an appropriate tuber size. With respect to the tuber size, smaller tubers are preferred as they can produce more stems per unit weight compared to bigger tubers (van Loon 2007).

Besides the previously mentioned quality determinants, there are several further factors which might influence on the potato tuber quality. However, not all determinants are objective of the present thesis why only a section of important quality determinants is considered.

Factors influencing on potato tuber quality

Tuber quality can be affected by several parameters such as the cultivar (Cabezas-Serrano et al. 2009; Elmore et al. 2015), the type and time of storage (Arvanitoyannis et al. 2008; Elmore et al. 2015), agronomic practices prior and during plant growth – for instance irrigation or tillage methods (Alva et al. 2002) – and tuber handling during and after harvest (Daniels-Lake et al. 2014; Peters 1996). According to Peters (1996) mechanical injuries, which can occur during or after harvest – for example whilst tuber grading – are the most serious threats for losses of marketable tubers. Such mechanical impacts can favor for instance the emergence of tuber cracks (Hiller et al. 1985). But also internal factors like changes in moisture content can favor the emergence of tuber cracks (Bohl and Thornton 2006). Indeed, the current knowledge regarding physiological reasons that make potatoes more susceptibly for mechanical impacts which can results in cracking of the tuber is rare.

With respect to agronomic practices prior or during plant growth the nutrient supply is a further central factor of influence (Westermann 2005). Potassium (K) is that mineral which is needed in the largest amount by the potato plant (Westermann 2005). The predominantly applied nutrients in potato production are nitrogen (N), phosphorus (P) and K (Ierna et al. 2011; Lin et al. 2004). While for K there has been profound research related to its functions and need for crop production – including potato – the role and importance of Mg often has been neglected (Cakmak and Yazici 2010; Guo et al. 2016). A search of the ISI Web of Science on 17 December 2017 at 11:00 h CET by using the topic key word 'potato' in combination with the title key word 'potassium' by simultaneous exclusion of 'magnesium' from the title (and vice versa) returned a total of 270 'potassium articles' but only 55 'magnesium articles' published since 1945. The search was filtered for the research areas 'agronomy', 'agriculture multidisciplinary', 'food science technology', 'plant sciences', 'environmental sciences', 'biochemistry molecular biology', 'soil sciences', and 'horticulture'. Moreover, each 'potassium article' was cited on average 9.52 times with 2571 total cites while each 'magnesium article' was cited on average only 5.25 times with 289 total sites. A further search of the ISI Web of Science on December 17 2017 at 11:10 h CET by using the topic key words 'potato' and 'quality' in combination with the title key word 'potassium' by simultaneous exclusion of 'magnesium' from the title (and vice versa) returned a total of 43 'potassium articles' but only 12 'magnesium articles' published since 1945. The search was filtered for the research areas 'agronomy', 'agriculture multidisciplinary', 'food science technology', 'plant sciences', and 'biochemistry molecular biology'. Each 'potassium article' was cited on average 14.19 times with 610 total cites while each 'magnesium article' was cited on average only 6.67 times with 80 total sites. Finally, first a search of the ISI Web of Science on December 17 2017 at 11:20 h CET by using the topic key words 'potato' in combination with the title key

words 'potassium' and 'magnesium' returned a total of only 3 'potassium and magnesium articles' which were sited on average 3 times with 9 total sites. Second, a search of the ISI Web of Science on 17 December 2017 at 11:25 h CET by using the topic key words 'potato' and 'quality' in combination with the title key words 'potassium' and 'magnesium' returned a total of 20 'potassium and magnesium articles' which were sited on average 10 times with 200 total sites. Both search (topic key word 'potato' in combination with title key words 'potassium' and 'magnesium' and topic key words 'potato' and 'quality' in combination with title key words 'potassium' and 'magnesium') were filtered for the research areas 'agronomy', 'agriculture multidisciplinary', 'food science technology', 'plant sciences', 'soil sciences', 'horticulture' and 'biochemistry molecular biology'.

These findings emphasize that there is huge lack of research and awareness about the importance of Mg for potato production and especially for potato quality. Besides, the outcomes of the search of the ISI Web of Science illustrate, that there has been only less research about the importance of K in combination with Mg for potato production and potato quality since 1945. Thus, there is a high need for current research about the importance and effect of Mg but also of K and Mg in combination for potato production and quality.

Roles of K and Mg in plant growth and metabolism

Both K and Mg are essential macronutrients for plant growth and are needed for a myriad of processes in plant metabolism (Marschner 2011). A main focus of this thesis is set on the roles of K and Mg for photosynthesis and the partitioning of photoassimilates from source to sink organs. Potato tubers are strong sink organs. Thus, an impact of the K and Mg supply on potato tuber development and likely quality can be expected. K has an outstanding role due to its osmotic properties in plants. Based on these properties it facilitates cell and root elongation (Mengel and Arneke 1982; Song et al. 2017), leaf area expansion (Jordan-Meille and Pellerin 2004), and plant movements such as stomata opening and leaf movement (Ahmad and Maathuis 2014). With regard to the mentioned functions K is crucial for photosynthesis for two main reasons: First, K ensures CO_2 diffusion through the leaf mesophyll (Jákli et al. 2017) and second, K is thought to cause a reduction in the activity of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) which catalyzes the first step in CO_2 fixation (Hu et al. 2016). This may be attributed to a decrease of CO_2 at the catalytic site of the enzyme based on a restricted CO_2 diffusion through the leaf mesophyll (Asif et al. 2017; Oosterhuis et al. 2013). The predominant role of K in source to sink transport of assimilates is likewise based on its previously mentioned function, namely its osmotic properties. Here, K establishes an osmotic gradient

which is causing a driving force for sucrose, the main transport form of carbohydrates in the phloem (Cakmak et al. 1994a; Hayashi and Chino 1990; Vreugdenhil 1985).

Mg is activator for a huge number of enzymes (Senbayram et al. 2015; Verbruggen and Hermans 2013). One of these enzymes is Rubisco (Belknap and Portis 1986) what makes Mg essential for photosynthesis. Beside, Mg is central atom of chlorophyll (Walker and Weinstein 1994) why it may additionally influence on photosynthesis. A further major role of Mg is located in the loading of the phloem why it is pivotal, like K, for the source to sink transport of assimilates in plants. Here, Mg is required by ATPases as allosteric activator. These ATPases create a proton gradient that provides energy for the phloem loading process (Hermans et al. 2005).

Finally, nutrient shortages, including K and Mg, have been shown to negatively impact on the plants root architecture (Cakmak et al. 1994b; Gruber et al. 2013; Mengutay et al. 2013; Sattelmacher et al. 1993). Cakmak et al. (1994b) refers this to a negatively affected photoassimilate partitioning which has been caused by K and Mg deficiency.

Impact of individual and interactive effects of K and Mg nutrition

Mineral nutrition can significantly affect the plant´s mineral status and in turn plant growth (Fageria 2001; White et al. 2009). It was shown that mineral nutrition of N, P, K, Calcium (Ca) and Mg can increase the particular element concentrations in tubers (for detailed literature references see White et al. (2009)). However, the application of one nutrient can change the concentrations of other minerals by affecting the absorption, distribution or function of another nutrient (Robson and Pitman 1983; White et al. 2009). These nutrient interactions can be of synergistic, antagonistic but also neutral nature. Interactions between nutrients are often observed between ions of similar chemical properties, such as K, Mg and Ca (Jakobsen 1992; Robson and Pitman 1983) as they might compete for the same uptake mechanism from the soil solution (Mayland 1990). With respect to potato, the interaction between K and Mg often has been research issue – however with contradictory outcomes: Hossner and Doll (1970) examined an antagonistic effect between K and Mg in form of decreasing tuber yield under decreasing Mg but increasing K plant mineral status. Contrary, Allison et al. 2001 concluded, that there is no interactive effect between K and Mg. Ding et al. (2006) could determine a synergistic effect of increasing Mg supply on the uptake and translocation of K from the root to shoot – though, this study was conducted with rice (*O. sativa* L. ssp. *Japonica)* plants.

Objectives of the thesis

An initial objective of the present thesis is to review the current state of knowledge about i) the importance of K and Mg for plant growth in general and for potato production in particular. Furthermore, ii), it is aimed to point out the current state of knowledge about the importance of K and Mg for potato quality. These aspects beside the importance of other nutrients than K and Mg are reviewed in the first two chapters of this thesis. The following chapters deal with the subsequent mentioned research objectives:

1. The functional impacts of K and Mg on photosynthesis and the partitioning of photoassimilates from source to sink organs are well resolved. However, it is unclear to which extent a K or Mg deficiency affect these processes in potato. Moreover, as tubers are strong sink organs for photoassimilates, an impairment on tuber development and quality is expected.

   Thus, central objectives of this study are:

   1a) Examining the severity of photosynthetic restriction and parameters, which give indication about the source to sink transport of photoassimilates under K and Mg deficiency.

   1b) How K and Mg restriction affect tuber development and quality.

2. Several studies in literature are available about nutrient uptake interactions between K and Mg, though with contradictory outcomes: Some studies report about antagonistic nature between K and Mg, some could not determine an interaction at all and some even demonstrated a synergistic effect. Therefore, the K and Mg status of different plant tissues under various combined K and Mg supplies is investigated to preserve clarification about the nature of interactive effects between K and Mg in potato.

3. Common bean (*Phaseolus vulgaris*), wheat (*Triticum aestivum*), maize (*Zea mays*) and the model plant Arabidopsis show a reduced root growth under Mg deficiency (Cakmak et al. 1994b; Gruber et al. 2013; Mengutay et al. 2013). This was never reported for potato. Thus, further aims of this thesis are

   3a) Testing if Mg deficiency causes a reduced root growth in potato.

   3b) Examining if such a putative root growth reduction can be ameliorated by Mg resupply via roots or leaves, respectively.

4. The absence of superficial blemishes such as tuber cracks is an important quality determinant of potatoes. Knowledge regarding physiological reasons that make potatoes more susceptibly for mechanical damage, which can result in cracking or fracture of the tuber skin, is rare. Therefore we aimed to elucidate:

   4a) Physiological parameters that might be linked with the resistance of tubers against mechanical impacts.

   4b) If a K and Mg supply is affecting these physiological parameters.

Chapter 2

The importance of nutrient management for potato production
Part I: Plant nutrition and yield parameters

Mirjam Koch, Marcel Naumann, Elke Pawelzik, Andreas Gransee, Heike Thiel

Submitted

The importance of nutrient management for potato production

Part I: Plant nutrition and yield parameters

Mirjam Koch[1], Marcel Naumann[1], Elke Pawelzik[1*], Andreas Gransee[2], Heike Thiel[2]

[1] Quality of Plant Products, Department of Crop Sciences, Faculty of Agricultural Sciences, University of Goettingen, Carl-Sprengel-Weg 1, 37075 Goettingen

[2] K+S KALI GmbH, Bertha-von-Suttner-Str. 7, 34131 Kassel, Germany

*Corresponding author: epawelz@gwdg.de

Abstract

Research from the last few decades has shown that, in potato production, optimal yield and optimal quality do not necessarily correlate. Agronomic strategies in potato production have mainly focused on improving yield and related parameters. In recent years, however, the quality aspect attracts more attention. As part of a successful agronomic strategy, adequate nutrient management of the potato crop is essential throughout the whole growth period. In this review, the importance of balanced fertilization for potato yield formation and yield security is addressed by taking advantage of the results of own field trials and current literature. Due to their various functions in plant metabolism, the impact of plant nutrients on specific yield parameters is complex, particularly under abiotic and biotic stress conditions. Specific and non-specific nutrient interactions in the soil and the plant have to be taken into account as well. In conclusion, the development of site-specific fertilization recommendations as part of an agronomic strategy strongly depends on soil and plant nutrient status.

Keywords: productivity; yield; nitrogen, phosphorus, magnesium; potassium

Introduction

Potato (*Solanum tuberosum*) is a highly attractive crop in agricultural production systems since it combines an extraordinarily high yield potential of, on average, more than 45 t ha^{-1} in high-input agriculture (Table 1) with a high nutritional value. For example, it is a good source of energy, minerals, proteins, fats, and vitamins (Ekin 2011, Drewnowski and Rehm 2013; King and Slavin 2013). Besides, potatoes are not just an important food source (Andre et al. 2014). They are also increasingly serving as feedstock for industrial products (Izmirlioglu and Demirci 2015; Jagatee et al. 2015). Therefore, unlike most other crops, potatoes have an unusually high range of utilization possibilities, which makes their production even more attractive (Stearns et al. 1994; Feltran et al. 2004; Kaur and Singh 2009). Table 1 summarizes data on the potato production in different regions of the northern hemisphere and Africa. These data base on cultivation area and taking the top five countries into account as well as the total potato production worldwide.

The yield, a potato crop can potentially realize at a specific production site, is mainly determined by its specific genetic background (Evans and Fischer 1999). There is a gap between the actual yields and the yield potential (Van Keulen and Stol 1995; Michel 2015). According to the yield potential concept, the potential yield is never fully reached in natural production systems, as biotic and abiotic factors, interfering with the potato crop negatively affect plant growth and tuber development. Important biotic stress factors in potato production include late blight (caused by *Phytophthora infestans*) (Nowicki et al. 2012) and other fungal infections, like early blight (caused by *Alternari solani*), silver scurf (*Helminthosporium solani*) and black scurf (*Rhizoctonia solani*), as well as *Fusarium* and *Verticillium* wilt (Rich 2013). Furthermore, other kinds of pathogens (Giordanengo et al. 2013), and various bacterial and viral diseases (Rich 2013) affect potato yield and production. The abiotic stresses that reduce yield include high radiation, heat and cold stress. But the most important abiotic factor affecting yield and quality is drought stress (van Loon 1981; Obidiegwu et al. 2015).

To a certain degree, growers can reduce the negative effects of the environmental impacts by using balanced agronomic management strategies. Apart from the choice of cultivar, plant protection, and continuous water supply, the most important agronomic measure for potato production is adequate nutrient management. An sufficient supply of mineral nutrients (1) fortifies the potato plants against adverse growth conditions (only well-nourished plants have the potential to withstand the challenges of climate change), (2) is crucial for achieving high yield, and (3) is essential for producing potatoes that meet the desired quality requirements. According to the law of the minimum developed by Carl Sprengel and, later, spread by Justus von Liebig in the early 19th century, optimal crop growth can take place only if all required

nutrients are at the optimum level (Sprengel 1828; cited in van der Ploeg et al. 1999; von Liebig 1841; von Liebig 1855). In detail, it states that plant growth is controlled not by the total amount of nutrients available, but by the amount of the scarcest nutrient. This law points to the importance of balanced nutrition for optimal plant growth. The law of the diminishing yield increase is of similar importance. It states that the higher the nutrient supply the lower the yield increase obtained from the increase in fertilization, which means that the yield response to fertilization follows a saturation curve (Spillman 1923). Both laws are the basis for modern approaches to develop fertilization recommendations—like the '4R plant nutrition concept' compiled by International Plant Nutrition Institute (IPNI), for example (IPNI 2012; Johnston and Bruulsema 2014).

In the following sections, this review aims to give an overview on the role of nutrients on yield formation, yield security and fertilization practice in potato production.

Table 1: Potato production details from Europe, America, Asia and Africa in total plus top five countries according to the cultivation area, the amount of harvested product, and the average yield in 1994 and 2014.

Country	Cultivation area (ha)*		Quantity (t)*		Average yield (t/ha)*		
	1994	2014	1994	2014	1994	2014	
Russia[1]	3,336,960	2,101,461	33,827,620	31,501,354	10.1	15.0	Europe
Ukraine	1,527,000	1,342,800	16,102,000	23,693,350	10.5	17.6	
Germany	322,775	244,800	10,635,400	11,607,300	33.0	47.4	
France	165,000	168,519	5,463,000	8,085,184	33.1	48.0	
Poland	1,697,247	276,927	23,057,540	7,689,180	13.6	27.8	
Total	9,795,116	5616844	138,208,334	124,542,089	14.1	22.2	
USA[2]	558,350	425,370	21,185,000	20,056,500	37.9	47.2	America
Peru	188,531	318,380	1,767,247	4,704,987	9.4	14.8	
Canada	132,900	138,942	3,676,600	4,589,200	27.7	33.0	
Brazil	171,853	132,058	2,488,461	3,689,836	14.5	27.9	
Colombia	184,397	107,598	2,938,631	2,157,568	15.9	20.1	
Total	1,721,011	1,576,901	38,591,256	42,241,119	22.4	26.8	
China[3]	3,207,600	5,645,000	43,800,000	95,515,000	13.7	16.9	Asia
India	1,047,100	2,024,000	17,392,400	46,395,000	16.6	22.9	
Bangladesh	131,245	461,710	1,438,055	8,950,000	11.0	19.4	
Iran	149,512	158,958	3,184,840	4,717,266	21.3	29.7	
Turkey	190,000	128,392	4,350,000	4,166,000	22.9	32.4	
Total	5,743,038	9,932,183	84,477,948	186,886,889	14.7	18.8	
Algeria	75,300	156,176	715,936	4,673,516	9.5	29.9	Africa
Egypt	64,779	172,005	1,324,649	4,611,065	20.4	26.8	
South Africa	55,197	63,907	1,316,000	2,247,495	23.8	35.2	
Rwanda	17,000	164,152	114,900	2,213,556	6.76	13.5	
Morocco	58,800	63,515	1,037,950	1,950,982	17.7	30.7	
Total	747,477	1,933,185	8,359,620	2,639,1538	11.2	13.7	
World	18,056,805	19,098,328	271,244,596	381,682,144	15.0	20.0	

[1] Russian Federation, [2] United States of America, [3] China, mainland

* All data were taken and re-calculated from faostat (http://faostat3.fao.org)

Roles of macronutrients in plant metabolism and their role in yield formation

Reports on the nutrient uptake and removal mainly rely on data produced decades ago. Therefore, a comprehensive study on the nutrient demand of and removal by modern varieties of potatoes is urgently needed. Perrenoud (1993) summarized the literature on the nutrient uptake of and removal by potatoes. The mean values are presented in Figure 1. From the removal per ton of tubers, the removal in kg ha^{-1} was calculated a tuber yield of 40 t ha^{-1}. The most important nutrients, as shown in Figure 1 (with the exception of sulphur), are highlighted with respect to their physiological functions in plant metabolism and for tuber yield formation in this review. Unfortunately, often less current literature is available dealing with nutrient functions in the potato crop. In this case, the most important nutrient roles are addressed exemplary on other crop plants with view on the importance for the potato crop. A critical review on all essential nutrients in potato growth is beyond the scope of this review.

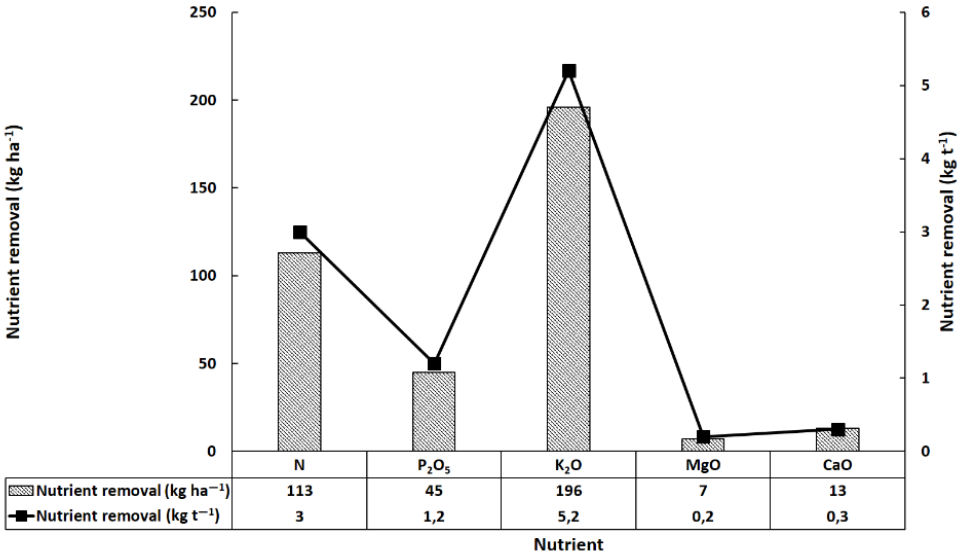

Figure 1: Removal of N, P_2O_5, K_2O, MgO, and CaO by potato tubers. Mean values per ton of tubers (as shown on the right axis), calculated according to Perrenoud (1993) [and literature cited therein]. Calculations on nutrient removal per ha (as shown on the left axis) were based on a 40 t ha^{-1} tuber yield.

Nitrogen

Nitrogen (N) is one of the most crucial macronutrients for plant growth and biomass development. It can limit potato yield formation most amongst all essential macronutrients (Bucher and Kossmann 2011; Silva et al. 2013). It has a decisive impact on the number of emerging leaves and the rate of leaf expansion, and, therefore, on the leaf area index (LAI) of plants. Hence, it has a positive impact on photosynthesis efficiency by increasing the interception rate of

radiation and photons (Vos 1995; Vos and van der Putten 1998; Mauromicale et al. 2006), and, as a consequence, on tuber yield formation (Ahmed et al. 2015). Besides this, N is mandatory for the plant as it is a component of chlorophyll, amino acids, proteins, nucleic acids, coenzymes, and membrane constituents (Andrews et al. 2013; Ahmed et al. 2015). Plants can use N in different forms. Their major sources are nitrate (NO_3^-) and ammonium (NH_4^+) (Silva et al. 2013). While adequate use of N fertilization can improve yield as well as plant quality, an inappropriate supply of N can lead to increasing vegetative growth but delayed flowering and impaired tuber formation (Nitsch 2003; Bucher and Kossmann 2011; Ahmed et al. 2015). In addition, an excessive supply of N can lead to the accumulation of reactive N compounds in the atmosphere or leaching to the groundwater, both of which have negative impacts on our ecosystems (Singh and Lal 2012 Silva et al. 2013). Leaching, in particular, is likely to occur under a high supply of N, as potatoes have shallow roots that are unable to capture N from deeper soil layers. Therefore, the potato crop can be referred to as N-inefficient crop (Cameron et al. 2013). Optimal N fertilization practices should be achieved to meet both economic and environmental demands (Zebarth et al. 2012). Therefore, an appropriate N supply should be based on calculations that meet the actual plant demand and should include other N sources—for example, delivered by catch crops or intercrops, like N-fixing leguminous plant species (Bucher and Kossmann 2011; Zebarth et al. 2012; Cameron et al. 2013). In order to meet the actual demand of the plant, splitting N application is commonly used approach (Kelling et al. 2015; Rens et al. 2016). Furthermore, optimal N usage can be improved upon by inducing and maintaining high plant growth and biomass production through appropriate irrigation strategies, controlling pest and observation of disease development, and avoiding nutrient deficiencies (Cameron et al. 2013).

Due to the disturbance of chloroplasts, N deficiency becomes obvious as leaf chlorosis that is equally distributed over the whole leaf. Unlike symptoms of potassium (K) or magnesium (Mg) deficiency, severe necrosis of the leaves due to N deficiency usually appears late in the growth stages. The symptoms of N deficiency may also be similar to ferric, calcium (Ca), or sulphur (S) deficiency. These symptoms occur first on younger leaves as those nutrients cannot be translocated within the plant (Mengel and Kirkby 2001).

Phosphorus

Phosphorus (P) is required in relatively high amounts by the potato crop compared to others (Figure 1) (Rosen et al. 2014). P serves various functions in plant metabolism, where the most prominent role is cellular energy transfer by dephosphorylation of Adenosine triphosphate (ATP) to Adenosine diphosphate (ADP), which is the primary source of energy in the processes of photosynthesis, respiration, or biosynthesis - like starch synthesis. Besides this, P is a

structural component of nucleic acids as units in deoxyribonucleic acid and ribonucleic acid molecules, of many coenzymes, and of phospholipids in biomembranes (Raghothama 2000; Marschner 2011; Rosen et al. 2014). Economically speaking, especially in the early growth states, P has a significant impact on number of potato tubers and settings (Jenkins and Ali 2000; Hopkins et al. 2014).

Most soils cannot sufficiently cover the P demand of potatoes or P may only be plant-available to a limited extend due to its absorption by soil particles, clay minerals, or Ca and Mg carbonates (Bucher and Kossmann 2011; Rosen et al. 2014). Besides this, similar to the N usage in deeper soil layers, P uptake is difficult for the potato crop due to its shallow and inefficient rooting system (Hopkins et al. 2014). However, there are various strategies for exploiting limited accessible P sources. Any factor that is able to increase the rooting zone can lead to better P absorption. Therefore, the best management practice, including the avoidance of root pruning by tillage and toxicities of salts or other compounds that can impair the root development, and pest and disease management in order to maintain healthy roots, are of central relevance (Hopkins et al. 2014). Another option is using the advantages of the symbiotic associations of potato roots with arbuscular mycorrhizal fungi (McArthur and Knowles 1993). These fungi colonize roots with hair-like hyphae, which increase the root area, and lead to higher water and nutrient uptake, especially the uptake of P. In turn, the fungi receive sugars in form of photosynthates from the plant (Smith and Smith 2012). Furthermore, the placement (banding or broadcast) and soil pH value seem to have an influence on P acquisition, but inconsistent results are noted in different studies, as described by Hopkins et al. (2014) and Rosen et al. (2014).

The potato plant can tolerate moderate P stress without any severe deficiency symptoms until photosynthesis and respiration processes are reduced heavily so much that carbohydrates start to accumulate. This becomes obvious in dark green to purple leaf discolorations, as described by Hoppo et al. (1999) and cited in Grant et al. (2001).

Potassium

Out of all the macronutrients, potassium (K) has the highest concentrations in potato tubers, accounting for about 400 mg per 100 g fresh weight (White et al. 2009) or for about 1.7% of dry matter (Schilling et al., 2016). In the remaining plant tissues, it is also the most abundant inorganic cation—in potato leaves with up to 6% of dry matter, for instance (Leigh and Wyn Jones 1984; Zorn et al. 2016). These facts are also reflected in the high amounts of K removal by potatoes (Figure 1). Beside this, K is one of the most important nutrients affecting potato tuber quality as is described e.g. by Zörb et al. (2014).

The major functions of K in plants are controlling enzyme activity, cation-anion homeostasis, and membrane polarization, or they are based on its osmotic nature, which is why it is needed for cell extension, turgor regulation, or stomatal movement (Walker et al. 1996; Liu et al. 2006; Wang and Wu 2013; Adams and Shin 2014; Shabala and Pottosin 2014). One important role of K for the potato crop in enzyme functions is, for example, stimulating the starch synthase for starch synthesis (Hawker et al. 1979). A sufficient supply of K is also needed for yield-decisive high biomass production and leaf area development. Under K deficiency, there can be a decreased number of leaves as well as a decrease in the leaf size. This can be attributed to K's role in osmoregulation and cell extension (Gerardeaux et al. 2010; Jákli et al. 2016). Besides the mentioned functions, K is crucial for photosynthesis and the distribution of photosynthates via the phloem. To maintain a proper working photosynthesis, an accurate working stomatal movement is needed to take up considerable amounts of CO_2 for fixation in the Calvin cycle (Cakmak 2005; Zörb et al. 2014). Moreover, the processes involved in photosynthesis require a fine-tuned pH regulation because photosynthetic enzymes need a specific pH to function efficiently (Rumberg and Siggel 1969; Woodrow and Berry 1988). For instance, this is true for ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) as a key enzyme involved in photosynthetic carbon fixation. However, the maintenance of photosynthesis is also dependent on the export of photosynthates from source to sink organs. Under K deficiency, there can be an accumulation of sucrose in leaves, which result in a decline in photosynthetic activity (Hermans et al. 2006). The accumulation of sucrose in the leaves of K-deficient plants occurs due to an impaired phloem loading and transport of sucrose in phloem. For phloem loading, K is again needed for stabilizing a specified pH value for energy-providing ATP production, whereas for distribution of sucrose within the phloem, K establishes the needed osmotic pressure (Cakmak et al. 1994a). Based on the mentioned roles of K in enzyme regulation, photosynthesis and partitioning of carbohydrates within the plant, it can be assumed that a K has central relevance in the potato crop for establishing desired tuber and starch yields.

In addition, the form of K application—for example, as sulphate or chloride—can have tremendous effects on assimilate distribution and, therefore, on the important quality aspects of potato. In general, independent of the K source that is supplied (either as K_2SO_4 or KCl), the yield can be increased with increasing K fertilization (Panique et al. 1997). But it is assumed that fertilization of K in chloride form leads to a higher osmotic potential in the crops, compared to the sulfate form, as the osmotically active chloride is accumulated in higher amounts than sulphate. This leads to higher water uptake and, therefore, higher vegetative growth. Higher vegetative growth rates, particularly of the above-ground plant parts, leads to an increased competition for assimilates between shoot and tuber, as the shoot is a strong sink for such assimilates. In addition, the chloride-induced high growth rates of the shoot as a result of

increased water uptake leads to a dilution of K (and other nutrients) in the plant. As K is important for phloem loading and distribution processes in plants, such reduced K concentrations in the plant matter could impair assimilate translocation to the roots and, therefore, to the tubers (Beringer et al. 1990).

When K is depleted in the potato plant leaves start to develop chlorosis, even on leaf edges or in the form of dots (Zorn et al. 2016). As K is phloem-mobile, the symptoms of K deficiency occur first on older leaves because K will be translocated from older to younger developing leaves. In addition, an increased root-to-shoot ratio can be observed (Cakmak et al. 1994a; Cakmak et al. 1994b).

Magnesium

Magnesium (Mg) can be designated as 'the forgotten element in crop production' as its supply and the need for are usually underestimated. But due to its several key roles, especially in photosynthesis, the partitioning of photoassimilates, protein synthesis, and enzyme regulation, Mg deficiency can lead to impaired growth and yield formation (Cakmak and Yazici 2010; Senbayram et al. 2015). Mg serves as a cation, together with K, in similar physiological processes—for example, in the regulation of the cation-anion balance—and as an osmotically active ion in the turgor regulation of cells (Marschner 2012). In addition, Mg contributes, like K, to maintain a stable pH for proper activity of photosynthetic enzymes—for example, for Rubisco (Woodrow and Berry 1988; Yuguan et al. 2009). Moreover, Mg specifically binds to RuBP, and thereby, enhances its catalytic activity (Belknap and Portis 1986). Besides, Mg is an allosteric activator of more than 300 enzymes (Verbruggen and Hermans 2013; Senbayram et al. 2015). The most commonly known function of Mg in photosynthesis is its role as a central atom of the chlorophyll molecule - the organic molecule capable of scavenging sunlight and transforming it into electron transport, and, hence, chemical energy (Walker and Weinstein 1994; Verbruggen and Hermans 2013). In protein synthesis, Mg is vital for bridging two subunits of ribosomes - the location of the translation of proteins - to its active form (Sperrazza and Spremulli 1983). One more essential role that Mg shares with K is located in the partitioning of carbohydrates. Mg is required for phloem loading with sucrose as it is an allosteric activator of ATPases, which create a proton gradient that provides energy for the transport of sucrose and protons via sucrose/H^+ symporters (Hermans et al. 2005). As pointed out, Mg serves like K in crucial functions for photosynthesis and carbohydrate partitioning, why it can be presumed that also Mg is of main importance for establishing favored tuber and starch yields.

Cakmak et al. (1994a) and Ceylan et al. (2016) reported as a consequence of impaired phloem loading that plants which were deficient in Mg (and also K) accumulated sucrose in the leaves, whereas simultaneously the concentration of

sucrose in the phloem sap decreased. Evidence was also provided that particularly a re-supply of Mg to Mg-deficient plants for only one day was very effective in restoring the phloem transport of sucrose (Cakmak and Kirkby 2008). This rapid correction of the phloem transport system following a re-supply of Mg indicates that foliar applications of soluble Mg fertilizers in field crops can provide a fast and effective remedial treatment for Mg deficiency.

Furthermore, there is evidence that Mg has an impact on root growth and morphology, but with contradictory results. Cakmak et al. (1994a, b) showed a decrease in dry matter production in the roots compared to the shoots of bean plants grown in a nutrient solution under conditions of Mg deficiency, while Hermans et al. (2005) documented almost no effect on root biomass development after transferring sugar beet plants into an Mg-depleted nutrient solution. This might be explained by the fact that both authors used different approaches: Cakmak et al. (1994a, b) induced Mg deficiency already at germination or at a very early growth stage, while Hermans et al. (2005) grew their plants first under conditions of sufficient Mg supply before transferring them into an Mg-depleted nutrient solution. It seems as if plants are able to overcome Mg depletion in the later growth stages without any severe impact on the root growth or morphology when they had been earlier sufficiently supplied with Mg. The symptoms of Mg deficiency as well as K deficiency, can first be observed on older leaves as Mg can be easily translocated to active growing plant parts in the form of intercostal leaf vein chlorosis (Cakmak and Kirkby 2008; White and Broadley 2009; Gransee and Führs 2013). It is likely, depending on growth conditions, that under Mg depletion, plants develop an increased root-to-shoot ratio (Cakmak et al. 1994a, b).

Potassium-magnesium antagonisms

The competition of cations for uptake is a well-known phenomenon (Jacoby 1961; Diem and Godbold 1993; Fageria 2001; Marschner 2011; Chen and Ma 2013). One of the most commonly observed phenomena based on cation antagonism is K-induced Mg deficiency. This could be the effect of the specificity of K transporters on the one hand and the unspecifity of Mg transporters on the other hand involved in K and Mg uptake from the soil solution. The delivery of K and Mg to the roots typically follows different mechanisms: While Mg mainly is delivered by massflow and to a smaller proportion by interception; K mainly is delivered by diffusion (Strebel and Duynisveld 1989; Barber 1995; Marschner 2011). To ensure delivery to the roots, plants need to decrease the K concentration in the soil solution of the rhizosphere in order to drive K flux to the roots via diffusion. In contrast, Mg is present in the soil solution in much higher concentrations. Hence, the delivery to the plant roots is mainly enabled by mass flow (Zhang and George 2002). It may occur that the delivery by mass flow is higher than the uptake by plants, which would result in the

accumulation of Mg in the rhizosphere (Zhang and George 2002). In addition, Mg adsorbs less to the soil matrix due to its high hydrated radius and therefore can be leached out what reduces, compared to K for instance, the availability of Mg to the roots (Deng et al. 2006). However, the main reason leading to different uptake rates of K and Mg may be due to the unspecificity of Mg transporters, which also take up, beside Mg, other cations like K. Therefore, under high plant available K concentrations in the soil solution Mg uptake can be blocked while K uptake can be advantaged by Mg transporters (Gransee and Führs 2013). At the same time there are existing very specific K transporters which ensure, depending on the K concentration in the soil solution, K uptake as well at low (HATS = High Affinity Transport System) as at high K concentrations (LATS = Low Affinity Transport System) (Britto and Kronzucker 2008). But these specific K transporters do not transport Mg (Gransee and Führs 2013). Hence, while the uptake of K is ensured - even under low K concentrations - due to the uptake by specific K transport systems as well as by unspecific Mg transporters, Mg uptake can be impaired even if there is enough Mg available in the soil solution due to the unspecificity of Mg transporters as well as of K transporters for Mg.

But with view on the described antagonistic effects, it is often wrongly concluded that particularly K and Mg should not be applied together in order to prevent antagonistic effects during uptake. However, this is the wrong conclusion, as can be seen in Figure 2: The yield of the control treatment receiving Mg in the form of 400 kg ha^{-1} as Magnesiumsulphat (ESTA® Kieserit) but no K was higher than the yield of the plants that received the highest amount of K in the form of 300 kg K_2O as K_2SO_4 ha^{-1} but no Mg. Moreover, in view of the comparably low soil Mg status, the high K supply further reduced Mg uptake by the potato plants. Hence, at least a slight Mg deficiency in the single K treatment could be expected, finally leading to a reduced yield. Only the combination of K and Mg supply revealed the highest yield.

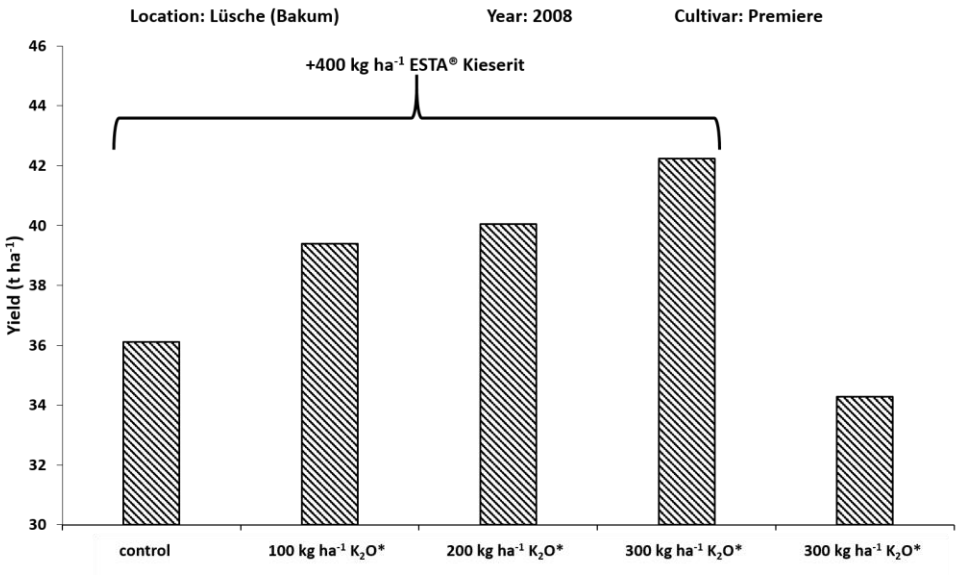

Figure 2: Effect of combined K and Mg fertilization on yield of potato. The experimental site was Lüsche (Bakum), Northwest Germany, predominantly characterized by silty sand. Soil analysis showed 13.6 mg K_2O 100 g^{-1} soil after calcium acetate lactate (CAL) extraction and 3.2 mg Mg/100 g^{-1} soil after $CaCl_2$ extraction; ESTA® Kieserit = 25% MgO (water-soluble) and 50% SO_3 (water soluble); *as KALISOP® gran. = 50 % K_2O (water-soluble) and 45% SO_3 (water-soluble)

Calcium

Calcium (Ca) is essential for the potato crop mainly due to its role in cell wall and membrane stabilization (Kirkby and Pilbeam 1984; White and Broadley 2003), its function as a counter-cation for inorganic and organic anions in the vacuole (White and Broadley 2003; Marschner 2011), and as a second messenger in intracellular signal transduction processes (Pottosin and Schonknecht 2007).

The most abundant polysaccharide of primary cell walls is pectin (Jarvis 1984). Due to its divalent nature, Ca is able to form a bridge between the galacturonates of pectin via carboxylate groups, thus contributing to the characteristic structure of cell walls (Subramanian et al. 2011). Besides the structural function in cell walls, Ca is fundamental for the stability of membranes. Here, it bridges the phosphate and carboxylate groups of phospholipids and proteins at membrane surfaces (Legge et al. 1982; Kirkby and Pilbeam 1984). Based on these roles for stabilizing membranes it can be suspected that Ca is also of importance for establishing and maintaining potato skin firmness, for instance.

Ca has extremely low cytosolic concentrations of less than 1 µM. A major part of Ca is present in bound form—to cell walls, for instance. However, the most water-soluble Ca is stored in vacuoles (Pottosin and Schonknecht 2007), where it contributes to the anion-cation balance (White and Broadley 2003; Marschner 2011). The resulting huge concentration differences between cytosol and vacuole form the basis for Ca's role as a second messenger (Pottosin

and Schonknecht 2007). Ca enables the plant to communicate information about the environment at the plant cell level (Whalley and Knight 2013). This forwarding of information can be triggered by different abiotic and biotic stimuli of the surrounding outside environment like, drought or oxidative stress as well as pathogens (McAinsh and Pittman 2009). Due to Ca´s roles in stabilizing the plant cell wall and membranes, and as a second messenger, Ca can contribute towards reducing disease severity (Ngadze et al. 2014).

The potato crop is known to tolerate low soil pH values and is often grown under very acidic soil conditions, for example at pH values of 4.6 (van Lierop et al. 1982; Lazarevic et al. 2014). Although liming usually can increase potato yields, people often refrain from liming these soils—as soils with higher pH-values could favor the development of common scab (*Streptomyces* spp.) (van Lierop et al. 1982; Waterer 2002). However, there may arise other and severe problems related to low soil pH conditions why it is difficult to determine a recommendation for an ideal pH-value for growing potatoes. The acidification of soils is frequently associated with deficiency of essential plant cations like Ca and Mg due to an antagonistic and inhibited uptake of these cations by metals like aluminum (Al) and manganese (Mn). Moreover, Al and Mn can cause toxic reactions in the plant. Therefore, under acidic soil conditions, liming with materials such as $CaCO_3$, CaO, or $Ca(OH)_2$ can not only improve the supply of Ca but also neutralize the soil pH and reduce the risk of Al or Mn toxicity in the plant (Mengel and Kirkby 2001; Lazarevic et al. 2014). On the other hand, when pH is raised it is possible that essential plant nutrients—like phosphorus or zinc—can be less plant available (Haynes 1990).

Ca moves within the plant via the xylem; therefore, Ca transport strongly depends on the transpiration of the plant (White and Broadley 2003; Subramanian et al. 2011). There are studies available that indicate Ca concentrations also in phloem sap but without further transport (Clarkson 1984). Clarkson (1984) argue these observations with the fact that Ca easily interacts with macromolecules and therefore transport must occur along extracellular pathways together with water. In addition, Ca cannot be translocated from older to younger leaves, as Ca is not mobile within the phloem and young leaves usually have a low transpiration rate. Consequently, deficiency symptoms regularly occur first on young leaves (White and Broadley 2003). Potato tubers have very low Ca concentrations, which can also be attributed to Ca transport mainly occurring via the xylem and the fact that tubers transpiring very less. The most Ca is distributed in the aboveground parts of the plant (Ozgen et al. 2006; Kärenlampi and White 2009). Besides growth reduction, a Ca deficiency can appear as browning phenomena or severe necrosis of the plant tissue (Brown et al. 2012).

Sulphur

Compared to other crops, like the *Brassica* species, potato has a comparatively low demand for S, but several high-yielding years can remove considerable amounts of S from the soil (Barczak and Nowak 2015; Klikocka et al. 2015; Koprivova and Kopriva 2016). In addition, S is essential for many cellular metabolites and, therefore, often represents the nutrient that limits plant yield and quality (Koprivova and Kopriva 2016). For instance, S is a component of amino acids like methionine and cysteine, which are the essential building blocks of proteins (De Kok et al. 2005; Galili and Amir 2013) or of the vitamins biotin and thiamine (Imsande 1998).

Although atmospheric S can be absorbed by higher plants in the form of SO_2, the highest amount of S is absorbed by the roots (De Kok et al. 2005). Atmospheric S concentrations strongly depend on anthropogenic SO_2 emissions and vary among continents and regions (Smith et al. 2011). While there has been a decrease in emissions by up to 50% in the last years in USA, Canada, and Central and Western Europe, there has been a two or three fold increase in emissions in Africa, China, Australia and New Zealand, for instance. Plants with S deficiency develop a similar yellowish phenotype, as described under N deficiency, for example. Both are based on a loss of chlorophyll. Though under S deficiency there is no direct impact on chlorophyll, an S deficiency inhibits the synthesis of thylakoid membranes and, therefore, promotes chlorophyll deficiency (Imsande 1998). S can be translocated within the plant via both phloem and xylem although, translocation via the phloem from older to younger leaves can be restricted. This is why deficiency symptoms (as yellowing similar N deficiency) often occur first on younger leaves (Mengel and Kirkby 2001).

Approaches to develop fertilization recommendations

There are numerous approaches for developing fertilization recommendations. Describing such approaches is beyond the scope of this review but they are described in detail by Marschner (2011), for instance. The most used approaches are soil analysis, plant analysis, or both in order to get information on the potential and/or actual nutritional level at a given production site. Some approaches include yield expectations, crop rotation and fertilization history, and additional site-specific parameters as well (Table 2). In general, both plant and soil analyses have advantages and disadvantages. Soil analysis gives an idea of the potential actual nutrient availability to the crop, but cannot forecast the availability. Plant analysis gives a good indication of the actual nutritional level of the crop, but does not provide information on the actual availability of nutrients to the crop. Hence, where applicable, soil and plant analysis in combination—when performed regularly—allows the development of the most reliable fertilization recommendations.

Table 2: Fertilization recommendations of different production areas in Europe, South Africa, and India. Shown are the locally recommended amounts of nutrients for potato production derived from the region-specific fertilization recommendation system. The procedure applied to develop a fertilization recommendation differs among regions.

Country/Region	Soil type	Recommended fertilization dose (kg ha^{-1})				
		N	P_2O_5	K_2O	MgO	CaO
Germany (Agricultural Chamber of Lower Saxony)	Varying	[1]160	[2]70—100	80—300	60	-
Germany (Agricultural Chamber of North Rhine-Westphalia)	Varying	[1]120—160	[2]	150—300	70	-
United Kingdom (DEFRA recommendation system)[3]	Varying	40—270	0—250	0—360	0—120	-
Netherlands	Varying	0 – 140[4]	20—185	0—320 (440)	0—200	
India (North-western hill zone) [5]	Acidic hill soil	120—150	100—150	120	-	-
India (North-eastern hill zone)	Acidic hill soil	100—120	120—150	60	-	-
India (North-western, -eastern and -central plain zone)	Alluvial	180—240	80—100	100—150	-	-
India (Plateau zone)	Black	100—120	60	60	-	-
India (Nilgiri zone)	Acidic hill	90—120	135—150	90	-	-
South Africa[6]	Varying	110—130[7]	70—300[8]	60—340[9]	0—105[10]	0—1,125

[1] Desired value, adaptations are needed according to the site-specific fertilization and crop rotation history and potato variety.

[2] Based on soil content class 'C'. Soil content classes were established empirically by conducting field trials for a wide range of soil types (explaining the wide range of some recommendations). Content classes are named A—E with A being very low and E very high. For content class 'C', fertilization at the height of nutrient removal from the field is recommended. Nutrient removal thereby depends on the expected yield level.

[3] The wide application ranges are a consequence of including agronomic factors like the length of the growing season (<60 to >120 days), the variety, and the UK-specific Soil Index system and the Soil Nitrogen Supply (SNS) Index system (taking soil type, rainfall, etc., into account). Values are calculated on a total yield of 50 t ha^{-1}.

[4] Calculations based on studies conducted by the University of Wageningen, including N_{min}, organic fertilization history, and intended use of potato (starch or fresh market potatoes), for P and K the water-extractable P, the HCl-extractable K, the NaCl-extractable Mg, and the demand of the crop (potato) is taken into account. In brackets: river and marine clay. Ca is not mentioned; instead, it is stated that Ca is typically sufficiently supplied with liming and/or fertilizers together with N or P.

[5] Official recommendation of the Central Potato Research Institute (CPRI), a federal research organization with a mandate on potato crop research.

[6] Fertilization guidelines according to the Potatoes South Africa and the National Potato Working Groups in South Africa (http://nbsystems.co.za/potato/index_12.htm)

[7] All nutrients are based on the yield potential of 30 t ha^{-1} and the clay content of the soil und rain-fed production

[8] Based on soil analysis according to Bray 1-2, Olsen, and AMBIC 1.

[9] Calculations for K and Ca based on cation exchange capacity (K: 80 mg/kg, Ca: 750 mg/kg, Mg: 121 mg/kg, Na: 77 mg/kg, H: 0.18 me%); H^+ expressed as percentage milli-equivalents (me%); the fertilization recommendation range shown here covers cation exchange capacity of me greater and smaller six

[10] For Ca and Mg, no yield potential, but only the soil analysis is taken into account. The values shown here cover the range of soil contents.

Conclusion

Beside other agronomic strategies, an adequate supply of nutrients is of main importance for achieving desired potato yield. In order to find the optimal level of nutrient supply it is important to understand and know basic laws of nutrient management, the individual physiological functions of each nutrient and resulting features, like nutrient antagonism for instance. Based on this fundamental knowledge the potato grower can decide for an accurate choice and application of fertilizers.

Chapter 3

The importance of nutrient management for potato production
Part II: Plant nutrition and quality parameters

Marcel Naumann, Mirjam Koch, Heike Thiel, Andreas Gransee and Elke Pawelzik

Submitted

The importance of nutrient management for potato production

Part II: Plant nutrition and quality parameters

Marcel Naumann[1], Mirjam Koch[1], Heike Thiel[2], Andreas Gransee[2] and Elke Pawelzik[1*]

[1] Quality of Plant Products, Department of Crop Sciences, Faculty of Agricultural Sciences, University of Goettingen, Carl-Sprengel-Weg 1, 37075 Goettingen

[2] K+S KALI GmbH, Bertha-von-Suttner-Str. 7, 34131 Kassel, Germany

*Corresponding author: epawelz@gwdg.de

Abstract

In the first part of these reviews, the focus was on yield and related parameters, as affected by nutrient management, which formed part of an agronomic strategy for potato production. The focus of the second review is on the quality of potato production. The term ‘quality’ is a complex parameter in potato production and the desired quality traits depend heavily on the intended use. Important quality traits for potatoes are dry matter and starch content, as well as firmness and resistance against mechanical stress—for example, during harvest. These quality traits are closely interrelated. It has been demonstrated that all these parameters are also strongly linked to the nutrient status of the plant and/or the tubers. Another important factor is the susceptibility to the formation of discolorations in potatoes for both fresh market and processing. In principle, enzymatic and non-enzymatic processes cause such undesired discolorations as ’black spot bruising‘ and ’after-cooking darkening‘. The potential of formation of carcinogenic compounds like acrylamide from precursors during the deep-frying of potato products and the accumulation of toxic substances like glycoalkaloids represent important quality criteria. The effect of fertilization management on these various quality aspects is addressed and important nutrients are highlighted.

Keywords: nutrient management, potato quality parameters, discoloration, fresh market, processing quality

Introduction

The nutrient composition and other quality traits of potato tubers are influenced by the supply and availability of macro- and micronutrients. However, the impact of nutrients on potato quality is influenced or overlapped by many other factors. The fertilization management and nutrient availability for the plant has a certain effect on tuber yield and size as well as on the content of N-compounds (Pawelzik and Möller 2014). Many studies emphasize besides the nutrient management the effect of individual characteristics of the cultivar and/or interaction with environmental factors (e.g. Bártová et al. 2013; Lombardo et al. 2013; Brazinskiene et al. 2014). The aim of the second part of this review is to evaluate the current state of knowledge about the functions of potassium, magnesium, and nitrogen in plant physiology with focus on potato quality formation but not in relation to interactions with other environmental factors.

Important potato quality traits

Particularly in potato production, the term ‘quality’ is a multifaceted trait that depends heavily on the intended use of the final product (Talburt and Smith 1987; Hiltrop 1999; Gerendas and Führs 2013). For potatoes used for fresh consumption, among the external quality parameters, even the cooking type—described as floury or mealy, medium, waxy or hard-boiling—is important. The cooking type as an internal quality trait is mainly determined and influenced by the starch content, which, in turn, is positively correlated with the specific gravity and the dry matter content of the tubers (Smith 1977; Talburt and Smith 1987; Feltran et al. 2004). When potatoes are produced for starch production, the starch concentration in the tubers is the most important quality parameter. Meanwhile, the dry matter content represents an important quality criterion when producing potatoes for further processing, such as for French fries or crisps. High dry matter content and its distribution within the tuber ensure a lower oil absorption, which results in a higher yield per unit of oil and improves the texture and shape of the product (Kita 2014). In addition to the various internal quality traits described here, the tendency of potatoes to form undesirable discolorations of various origins represents an important quality criterion. The mechanical impact on potato tubers during harvest and post-harvest handling causes, besides external damage and physiological aging during storage, also the internal discoloration of tuber tissue. Enzymatic oxidative processes lead to black spot incidence, especially in the tissue beneath the perimedullary tissue—inside the vascular ring (Baritelle and Hyde 2003). Upon mechanical impact, free phenolic compounds are oxidized by polyphenol oxidases (PPOs) to dopaquinone. These will be transformed to the dark pigment melanin (McGarry et al. 1996).

Figure 3 shows a schematic illustration of these processes. The same reaction occurs during the processing of raw potatoes and it is called as raw pulp discoloration. Beside enzymatic caused reactions the discoloration of potato tuber products can be caused non-enzymatically during the Maillard reaction and as after-cooking darkening. The Maillard reaction takes place during the frying and baking of potato products (crisps, French fries, baked potatoes), processes that involve reducing sugars (e.g. glucose, fructose) and amino acids. This non-enzymatic browning reaction influences flavor, color, and aroma formation (Belitz et al. 2009). When the reducing sugars specifically react with asparagine, the reaction intermediates may form acrylamide. Acrylamide is known to be neurotoxic and carcinogenic, thus indicating potential risks to human health (Rice 2005; Medeiros Vinci et al. 2012). The after-cooking darkening of potato tubers is an undesirable quality trait, which may occur when tubers are exposed to air after boiling (Wang-Pruski and Nowak 2004). The darkening is a result of the reaction of chlorogenic acid and ferric ions in presence of oxygen, leading to a bluish-grey color (Smith 1977).

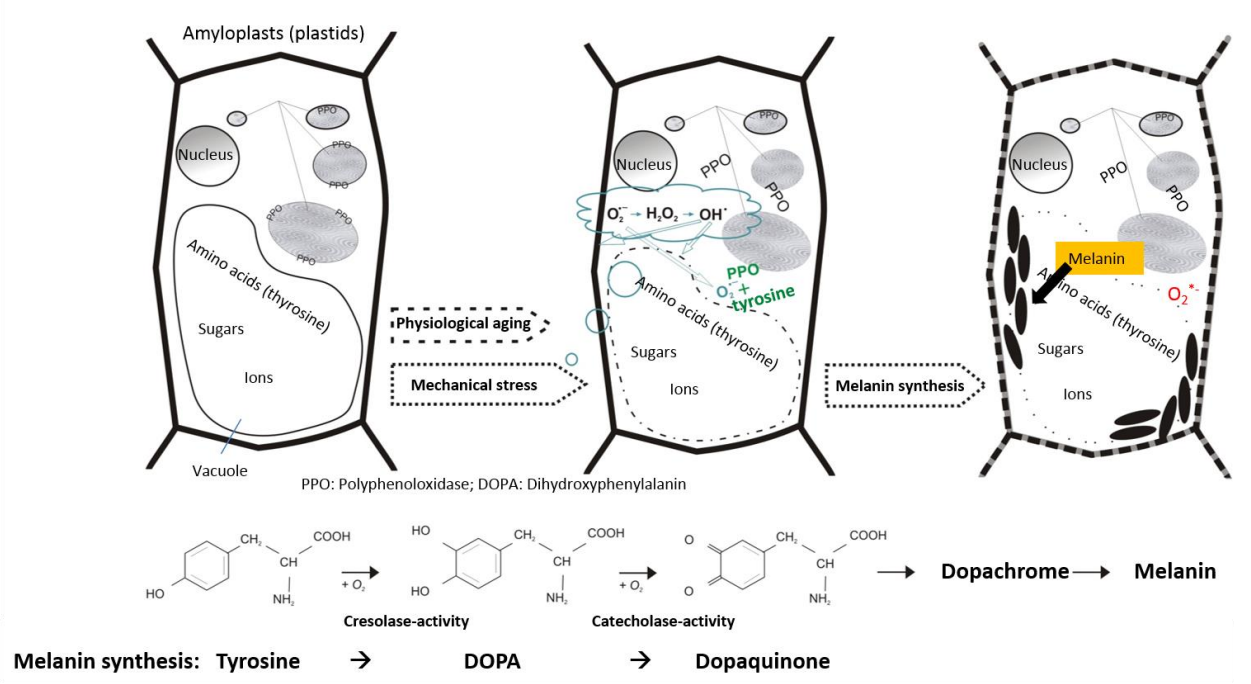

Figure 3: Mechanism leading to black spot formation (adapted from Ernst et al. (2008)).

Glycoalkaloids are potentially health-threatening compounds in potatoes. They occur in the tubers mainly as alpha-solanine and alpha-chaconine. A glycoalkaloid content higher than 100 mg/kg fresh weight (FW) leads to a bitter flavor

in potatoes (Friedman 2006). Most importantly, as they are toxic for humans (McMillan and Thompson 1979), the recommended safety level for human consumption is 200 mg/kg FW since many years (FAO/WHO 2011).

In addition, the accumulation of glycoalkaloids is associated with the greening of tubers (Maga and Fitzpatrick 1980), as both are light-induced processes (Bamberg et al. 2015). But a link between the two processes does not exist (Edwards et al. 1998). The greening of tubers occur due to non-toxic chlorophyll formation, and therefore, greening can be used as a helpful indicator that tubers have been exposed to light and, thus, should not be consumed anymore (Bamberg et al. 2015). But glycoalkaloid formation can also occur in even the non-green parts of tubers. That is why it is agreed that glycoalkaloid formation and the greening of potatoes are physiologically unrelated processes (Dao and Friedman 1994; Edwards and Cobb 1999). Figure 4 gives an overview about potato tuber properties as affected by important macronutrients. Particularly the fertilization strategy has a substantial impact on important potato quality parameters (Marschner 2012). Especially for the macronutrients K, Mg and N various studies over the last 40 years showed a direct impact on important quality traits of potatoes. But the results of these studies usually show varying responses to nutrient supply, as illustrated for Mg in Table 3.

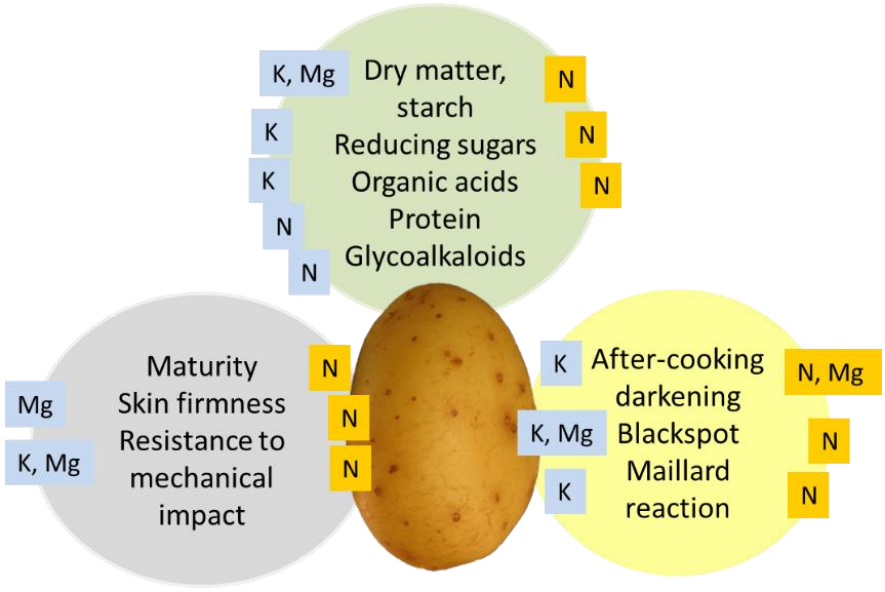

Figure 4: Potato tuber quality properties as affected by macronutrient supply: traits (grey), main compounds (green) and susceptibility to discoloration (yellow) of tubers and food. Blue: positive effects, orange: negative effects of minerals.

Table 3: Contribution of increasing Mg supply to yield, quality formation, and storability of potato tubers shown as relative changes compared to the control; green-red scale represents increased or decreased of the trait, while yellow represents no change.

Trait	Changes by increasing Mg supply compared to control samples	Mg supply, field (F), or pot (P) experiments	References
Dry matter	+ (40—50%)	0—0.3 g/pot, (P)	Addiscott (1974)
	∞	0—60 kg/ha, (P)	Miča (1979)
	+ (5—8%)	0—100 kg/ha, (F)	Poberezny and Wszelaczynska (2011)
	∞	0—60 kg/ha, (F)	Miča and Vokal (1983)
Starch	∞	0—60 kg/ha, (P)	Miča (1979)
	+ (0.5 %)	0—100 kg/ha, (F)	Poberezny and Wszelaczynska (2011)
	∞	0—60 kg/ha, (F)	Miča and Vokal (1983)
Nitrate	- (0.5—10%)	0—75 kg/ha, (F)	Rogozińska et al. (2005)
	∞	0, 56 kg/ha, (F)	Mondy and Ponnampalam (1985)
Glycoalkaloids	+ (70—200%)	0—112 kg/ha, (F)	Evans and Mondy (1984)
	+ (50—70%)	0, 56 kg/ha, (F)	Mondy and Ponnampalam (1985)
	∞	0—40 kg/ha, (F)	Rogozińska and Wojdya (1999)
Phenols	- (10—20%)	0, 56 kg/ha, (F) 0—112 kg/ha, (F)	Mondy et al. (1987) Klein et al. (1981)
Lipids	+ (0.5—10%)	0, 56 kg/ha, (F) 0—112 kg/ha, (F)	Mondy et al. (1987) Klein et al. (1981)

Changes in yield and content of quality traits: + increase, - decrease, ∞ no trend

The following passage aims to provide an overview of the most crucial impacts of K, Mg, and N on potato quality traits while considering results that are either contradictory or could not yet to be proven.

Potassium

Potassium (K) has an important impact on tuber quality. It acts as an osmotically active ion so that its accumulation in the cytosol drives water uptake into the cell and increases the cell turgor. Also, it contributes substantially to the equilibrium of soluble and insoluble ions (Marschner 2011). The positive effect of K supply on the content of organic acids as ascorbic acid in the tuber is well known (e.g. Hamouz et al. 2009). An average K concentration in tubers of about 2.2—2.5 % dry weight (DW) is assumed to be optimal for high yield and good quality (Winkelmann 1992). Field trials conducted by K+S KALI GmbH in Germany in 2002 and 2004 have also shown that an increased K supply increased the ascorbic acid concentration in tubers (Figure 5). By increasing the cell turgor in the tuber the risk of

internal enzymatic discoloration (black spot; shown in Figure 3) caused by mechanical impact stresses potentially decreases (Praeger et al. 2009) (Figure 6). As ascorbic acid counteracts the formation of reactive oxygen species, it may be involved in limiting the enzymatic formation of melanin (Delgado et al. 2001). In addition, high ascorbic acid contents in potato tubers can be regarded as a positive quality trait because the antioxidative capacity of ascorbic acid has a positive impact on human health as well (Delgado et al. 2001).

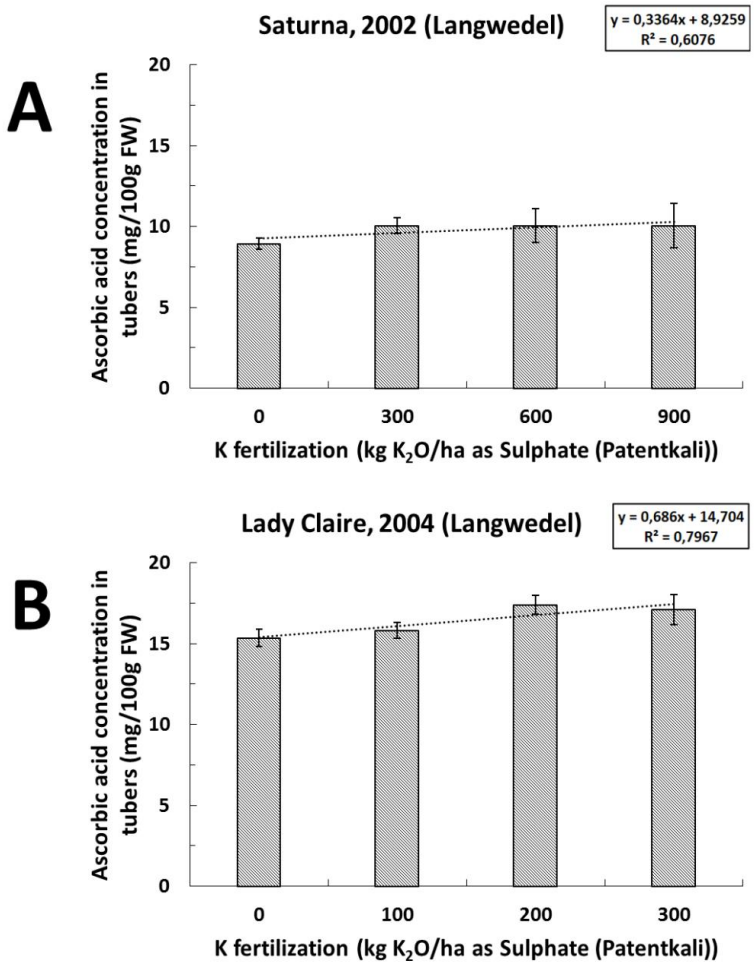

Figure 5: Effect of increasing K supply on the ascorbic acid content of potato tubers; (A) cultivar: Saturna; year of cultivation: 2002; experimental site: Langwedel (Lowery saxony, Germany); (B) cultivar: Lady Claire; year of cultivation: 2004; experimental site: Langwedel (Lowery saxony, Germany).

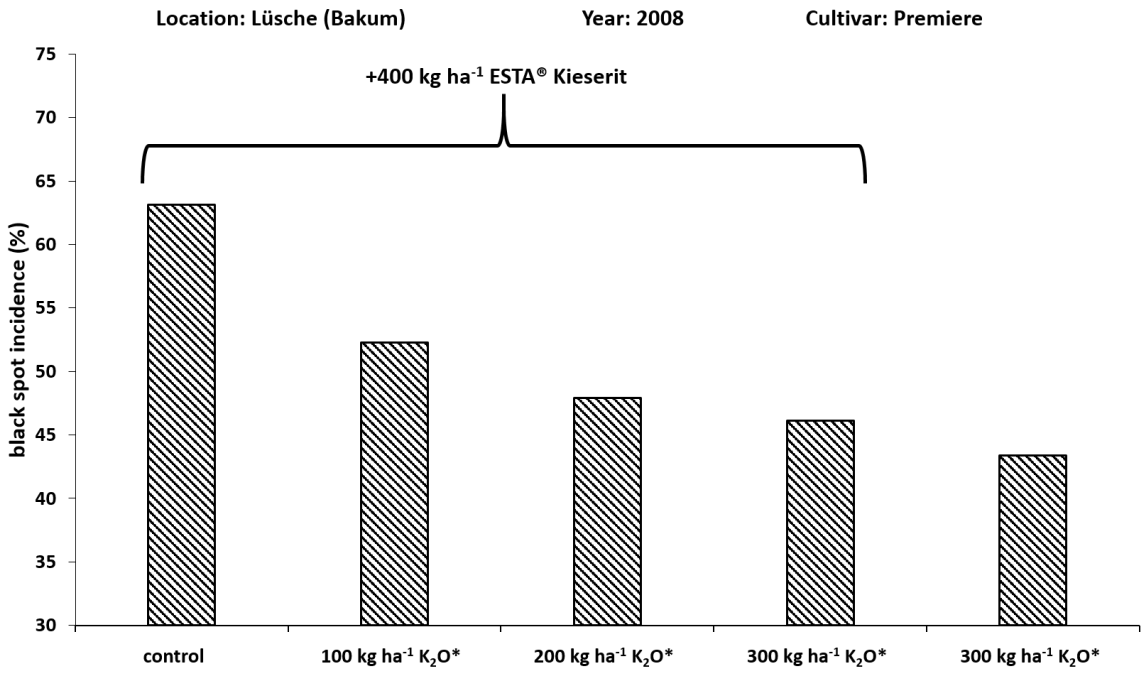

Figure 6: Effect of combined K and Mg fertilization on black spot incidence. The experimental site was Lüsche (Bakum), Northwest Germany, predominantly characterized by silty sand. Soil analysis showed 13.6 mg K_2O 100 g^{-1} soil after calcium acetate lactate (CAL) extraction and 3.2 mg Mg/100 g^{-1} soil after $CaCl_2$ extraction; ESTA® Kieserit = 25% MgO (water-soluble) and 50% SO_3 (water soluble); *as KALISOP® gran. = 50 % K_2O (water-soluble) and 45% SO_3 (water-soluble).

Increasing K concentration in tubers, generated by K supply, lead to lower content of reducing sugars (Figure 7) which are important precursors of acrylamide formation during Maillard reaction (Matthäus and Haase 2014). The cause of the after-cooking darkening can be encountered through high contents of citric acid, as citric acid competes with the phenolic compound chlorogenic acid to bind ferric ions (in fact, citric acid is in plants the transport form of Fe) (Wang-Pruski and Nowak 2004). Indeed, in potato, a positive correlation between the K content in tubers and the citric acid content was also found in field trials in 2002 and 2004 (Figure 8).

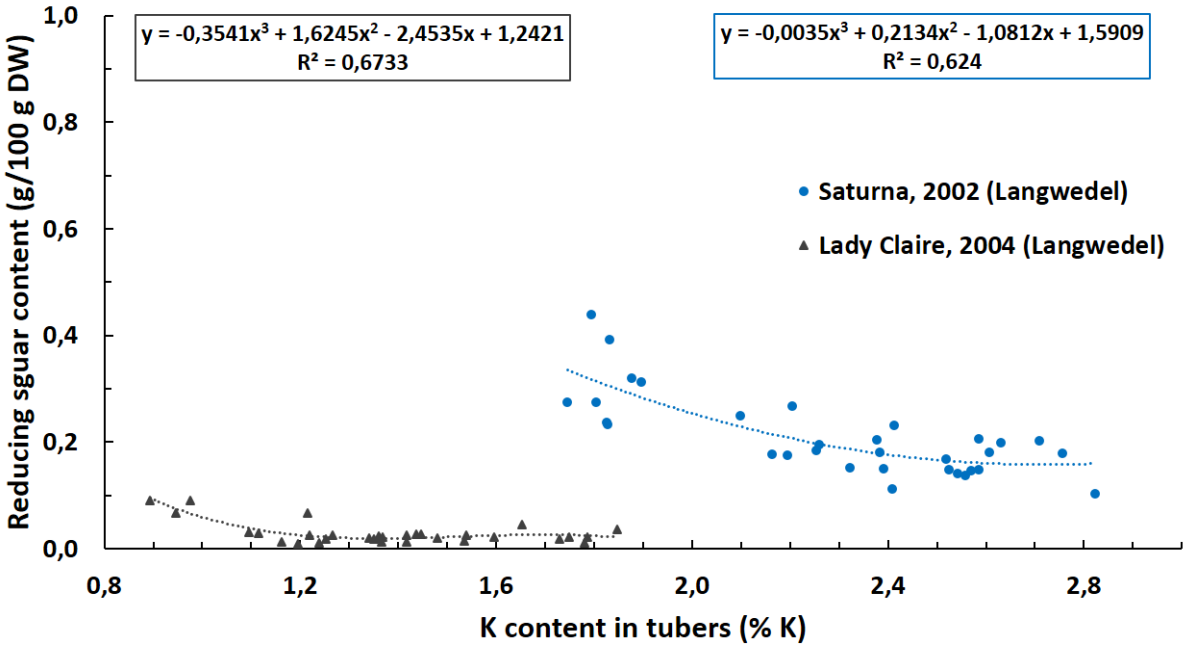

Figure 7: Effect of increasing K concentration in potato tubers on the reducing sugar content of potato tubers. Data from K+S KALI GmbH, unpublished.

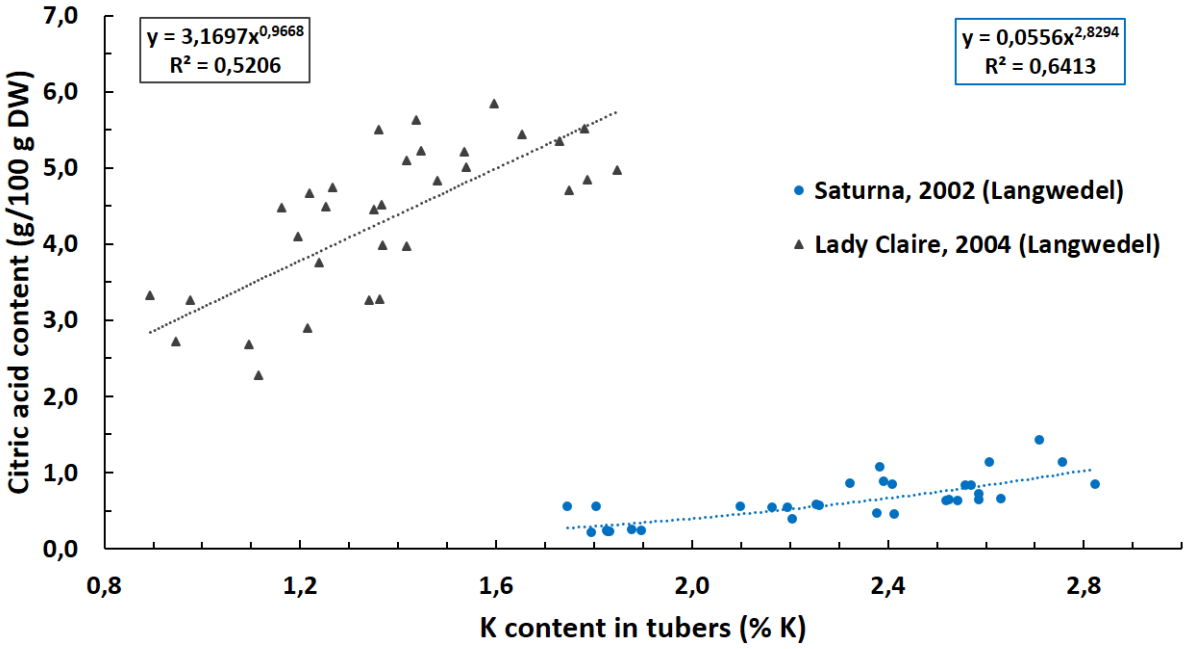

Figure 8: Effect of increasing K concentration in potato tubers on the citric acid content of potato tubers. Data from K+S KALI GmbH, unpublished.

As K is involved in many physiological processes, including enzyme-activation processes, a deficiency of K can lead to the accumulation of low-molecular-weight compounds, such as soluble sugars, organic acids, or amino acids, and decrease the synthesis of high-molecular-weight compounds, such as proteins, starches, or cellulose (Wang et al. 2013). For instance, K is required for the activity of starch synthase; therefore, a deficit of K can limit the formation of starch (Nitsos and Evans 1969; Subramanian et al. 2011), impair the ATP formation and the phloem loading of carbohydrates and increase the plant respiration as well (Römheld and Kirkby 2010; Marschner 2011); hence, the formation of potato tubers can be delayed and restricted, particularly under very severe K deficiency stress. Considering the effect of K supply on glycolalkaloids, Ahmed and Müller (1979) ascertained a decreasing effect of increasing K supply on the glycoalkaloid content of tubers, whereas the contents in leaves and stems remained unaffected. The storability of potatoes is positive influenced by K supply. Poberezny and Wszelaczynska (2011) showed that intermediate K doses ranging from 0—240 kg K_2O ha^{-1} (optimum: 160 kg K_2O ha^{-1}) reduced fresh weight losses in two mid-early cultivars during their storage for six months.

The **form of K application** particularly—for example as sulphate or chloride—has a significant impact on tuber quality traits. Figure 9 summarizes the effect of different K fertilizers on yield, starch yield, and starch content. Independent of the K-form supplied (either as K_2SO_4 or KCl), the yield is increased with increasing K fertilization. However, fertilization with KCl reduced the starch content of the potatoes by about 2%, finally leading to a starch yield that was about 1 t ha^{-1} lower than after K application in the sulphate form. What could be the reason for this phenomenon? It is assumed that application of K in chloride form leads—in comparison to the sulphate form—to a lower osmotic potential in crops, as the osmotically active chloride is accumulated in higher amounts than sulphate; subsequently, it leads to a higher water uptake and, therefore, a higher vegetative growth. Higher vegetative growth rates, particularly of the above-ground plant parts, lead to an increasing competition for assimilates between shoot and tubers, as the shoot is a strong sink for such assimilates K is also osmotically active (Marschner 2011). Hence, a very high accumulation of K in tubers leads to an increased uptake of water by the tuber, which can result in a dilution of the starch content independent of the form of K application.

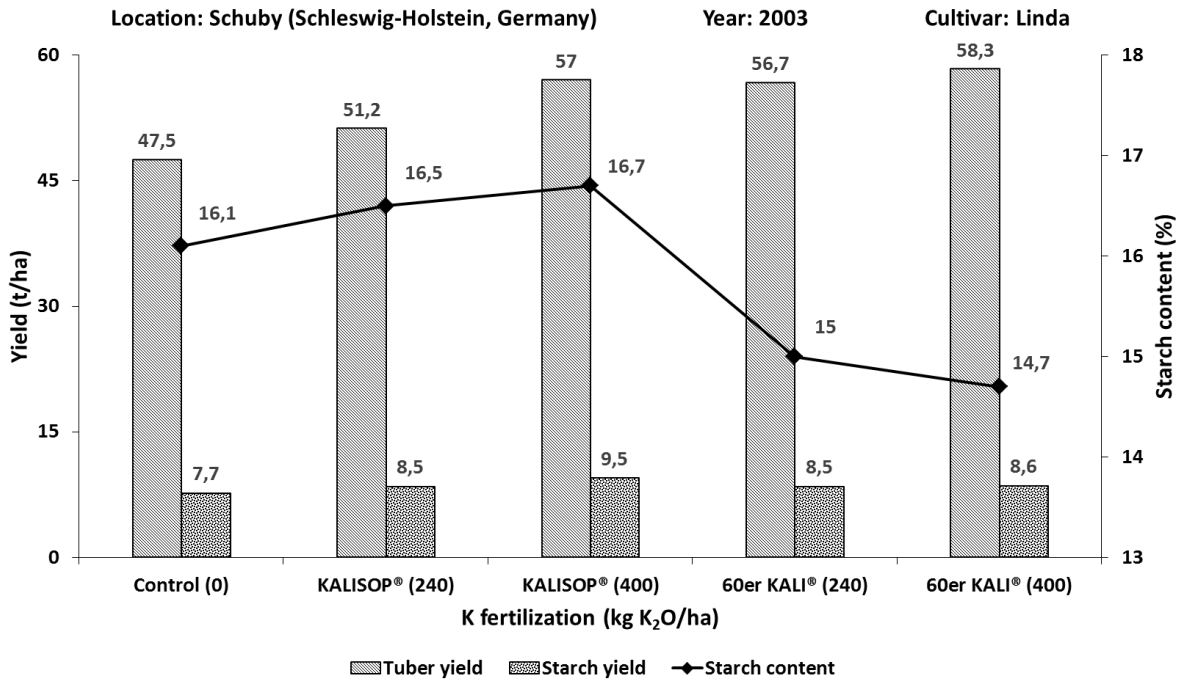

Figure 9: Effect of increasing K supply either as sulphate or as chloride on yield, starch yield, and starch content of potato; Mg supply in all variants: 320 kg ha-1 ESTA® Kieserit gran.. Data from the Agricultural Chamber of Lower Saxony, Germany, 2003.

Magnesium

Limited studies are available to review the functions of Mg on tuber quality. Mg might contribute to the stabilization of cell wall associations (Andersson et al. 1994) and it can be assumed that Mg tends to improve the resistance towards mechanical stress that affect tubers. Findings regarding the effect of Mg supply on enzymatic discoloration and the accumulation of minor compounds are not consistent, as reviewed by Gerendas and Führs (2013). For example, Klein et al. (1981) found that fertilization with $MgSO_4$ reduced enzymatic discoloration and the concentration of phenolics, whereas Mondy et al. (1967) showed a positive correlation between them. These contradictory results may indicate that possible interactions with other production system-related factors may mask the involvement of Mg in this specific quality response. It is commonly known that the enzymatic cascade finally leading to melanin formation and, subsequently, to black spot occurrence is inhibited by a low pH value and antioxidants (Altunkaya and Gökmen 2008). As proof of concept, increasing citric and/or ascorbic acid in the tubers contribute to the reduction of enzymatic discolorations. The synthesis of ascorbic acid originates from glucose (Marschner 2011), and a positive influence of favorable environmental conditions for photosynthesis (e.g. high light intensity) on ascorbic acid concentrations in various crops was reported (e.g. Noctor and Foyer 1998). The significance of Mg for assimilation and carbohydrate

translocation may imply a positive effect of increased Mg supply on ascorbic acid formation. However, Mondy and Ponnampalam (1986) did not observe significant effects of increasing Mg supply on the concentration of ascorbic acid, which agrees with the early reports of (Karikka et al. 1944). Gerendas and Führs (2013) concluded from these contrasting results on phenol and ascorbic acid contents with respect to the occurrence of black spots that all these parameters are associated with several environmental factors that were not controlled in the field experiments referred to and therefore these factors may have masked the effect of Mg.

With respect to non-enzymatic browning, to our knowledge, no results have been published yet on the effect of Mg supply on the content of reducing sugars, asparagine or acrylamide formation in tubers and processed food, even though an effect can be expected considering the Mg function in protein biosynthesis and carbohydrate partitioning (Gerendas and Führs 2013). Future studies are necessary to clarify this point.

Numerous reports are available on the effect of Mg supply on glycoalkaloid accumulation in potato tubers. Evans and Mondy (1984) as well as Mondy et al. (1987) observed a significant increase in glycoalkaloid concentration in tubers (see Table 3). The authors suggested that this is due to a stimulation of sugar metabolism, and/or an increase in amino acid production. This theory is supported by reports referring to the same field experiments, where it was shown that Mg application increased both the total N and the protein concentration (Klein et al. 1982; Mondy and Ponnampalam 1985). Thereby, the maximal total amino acid concentration correlated with the maximal total glycoalkaloid concentration (Evans and Mondy 1984). However, contradictory results were described by (Rogozińska and Wojdya 1999). They found no influence of the Mg supply on the glycoalkaloid concentration of potato tubers.

Regarding the storability of potatoes, also very limited results on the effect of Mg are available. However, in the above cited study, Poberezny and Wszelaczynska (2011) showed that intermediate Mg doses ranging from 0—100 kg MgO ha^{-1} (optimum: 60 kg MgO ha^{-1}) reduced similar to K also fresh weight losses during six months of storage.

Nitrogen and interactions with potassium

Nitrogen is essential for many physiological functions in the cell and subsequently, for plant growth and yield formation (see part I of the review). However, many quality traits are affected adversely (Figure 4). It is obvious that the N nutrition has a substantial impact on the formation of amino acids (Marschner 2012). Potato tubers contain considerable amounts of free amino acids (Farré et al. 2001); thereby, the amino acid pattern is typically characterized by high amide contents which include mainly asparagine and glutamine. About 14—31% of the total amino acids in tubers were shown to be asparagine (Elmore et al. 2015). An accumulation of particularly asparagine in response to a

high N supply has been observed, which is typically referred to the favorable low C/N ratio of this storage and transport form of N in plants (Muttucumaru et al. 2013). As mentioned, the formation of acrylamide is specifically formed by the reaction of reducing sugars with asparagine (Matthäus and Haase 2014). Therefore, the formation of acrylamide also depends heavily on the N nutrition (De Wilde et al. 2006). This is particularly true during a K deficiency, as not only the production of amides is increased by a high N supply, but also the transformation of amides into proteins is reduced by a K deficiency. Therefore, in principle, the higher the N/K supply ratio, the higher is the risk of acrylamide formation. Decreasing the ratio by decreasing the N supply and increasing the K supply instead reduces the risk of acrylamide formation (Gerendás et al. 2007).

Other nutrients

Beside potassium, magnesium and nitrogen, further nutrients are having tremendous impact on quality formation in potato. Calcium (Ca) is needed for cell wall and membrane stabilization (Palta 2010; Hirschi 2004). In cell walls Ca contributes to their characteristic structure by bridging galcturonates of pectin via carboxylate groups (Subramanian et al. 2011) while membrane stabilization is caused by bridging the phosphate and carboxylate groups of phospholipids and proteins at membrane surfaces (Legge et al. 1982; Kirkby and Pilbeam 1984). Based on these functions for cell wall and membrane stability it can be expected that Ca is essential for establishing and maintaining potato skin firmness and in addition giving tubers higher resistance against pathogens as for example has been shown by McGuire and Kelman (1984). They found a reduced severity of bacterial soft rot caused by *Erwinia carotovora* pv. *atroseptica* with increased calcium concentrations of tubers. Unfortunately potato tubers showing naturally very low Ca contents which can be contributed to the fact that Ca is mainly transported together with water via the xylem and potato tubers are transpiring very less (White and Broadley 2003; Subramanian et al. 2011). Ca deficiency can even lead to cell death (Palta 2010) and causing therefore internal brown spots for instance which can also reduce potato tuber quality (Clough 1994). But already Collier et al. (1978) could show that an additional supply of Ca can increase tuber Ca concentrations and reduce the occurrence of internal brown spots. Moreover studies by Kratzke and Palta (1986 and 1985) and Palta (2010) could show that Ca concentrations of tubers can be increased if Ca is directly applied to the tuber-stolon area.

Beside nitrogen also sulphur (S) has decisive impact on amino acid formation and hence protein synthesis. Therefore under S-deprivation the proportion of S-containing essential amino acids, namely cysteine and methionine, can be reduced while the proportions of other amino acids can be increased (Eppendorfer and Eggum 1994; Marschner 2011). As described above acrylamide is formed by reducing sugars reacting with asparagine. Prosser et al. (2001) are

discussing different studies with different cultures than potato which observed under S-deficiency an increase of the transport amino acids glutamine and asparagine. In potato, Elmore et al. (2007) could show a variety dependent increase of acrylamide precursors under S deprivation but no increase of acrylamide itself. They arguing their findings that the acrylamide formation depends on the separate amounts of amino acid and sugar precursors and that in their case of study precursor amino acids were present in a much higher amount than precursor sugars which may also react with acrylamide non-precursor amino acids.

Up to 75 % of the potato tuber is formed by carbohydrates while starch represents the predominant carbohydrate (McGill et al. 2013). Potato starch quality is dependent on different physical and chemical characteristics which are mainly determined by its amylose content, granule size and glucose-6-phosphate content (Christensen and Madsen 1996; Haase and Plate 1996). The bound phosphorus (P) in starch, mainly present as glucose-6-phosphate, is responsible for its unique properties in view of gelatinization temperatures and cross linking ability (Christensen and Madsen 1996). ThereforeTherefore, also P is of central relevance for potato tuber quality development, especially in case of potatoes for starch production.

Conclusion

An adequate supply of potatoes with nutrients is important for achieving not only high yield but also the desired quality. Besides appropriate nutrients and their ratios even the choice of fertilizer can be of particular relevance. Among the principles of adequate potato nutrition, other agronomic measures like choice of cultivar and plant protection need to be considered as well.

Chapter 4

Differential effects of varied potassium and magnesium nutrition on production and partitioning of photoassimilates in potato (*Solanum tuberosum* L.) plants

Mirjam Koch, Matthies Busse, Marcel Naumann, Bálint Jákli, Inga Smit, Ismail Cakmak, Christian Hermans and Elke Pawelzik

Submitted

Differential effects of varied potassium and magnesium nutrition on production and partitioning of photoassimilates in potato plants

Mirjam Koch[1*], Matthies Busse[1], Marcel Naumann[1], Bálint Jákli[2], Inga Smit[1], Ismail Cakmak[2, 3], Christian Hermans[4] and Elke Pawelzik[1]

[1] Department for Crop Sciences, Division Quality of Plant Products, Carl-Sprengel-Weg 1, 37075 Göttingen, University of Göttingen, Germany
[2] Institute of Applied Plant Nutrition, Carl-Sprengel-Weg 1, 37075 Göttingen, Germany.
[3] Biological Sciences and Bioengineering Program, Faculty of Engineering and Natural Sciences, Sabanci University Tuzla, Istanbul, Turkey.
[4] Laboratory of Physiology and Molecular Genetics of Plants, Interfaculty School of Bioengineers, Université libre de Bruxelles, Campus plaine CP 242, Bd du triomphe, 1050 Brussels, Belgium.

[*] Corresponding author: Mirjam Koch, Department for Crop Sciences, Division Quality of Plant Products, Carl-Sprengel-Weg 1, 37075 Göttingen, University of Göttingen, Germany. Tel.: 49(0)551-39-25568. Fax: 49(0)551/39-25570. Email: mirjam.koch@agr.uni-goettingen.de.

Keywords

Mineral deficiencies, nutrient interaction, potato, sugar transport systems, source–sink relationship

Abstract

Potassium (K) and magnesium (Mg) are essential macronutrients for plants; they play crucial roles for photoassimilate production and transport. The knowledge on both individual and interactive effects of K and Mg nutrition in potato is limited. As potato tubers are strong sink organs for photoassimilates, we aimed to determine if and how K- or Mg-deficiency impairs photoassimilate production and transport, and consequently, plant and tuber development. Potato plants were grown in pots using sand under various K and Mg supplies. They were surveyed for biomass production, CO_2 net assimilation, leaf sugar concentrations, and transcript levels of H^+/sucrose symporters in leaves. Both K- and Mg-deficiency reduced CO_2 net assimilation and biomass production, with stronger reductions in case of K-deficiency. Sugars accumulated in leaves of K- and, more importantly, of Mg-deficient plants. Low K supply resulted in increased transcript levels of H^+/sucrose symporters, with less expression under Mg-deficiency. The latter case probably was caused by an impaired sucrose transport already at an earlier step, namely the efflux of sucrose from mesophyll cells into the apoplasm. Thus, we assume that K- and Mg-deficiency caused sugar accumulation in seperated cell compartments of source leaves leading to a different impact on the gene expression of sucrose transport systems. Tuber

sugar and starch concentrations, however, remained unaffected under the various treatments. Nevertheless, the total amount of tuber sugar and starch per plant decreased significantly upon K- and Mg-deficiency.

Abbreviations

Ct, cycle threshold; DAP, days after planting; E, primer efficiency; G6P-DH, glucose-6-phosphate dehydrogenase; HEPES, hydroxyethylpiperazine-ethanesulfonic acid buffer; HK, hexokinase; INV, invertase; OD, optical density; PGI, phosphoglucose isomerase; rpm, rotations per minute; StSUT, *Solanum tuberosum* sucrose transporter

Introduction

Potato (*Solanum tuberosum* L.) can produce a more nutritionally important biomass in a shorter period of time than cereals, which makes potatoes one of the most important non-grain foods in the world (Rajiv and Kawar 2016). Furthermore, potato tubers offer excellent nutritional value with the potential to contribute to global food and nutrition security (Camire et al. 2009).

To ensure the successful cultivation of potatoes, careful consideration of cultivar choice and agronomic management are essential (Firman and Allen 2007; Kirkman 2007). In particular, a balanced fertilization is crucial for the mineral nutrition of that crop (Firman and Allen 2007). Among macronutrients, nitrogen (N) (Silva et al. 2013), phosphorus (P) (Rosen et al. 2014), potassium (K) (Panique et al. 1997) and, magnesium (Mg) (Mondy and Ponnampalam 1986) are of central importance to ensure a better productivity and quality in potato. While there is an abundance of literature on the effects of N and P, knowledge on the interaction between K and Mg nutrition is limited. Potassium acts as the main osmoticum to maintain a better cell growth and turgor pressure (Mengel and Arneke 1982; Anschütz et al. 2014), hydraulic conductance (Oddo et al. 2011; Chen et al. 2016), leaf expansion (Jordan-Meille and Pellerin 2004), root elongation (Song et al. 2017), transport of photoassimilates between source and sink organs (Cakmak et al. 1994b; Hu et al. 2017), and regulation of stomatal guard cells (Raschke 1975). Additionally, K is crucial for maintaining photosynthesis (Tränkner et al. 2018) by facilitating CO_2 diffusion through the leaf mesophyll (Jákli et al. 2017). Magnesium is important for the energy metabolism, light harvesting (Verbruggen and Hermans 2013), and photoassimilate allocation (Cakmak et al. 1994a). Due to greater sensitivity of sink organs to low Mg supply, significant impairments occur in development of sink organs in different plant species such as in root growth (Cakmak et al. 1994b; Farhat et al. 2016) and seed development (Ceylan et al. 2015).

In many crop species with sink organs that are of agronomical interest (e.g. tuber and taproot), a critical component of the photoassimilate partitioning between source and sink is the proton-driven sucrose symport (Van Bel 2003). This active transport system in the phloem couples sucrose translocation across the plasma membrane to the proton motive force generated by the H^+-ATPase, which requires Mg-ATP to function (Cowan 2002; Hermans et al. 2005). During Mg-deficiency, phloem loading is impaired and sucrose accumulates in the apoplasm (Hermans et al. 2005). As sucrose concentration builds up in leaves, greater expression levels of genes encoding H^+/sucrose symporters are observed in several plant species (Hermans et al. 2004; Hermans et al. 2005). A similar scenario is possible under K limitation, as K is necessary for not only phloem-loading but also the transport of sucrose within the phloem. The activity of the H^+-ATPases is dependent on a finely tuned pH value, for which K is needed. Furthermore, K establishes an osmotic potential within the phloem, which is needed to translocate sucrose from source to sink organs (Hayashi and Chino 1990; Cakmak et al. 1994a). Consequently, low K supply leads to the accumulation of sucrose in source leaves due to impaired sucrose-loading into the phloem and/or due to limited osmotic effects of K in the phloem sieve tubes. Besides, a reduction in phloem transport of sucrose could also be a consequence of a limited symplastic unloading of sucrose into the sink cells due to reduced sink strength (Hütsch et al. 2016).

Mineral elements can compete for root uptake (Fageria 2001). For example, an antagonistic interaction is reported between K and Mg. This can be attributed to different transport systems that are responsible for the uptake of these two elements. While putative transporters for Mg are unspecific and take up cations other than Mg, K transporters are very specific and the uptake of K is ensured under both low and high K concentrations in the soil solution (Senbayram et al. 2015). Nonetheless, there are also reports on the synergy between K and Mg. For instance, Ding et al. (2006) showed a synergistic mechanism of increasing Mg supply on K uptake and translocation in rice. Similar results were demonstrated by Narwal et al. (1985) in cowpea (*Vigna unguiculata* L. Walp.).

As potato tubers are strong sink organs, it seems that tuber yield and starch formation must be highly dependent on photosynthesis and the export of photoassimilates from source leaves. Owing to the indispensable functions of K and Mg in photosynthesis and translocation of photoassimilates in plants, this study focuses mainly on the impact of varied applications of K and Mg on CO_2 net assimilation and on parameters that provide indications about the partitioning of photoassimilates, such as soluble sugar concentrations and gene expression of H^+/sucrose symporters in source leaves, in potato. In light of this, plant shoot and root growth, tuber yield, and tuber sugar and starch formation were investigated. Furthermore, the changes in tissue concentrations of K and Mg were studied under different combined applications of K and Mg in order to collect further information about K and Mg interactions in potato plants.

Materials and methods

Plant growth conditions

Potato plants (*Solanum tuberosum* L.) of the cultivar "Laura" were grown for a period of 98 days individually in pots (capacity 11 L) filled with nutrient-poor sandy soil. The experimental design was completely randomized. For inducing germination, the tubers were stored for 10 days in darkness at room temperature. Tuber slices with one germ bud (~1 cm length) were planted. Plants were first cultivated in a greenhouse with an average temperature of 20°C, 48% relative humidity, and 12 h light (300 µmol m^{-2} s^{-1}; MASTER Agro 400 W, Philips, Netherlands) and 12 h darkness. After 27 days, the plants were transferred to an outdoor installation (mean temperature, precipitation, and irradiance are shown in under supplementary material (SM) SM_1). Five fertilization regimes of K and Mg were applied (Table 1) to 10 biological replicas: low K with sufficient Mg supply (K1+Mg), moderate K supply with sufficient Mg supply (K2+Mg) or low Mg supply (K2-Mg), high K supply with sufficient Mg supply (K3+Mg) or low Mg supply (K3-Mg). The two elements were applied in the form of K_2SO_4 or $MgSO_4.7.\ H_2O$ (Table 1). All quantities of other mineral elements applied to the soil are presented in SM_2. The soil K and Mg status before the fertilization treatment was 1.5 mg K 100 g^{-1} soil and < 1 mg Mg 100 g^{-1} soil.

Table 1: Overview of the K and Mg supply (mg kg^{-1} soil) before planting of the different fertilization treatments. * signifies additional 5 mg K kg^{-1} soil 27 DAP.

Fertilization treatment	K	Mg
K1+Mg	30 (+5*)	100
K2+Mg	300	100
K2-Mg	300	5
K3+Mg	600	100
K3-Mg	600	5

Phenotypic observation, shoot and root biomass recording, and root scanning

The whole plant phenotype was documented by taking pictures throughout the treatment. Changes in growth were recorded by measuring plant height and counting the internodes. At harvest, biomasses of leaves, roots, and tubers were measured separately and roots were stored at –20°C. Root scanning was conducted using a flat-bed scanner

(Epson Perfection V700 Photo, Epson, Germany) and analyzed with the software WinRhizo 2016 (Regent Instruments Inc., Québec City, Canada). Only half of each root was used and the total root length was calculated for the whole root on the basis of the determined dry weight of the scanned root part and the non-scanned root part.

Mineral analysis in plant tissues

Leaf and root samples were dried for four days at 60°C and crushed into fine powder. Tubers were cut into pieces and freeze-dried for four days in a freeze-dryer (EPSILON 2-40, Christ, Germany). Subsequently, the residual moisture was assessed by determining the weight of a subsample of the freeze-dried potato flour before and after drying for 12 hours at 105°C. Root samples were dried at 60°C for four days and later ground into 0.5 mm flour in a hammer mill (DFH 48, Culatti, Switzerland). Mineral concentrations were determined according to an adjusted method, as described by Wheal et al. (2011). 100 mg of each sample were digested in 4 ml of 65% (v/v) nitric acid and 2 ml of 30% (v/v) hydrogen peroxide for 75 min at 200°C and 40 bar in a microwave (Ethos 660; MWT AG, Switzerland). Afterward, the samples were filled up to 25 ml with distilled water. The element concentrations were measured with inductively coupled plasma optical emission spectrometry (Vista-PRO CCD Simultaneous ICP-OES; Varian Inc., USA).

Gas-exchange measurements and chlorophyll determinations in fully expanded leaves

Net CO_2 assimilation of fully expanded leaves (4 cm^2) was quantified by using a portable gas-exchange device (GFS-3000, Heinz Walz GmbH, Germany) under ambient temperature, relative humidity, and CO_2 concentration (~390 ppm), and light intensity of 400 µmol m^{-2} s^{-1} (cloudy condition) or 1,000 µmol m^{-2} s^{-1} (sunny condition).

For chlorophyll determination about 20 mg of leaf tissue was ground in liquid nitrogen and extracted successively twice with 80% (v/v) and a third time with 50% (v/v) ethanol. The samples were shaken in a heat block at 95°C for 30 minutes. After the third extraction step, the supernatants were combined, the pellet discarded, and the samples stored at –20°C until further analysis.

Chlorophyll was examined as described by Arsovski et al. (2018). For the results, the sum of chlorophyll *a* and *b* was considered.

Soluble sugar quantification in fully expanded leaves

The soluble sugars were determined following the procedure developed by Stitt et al. (1989) after some modifications. The same ethanolic extract as for chlorophyll extraction was used. Sugars were converted by the added enzymes

hexokinase (HK; Roche Diagnostics GmbH, Germany and Merck, Germany; EC number 2.7.1.1), phosphoglucose isomerase (PGI; Roche Diagnostics GmbH, Germany; EC number 5.3.1.9), and invertase (INV; Sigma Aldrich, USA; EC number 3.2.1.26). For dissolving the enzymes, a 100 m*M* hydroxyethylpiperazine-ethanesulfonic acid (HEPES) buffer (Roth, Germany) and a 3 m*M* $MgCl_2$ buffer (adjusted with KOH to pH 7) was used. Half of the samples were prepared with HK in suspension (Roche Diagnostics GmbH): 72 µl (108 units) HK was centrifuged for three min at 11 000 rpm and the pellet was dissolved in 120 µl HEPES-$MgCl_2$ buffer. The other half of the samples was prepared with HK in solid form (Merck, Germany): 0.50 mg was dissolved in 120 µl HEPES-$MgCl_2$ buffer. For preparation of PGI 36 µl (25.2 units), PGI was centrifuged for three minutes at 11 000 rpm and the pellet was dissolved in 120 µl HEPES-$MgCl_2$ buffer. For the preparation of INV, 8.3 mg (2,500 units) INV was dissolved in 120 µl HEPES-$MgCl_2$ buffer. A further needed enzyme was glucose-6-phosphate dehydrogenase (G6P-DH) (Roche Diagnostics GmbH, Germany; EC number 1.1.1.49), which was prepared together with 100 m*M* ATP (Sigma-Aldrich, USA) and 45 m*M* nicotinamide adenine dinucleotide phosphate (NADP) (Roche Diagnostics GmbH, Germany) to form a solution. For this, 85 µl (60 units) G6P-DH was centrifuged for three minutes at 11 000 rpm and the pellet was dissolved in 15.5 ml HEPES + $MgCl_2$ buffer, 480 µl ATP, and 480 µl NADP solution. Next, 50 µl of the ethanolic extract plus 160 µl of the G6P-DH–ATP-NADP solution was added per well on a 96-well plate and shaken for 10 minutes. The converted NADPH was quantified by measuring the OD at 340 nm in a plate reader (Epoch, 1402203, Biotek, USA) after reaching stable values.

NADPH was calculated with the help of Δ OD (used formula: µ*M* NADPH = Δ OD/(2.85*6.22)).

The calculated values were:

1 *M* NADPH derived from glucose/fructose = 1 *M* glucose/fructose.

1 *M* NADPH derived from sucrose = 0.5 *M* sucrose (1 mole glucose equivalent).

RNA extraction and quantitative real-time polymerase chain reaction

Total RNA was isolated from 100 mg leaf tissue using the innuPREP Plant RNA Kit (Analytic Jena AG, Germany) and cDNA was synthesized from 75 ng of the total RNA using the iScript cDNA Synthesis Kit (Bio-Rad Laboratories, Germany), according to the manufacturer's instructions. Prior to cDNA synthesis, the extracted RNA was quantified by using a Qubit® RNA HS Assay Kit and the samples were measured in a fluorimeter (Qubit 3.0 Fluorimeter, ThermoFisher Scientific, Germany). A real-time PCR detection system (CFX96, Bio-Rad Laboratories, Germany) was used to quantify the expression levels of *StSUT1* and *StSUT4*. For quantitative real-time PCR (qRT-PCR), 4 µl of

diluted cDNA was used for the reaction, together with 50 µ*M* target-specific primers (SM_3) and the fluorescent intercalating dye SYBR Green (SsoAdvanced™ Universal SYBR® Green Supermix, Bio-Rad Laboratories, Germany). The protocol is shown detailed in SM_4 and the primers listed in SM_3. The relative gene copy number of cDNA was normalized to the *St_UBIQUITIN* gene and relative quantification was performed using the ΔΔ *Ct*-method after Pfaffl (2007). The K2+Mg plants were used as the control. The relative expression levels of the K2+Mg plants were set to one.

Sugar and starch examination in tubers

Prior to starch and sugar determination, tubers were prepared as described for mineral analysis.

Starch was quantified according to ICC standard no. 123 (modified). In 100 ml flasks, 25 ml of hydrochloric acid was added twice to 1 g of potato flour, placed for 15 minutes in a scalding water bath (Memmert, Germany), and shaken for the first eight minutes. The flasks were filled up to 90 ml with distilled water and cooled to room temperature. Following this, 5 ml of tungstophosphoric acid ($H_3PW_{12}O_{40}$) was added and panned. Finally, the flasks were filled up to 100 ml with distilled water and the optical rotation was examined in polarized light in a polarimeter (Zeiss, Germany) at 589 nm.

Sugars were quantified by high-performance liquid chromatography (HPLC). For extraction, 0.4 g of potato flour was shaken with 4 ml of distilled water in 15 ml centrifugal tubes horizontally for one hour. To precipitate proteins, 0.5 ml Carrez I (3.6 g $K_4Fe(CN)_6$ in 100 ml distilled water) and 0.5 ml Carrez II (7.2 g $H_{14}O_{11}SZn$ in 100 ml distilled water) solutions were added in order, then mixed and centrifuged for 20 minutes at 5000 rpm. Supernatants were transferred in 10 ml flasks and the pellet was again dissolved in distilled water, shaken for one hour, and centrifuged for 20 minutes at 5000 rpm. Finally, the supernatants were combined. The flasks were filled up to 10 ml with distilled water. The samples were filtered with filter paper (Type 615, Macherey-Nagel, Germany) in screw cap tubes and stored at –20°C until the measurement.

For HPLC measurement, the samples were thawed. Next, 5 ml was vaporized using a rotary vacuum concentrator (RVC 2-25 CD plus, Christ, Germany) and filled with 1 ml of distilled water. The fivefold concentrated solution was filled using a 13 mm syringe filter holder (VWR International, USA) in 2 ml vials and the extract was quantified through HPLC (Jasco, Japan) (injection volume = 20 µl; eluent = 80% acetonitrile and 20% water; flow rate = 1 ml/min; column = LiChrospher 100; column temperature = 22°C; refractive index detector).

All biological replicates of tubers of K1+Mg plants were pooled to four samples as the tuber yields of the single plants were not sufficient. Tubers of all remaining treatments were not pooled.

Tuber dry matter and sugar and starch yield

An average of three to five tubers per treatment (the tuber quantity used was dependent on tuber size—e.g. three bigger tubers or five smaller tubers) was used. These were cut into pieces and the fresh sample weight of a subsample was determined. Afterward, the sample was dried at 60°C for 24 hours and subsequently at 105°C for four hours and the weight was determined. The tuber sugar and starch yields (g sugar or starch, respectively, per plant in dry matter [DM]) were calculated based on the tuber DM, the sugar and starch concentrations, and the tuber yield per plant.

Statistical treatment

Statistical analysis was performed using R software version 3.4.0 (R Core Team 2016). All data were checked for normal distribution and homoscedasticity. Then, ANOVA was performed to detect differences between treatments followed by multiple contrast tests. A non–parametric Kruskal-Wallis test was performed in the case that normality and/or homoscedasticity were not verified. All tests were performed on a significance level of $p < 0.05$ (unless otherwise indicated).

Results

Signs of nutrient deficiencies

The experimental plants were affected differentially in terms of expression of leaf symptoms under given experimental conditions. In K1+Mg plants, firs spot-like and leaf-edge necrosis and chlorosis became visible on the oldest leaves, which quickly developed into severe necrosis and chlorosis or total necrotic material (Fig. 1a). The K2 and K3+Mg plants appeared lush green and only their oldest leaves were senescent (Fig. 1b and d). For K2 and K3-Mg plants, clear chlorosis and flat spot-like necrosis were noted, especially on older leaves (Fig. 1c and e).

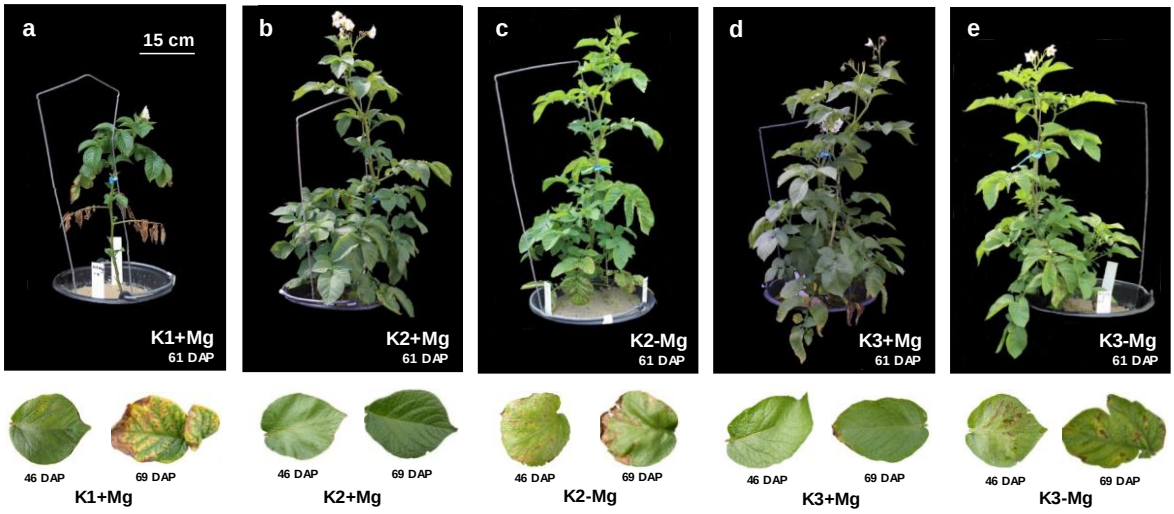

Figure 1: Plant phenotypes during K and Mg treatments. Pictures of whole potato plants were taken 61 days after planting (DAP) and close-ups of most recently expanded leaves on 46 and 69 DAP. Treatment description as in Table 1.

Plant growth and tuber yield

Shoot and root DM as well as total root length were significantly reduced in plants supplied with low K (K1+Mg), as compared to K2 and K3+Mg plants (Fig. 2a, b and c). Root DM and total root length were further reduced under low Mg supply (K2 and K3-Mg), but the difference was significant for root length only (Fig. 2b and c). The number of internodes (Fig. 2d) and plant height (Fig. 2e) were also significantly decreased in K1 compared to K2 and K3+Mg plants whereas Mg-deficient plants did not show a significant reduction in quantity of internodes as well as in plant height (data not shown). The shoot-to-root biomass ratio was increased especially in K-deficient (K1+Mg) and also in Mg-deficient plants (K2 and K3-Mg) (Fig. 2b). Both K- and Mg-deficient plants exhibited a significant reduction in tuber yield. However, low K supply reduced tuber yield by 89%, whereas low Mg supply led to only 14–16% of tuber yield reduction in K2 and K3 treatments (Fig. 2f).

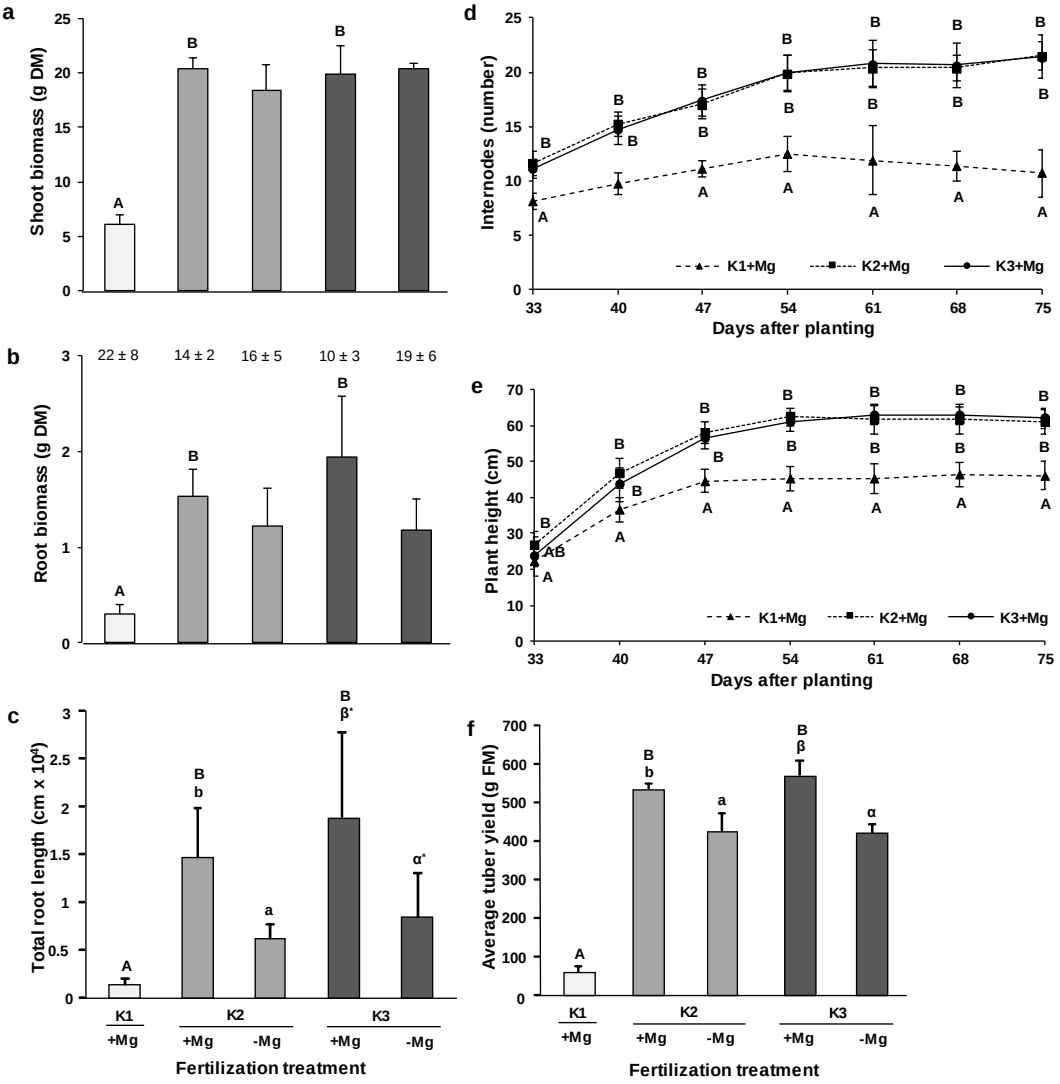

Figure 2: Effects of K and Mg treatment on biomass production and plant morphology. Shoot biomass (n = 8—10) (a), root biomass with shoot-to-root biomass ratios (mean ± SE values above bar plot; n = 5) (b), total root length (n = 5) (c), and tuber yield (n = 8—10) (f) at harvest. Number of internodes (d) and plant heights (e) (n = 8—10) on seven sampling dates after planting. Mean ± SE values. Capitals = significant differences between K treatments of +Mg plants. Small letters = significant differences between differing Mg treatments of K2 plants. Greek letters = significant differences between differing Mg treatments of K3 plants. No indication = no significant effect. $p < 0.05$; * = $p < 0.01$.

Potassium and magnesium status of fully expanded leaves

The K concentrations in leaves of K2 and K3+Mg plants were at least two times higher compared to those that received a low K supply (K1+Mg) (Table 2). On 69 days after planting (DAP), K1+Mg plants even exhibited seven times lower K concentrations compared to K2+Mg plants and nine times lower K concentrations compared to K3+Mg plants.

Plants fed with moderate or high K supplies (K2 and K3+Mg) did not show significant differences in this regard. The Mg concentrations of the same plants behaved in the opposite way: the plants with the highest K supply (K3+Mg) showed the lowest significant Mg concentrations while the plants with the lowest K supply (K1+Mg) showed the highest Mg concentrations (Table 2). The Mg concentrations of the K2 and K3-Mg plants were nearly one-tenth (K2+Mg vs. K2-Mg at 69 DAP) compared to the K2 and K3+Mg treatments (Table 2).

Potassium and magnesium status of plant organs

Leaves, tubers and roots of K-deficient (K1+Mg) plants had significantly lower K concentrations compared to K2 and K3+Mg plants, and Mg-deficient (K2 and K3-Mg) ones significantly lower Mg concentrations compared to K2 and K3+Mg plants (Fig. 3). These decreases were much more severe in leaves than in roots or tubers (Fig. 3). Considering Mg concentrations of K1+Mg plants, leaves revealed the highest significant Mg concentrations, while tubers and roots showed the lowest significant (one-tenth lower) Mg concentrations compared to leaves (Fig. 3b).

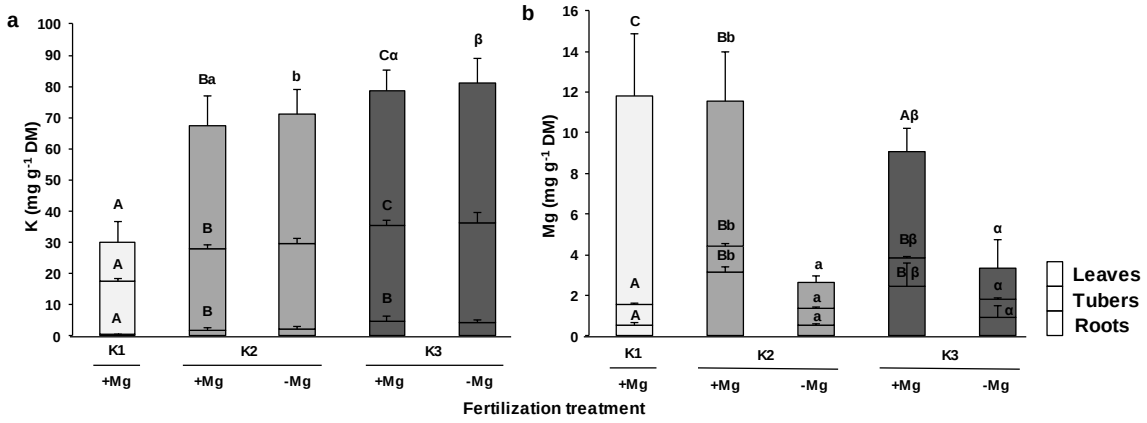

Figure 3: Effect of K and Mg treatments on element concentrations in leaves, tubers, and roots. K (a) and Mg (b) concentrations of fully expanded leaves (mean ± SE values averaged over all sampling dates; for data, see Table 2; n = 4—5) and tubers and roots after harvest (mean ± SE values; n = 8—10). Capitals = significant differences between K treatments of +Mg plants within one plant organ (leaves, tubers, or roots). Small letters = significant differences between differing Mg treatments of K2 plants of one plant organ. Greek letters = significant differences between Mg treatments of K3 plants within one plant organ. No indication = no significant effect.

Table 2: Effect of K and Mg treatments on element concentrations (mg g^{-1} DM) in leaf tissues on five sampling dates from day 34 until day 69 after planting (n = 4—5). Mean ± SE values. Capitals = significant differences between differing K treatments of +Mg plants. Asterisks = significant differences between K2 and K3-Mg plants. Small letters = significant differences in K2-Mg plants compared to K2+Mg plants. Greek letters = significant differences in K3-Mg plants compared to K3+Mg plants. No indication = no significant effect. DAP signifies days after planting.

K										
	Fertilization treatment									
DAP	**K1+Mg**		**K2+Mg**		**K2-Mg**		**K3+Mg**		**K3-Mg**	
34	21.61 ± 5.29	A	56.46 ± 1.69	B	54.37 ± 4.78		52.81 ± 4.31	B	44.12 ± 11.85	
41	16.33 ± 0.69	A	32.66 ± 2.36	B	35.10 ± 1.98		36.51 ± 1.29	B	38.46 ± 4.47	
48	8.29 ± 0.71	A	35.10 ± 4.20	B	38.16 ± 0.78		40.46 ± 2.37	B	41.96 ± 4.46	
55	14.42 ± 1.45	A	40.62 ± 2.04	B	40.73 ± 2.81	*	46.68 ± 3.28	B	51.51 ± 3.71	*
69	4.26 ± 0.51	A	33.11 ± 3.36	B	40.66 ± 5.26		41.59 ± 3.59	B	49.77 ± 1.98	
Mg										
34	8.64 ± 2.05	AB	5.55 ± 0.22	Bb	1.44 ± 0.12	a	4.62 ± 0.25	Aβ	2.79 ± 2.39	α
41	6.93 ± 0.85	B	4.43 ± 0.61	Ab	1.58 ± 0.08	a	3.99 ± 0.08	Aβ	1.52 ± 0.16	α
48	13.77 ± 0.78	C	7.01 ± 0.63	Bb	1.41 ± 0.14	a	5.73 ± 0.31	Aβ	1.48 ± 0.28	α
55	8.92 ± 1.32	B	7.99 ± 1.32	Bb	0.97 ± 0.12	a	4.95 ± 0.45	Aβ	0.74 ± 0.92	α
69	12.62 ± 1.46	B	10.74 ± 1.27	Bb	0.77 ± 0.23	a	7.09 ± 0.79	Aβ	0.75 ± 0.13	α

CO_2 assimilation rate and chlorophyll concentrations of fully expanded leaves

On 40 DAP, the CO_2 net assimilation rate of K1+Mg plants showed the lowest values while the CO_2 assimilation rate was the highest in the leaves of K2-Mg plants, but both were not significant (Fig. 4a). On 47 DAP, the CO_2 net assimilation rate of the leaves of K1+Mg plants was significantly lower compared to that of the K3+Mg plants. In addition, the leaves of the K3-Mg plants exhibited a lower CO_2 net assimilation compared to the K3+Mg plants, but without significance. On 83 and 84 DAP, further determinations of the CO_2 net assimilation rate between K2 and K3+Mg and K2 and K3-Mg plants were performed. The CO_2 assimilation rate decreased in K2-Mg as well as in the K3-Mg plants, but with a significant decrease only in the K3 plants.

The plants treated with a low K supply (K1+Mg) exhibited higher chlorophyll concentrations compared to the plants that received moderate (K2+Mg) or high (K3+Mg) levels of K on 41 and 55 DAP (Fig. 4b). However, the chlorophyll concentrations showed a significant decrease in K1+Mg-treated plants compared to the K2- and K3+Mg-treated plants on 69 DAP. There was no significant difference in the chlorophyll concentrations of leaves between the plants that received moderate (K2+Mg) or high (K3+Mg) supplies of K, but an increase in the chlorophyll concentrations was observed from 41 till 69 DAP. Lower chlorophyll concentrations were detected in the K2 and K3-Mg plants (Fig. 4c). However, these differences were not significant.

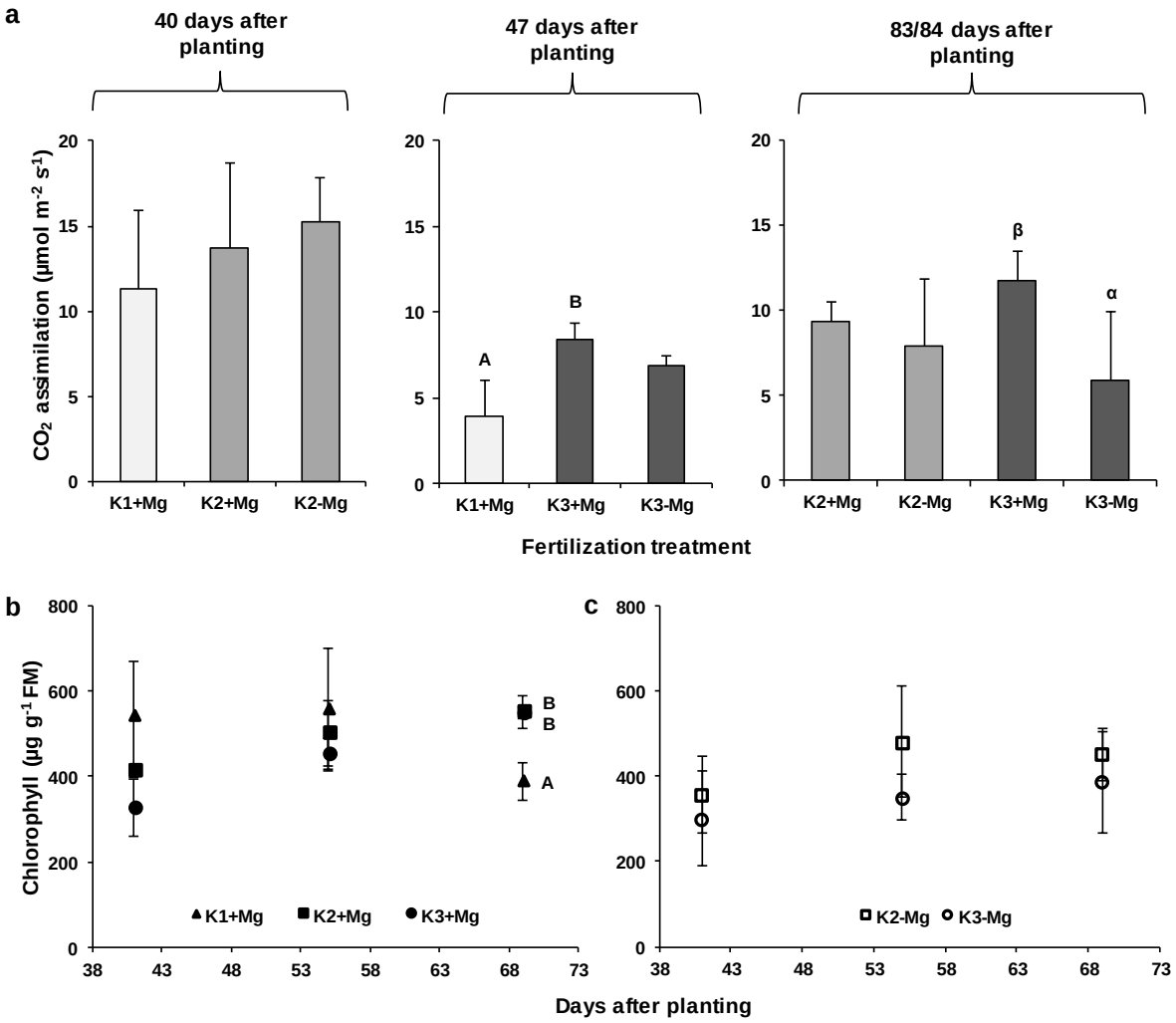

Figure 4: Effect of K and Mg treatments on CO_2 net assimilation and leaf chlorophyll concentrations.

CO_2 net assimilation rate of fully expanded leaves over time (a) of K2+Mg plants compared to K1+Mg and K2-Mg plants on day 40 after planting, of K3+Mg plants compared to K1+Mg and K3-Mg plants on day 47 after planting, and of K2+Mg/K3+Mg plants compared to K2-Mg/K3-Mg plants on days 83/84 after planting (K2 and K3+Mg were measured on day 83 and K2 and K3-Mg plants were measured on day 84 after planting), and chlorophyll concentrations in fully expanded leaves on days 41, 55, and 69 after planting of K1, K2, and K3+Mg (b) and K2 and K3-Mg plants (c) (n = 4—5). Mean ± SE values. Capitals = significant differences between differing K treatments of +Mg plants. Greek letters = significant differences between differing Mg treatments in K3 plants. No indication = no significant effect.

Soluble sugars in fully expanded leaves

The total soluble sugars increased in the leaves of K1+Mg and of K2 and K3-Mg plants compared to K2 and K3+Mg plants (Fig. 5a). While this observation was not significant on 41 DAP, the total soluble sugars significantly increased in leaves of K1+Mg-treated plants compared to K2 and the K3+Mg-treated plants, and in the leaves of K2 and K3-Mg-treated plants compared to K2 and K3+Mg-treated plants on 69 DAP. At the same time, the sum of hexose sugars (glucose and fructose) was higher in K1+Mg plants and in K2 and K3-Mg plants but significant only on 69 DAP.

Relative gene expression of the H^+-sucrose cotransporters StSUT1 and StSUT4

The relative transcript levels of the sucrose cotransporter *StSUT1* and *StSUT4* in leaves showed an up-regulation in K1 and K3+Mg plants compared to control plants (K2+Mg) on 41 and 69 DAP (Fig. 5b). In the first case, the sucrose cotransporter *StSUT4* showed a more than 150-fold increase on 69 DAP. The increase of transcript levels of both genes was more modest in Mg-deficient plants (K2 and K3-Mg) (Fig. 5c) compared to both low K (K1+Mg) and high K supplied plants (K3+Mg) (Fig. 5b). The relative transcript levels of the sucrose cotransporter *StSUT4* were higher compared to the relative transcript levels of the sucrose cotransporter *StSUT1* in K low (K1+Mg), in K high (K3+Mg) and in Mg deficient plants (K2 and K3-Mg) on 41 and 69 DAP (Fig. 5b and c).

Tuber DM, sugar and starch

The sugar and starch yields per plant revealed significant differences between the various fertilization treatments. First, K2 and K3+Mg showed significant higher yields of hexose sugars (glucose and fructose) as well as of the sum of all sugars (glucose, fructose and sucrose) per plant compared to K1+Mg plants (Fig. 6a). Second, K2 and K3+Mg plants exhibited significant higher starch yields per plant in comparison to K1+Mg plants (Fig. 6b). Besides, plants with sufficient Mg supply (K2 and K3+Mg) showed significant higher starch yields compared to Mg-deficient plants (K2 and K3-Mg) (Fig. 6b). However, the concentrations of the sum of sugars (glucose, fructose, and sucrose) as well as of the sum of hexose sugars (glucose and fructose) and of starch in tubers did not show significant differences across the fertilization treatments (SM_5b and SM_5c). Only a slight tendency can be reported in the form of lower concentrations of hexose sugars in plants with high K and sufficient Mg supply (K3+Mg) compared to the other treatments (SM_5). Besides, there was no effect of the different K and Mg treatments on tuber DM (SM_5a).

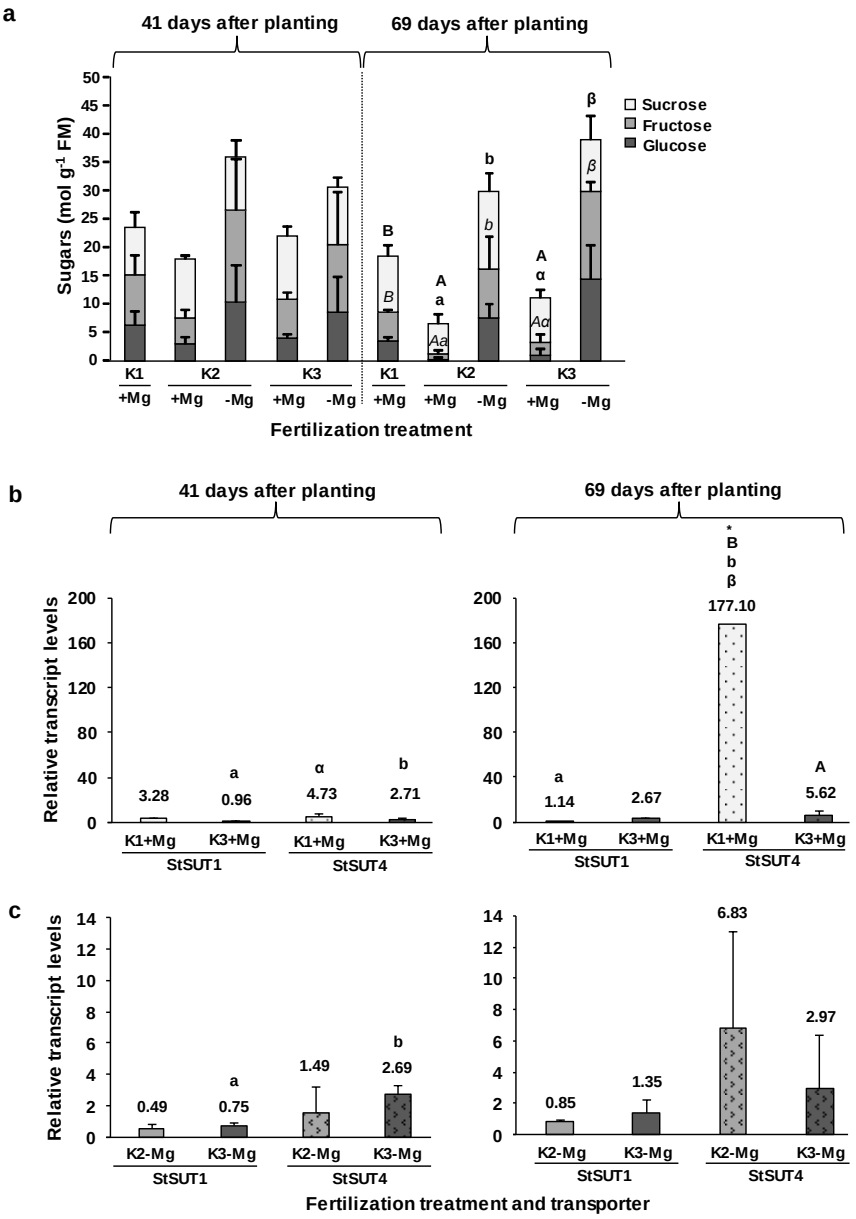

Figure 5: Effect of K and Mg treatments on soluble sugar concentrations and transcript levels of genes encoding H^+/sucrose symporters in leaves. Total soluble and hexose sugar concentrations in fully expanded leaves of all fertilization treatments on day 41 and 69 after planting (a) (n = 4—5). Mean ± SE values. Capitals = significant differences between differing K treatments of +Mg plants. Small letters = significant differences between differing Mg treatments of K2 plants. Greek letters = significant differences between differing Mg treatments in K3 plants. Non-italic letters = significant differences between total soluble sugars. Italic letters = significant differences between hexose sugars. Transcript levels of the H^+/sucrose symporters *StSUT1* and *StSUT4* in fully expanded leaves of K-depleted plants (K1+Mg) (b) and of Mg-depleted plants in the medium (K2-Mg) and high (K3-Mg) K levels (c) compared to control plants (K2+Mg) on day 41 and 69 after planting (n = 1—5). Mean ± SE values. Asterisks = significant differences to control plants. Capitals = significant differences between K1+Mg and K3+Mg plants. Small letters = significant differences between transporters at one sampling date and of one fertilization treatment. Greek letters = significant differences between 41 and 69 days after planting of one transporter and fertilization treatment. No indication = no significant effect.

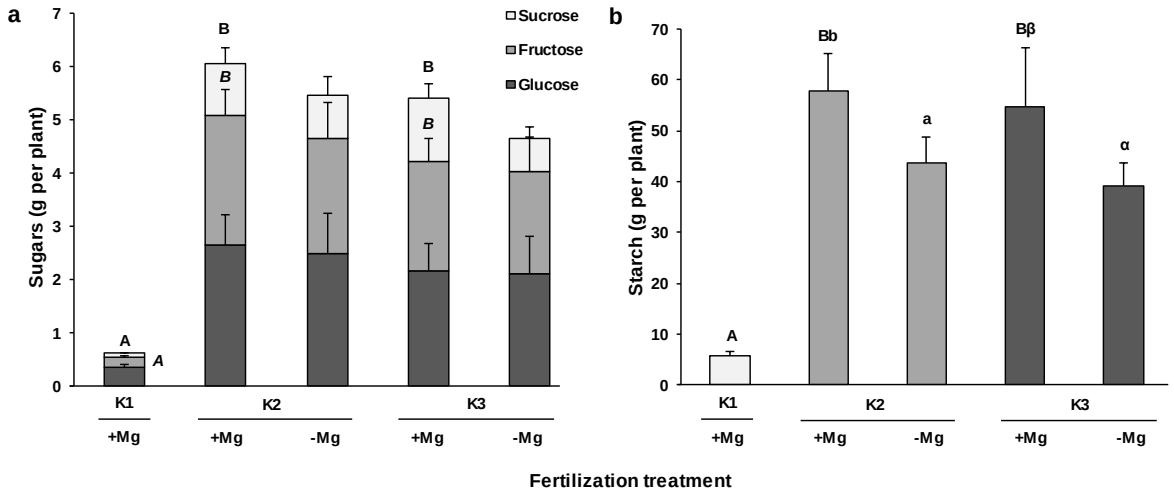

Figure 6: Effects of K and Mg treatments on tuber sugar and starch yields per plant. Yields of sugar (glucose, fructose, and sucrose) (a) and starch (b) in tubers of all fertilization treatments at harvest (n = 8—10). Mean ± SE values. Non-italic capitals = significant differences in the sum of sugars (glucose, fructose, and sucrose) between differing K treatments of +Mg plants. Italic capitals = significant differences in the sums of hexose sugars (glucose and fructose) between differing K treatments of +Mg plants. Small letters = significant differences between differing Mg treatments of K2 plants. Greek letters = significant differences between differing Mg treatments in K3 plants. No indication = no significant effect.

Discussion

Our experimental set-ups were suitable to impose K and Mg deficiencies in potato plants. Indeed, the K concentrations in leaves of K1+Mg plants were below levels which are considered to ensure a sufficient supply with K of the potato plant (Table 2), which should be above 30 mg K g^{-1} DM (Bergmann 1993; von Wulffen et al. 2008). The same is true for Mg concentrations in leaves of Mg-limited plants (K2 and K3-Mg) (Table 2), which should be higher than 2 mg Mg g^{-1} DM (Bergmann 1993; von Wulffen et al. 2008).

Shoot and root growth decreased under Mg- and especially under K-deficiency

Plants fed with low K supply showed decreased shoot and root biomasses, plant heights, and internode numbres compared to those with sufficient or high K supplies (Fig. 2). Such decreases under low K supply are well known, as shown by Cakmak et al. (1994a) in bean (*Phaseolus vulgaris* L.) and Jákli et al. (2016) in spring wheat plants (*Triticum aestivum* L. *var. Sonett*). In Mg-depleted plants, we observed no significant effect on the aboveground biomass production (Fig. 2a, d and e) for the duration of the treatment. The total root biomass decreased during K and Mg deficiencies, although not significantly in the latter case, and the shoot-to-root biomass ratio raised consequently (Fig.

2b). Moreover, the root length significantly decreased in K- as well as in Mg-deficient plants (Fig. 2c). Likewise, Kellermeier et al. (2013) documented a strong reduction of root elongation in K-deficient *Arabidopsis thaliana*; Silva et al. (2005) demonstrated increasing root lengths with increasing supply of Mg in soybean (*Glycine max*. L. *Merr*.). Similar to our results, Mengutay et al. (2013) noted a higher sensitivity of the root compared to the shoot growth in Mg-deficient wheat (*Triticum aestivum* ev. Adana 99) and maize plants (*Zea mays* ev. Shemal).

K showed an antagonistic effect on Mg in shoots but a synergistic effect on Mg in roots and tubers

While Mg concentrations decreased in leaves, there was no Mg decrease in the roots and tubers under high K supply (Fig. 3b). Conversely, the highest significant Mg leaf concentrations were determined in K-deficient plants (Table 2 and Fig. 3b). When faced with restriction of major cationic nutrients like K, plants usually absorb higher amounts of other cationic nutrients than the one under restriction (Kirkby and Mengel 1967). This could explain why the K-deficient plants revealed higher Mg (Table 2 and Fig. 3b) as well as higher Calcium concentrations in the leaves (SM_6). The lower Mg concentrations in the leaves, especially in K3+Mg plants, might have resulted from an antagonistic interaction between K and Mg during root uptake. The occurrence of an Mg-deficiency risk in plants due to high K supply has often been reported (Ding et al. 2006; Senbayram et al. 2015). However, tubers and roots do not show any significant decrease in the Mg concentrations in plants with a high K supply (Fig. 3b). This is probably due to the usually much lower amounts of K in roots compared to shoots (Fig. 3a) (White 1997; Karley and White 2009). Both effects, antagonism and synergism, seem related: Increasing K concentrations led to a depletion in Mg leaf concentrations while the Mg root and tuber concentrations increased compared to the Mg leaf concentrations.

Interestingly, under K- and Mg-deficiency, the quantitative highest proportion of decreasing K and Mg concentrations can be allocated to the leaves, while the decrease in K and Mg concentrations in tubers was quantitatively less (Fig. 3). It is conceivable that the plant strives to save its reproductive organs by investing higher amounts of nutrients in the tubers rather than in the roots and leaves.

Potassium-deficiency reduced photosynthesis while Mg-deficiency caused a reduction only late in growth stage

During K-deficiency, lower photosynthetic rate is mirrored by lower shoot biomass production (Fig. 2a and 4a). This confirms earlier reports on cotton (Zhao et al. 2001) and sunflower (Jákli et al. 2017) plants fed with a low K supply. Mg-deficient plants did not show a significantly decreased CO_2 net assimilation rate at the earlier growth stages (40 and 47 DAP). However, there was a decrease in CO_2 net assimilation in Mg-deficient leaves at a later growth stage

(Fig. 4a). Similar findings were presented by Hermans et al. (2005), who detected a decrease in photosynthetic electron flux in the photosynthetic reaction centers PS II and I in Mg-deficient sugar beet plants (*Beta vulgaris* L. ev. Adonis). The fact that CO_2 net assimilation was not restricted under Mg-deficiency in the early growth stages may explain why these plants did not suffer the same loss of photosynthetic active biomass compared to the K-deficient plants (Fig. 2a). Interestingly, higher concentrations of chlorophyll were found in the lowest K-treated plants compared to the medium and high K-treated plants on the early sampling dates (Fig. 4b). This is probably because leaf expansion in the K-depleted plants was restricted, which resulted in higher chlorophyll concentrations compared to plants given higher K treatments. Moreover, chlorosis and necrosis were less developed at these earlier growth stages (Fig. 1a).

Soluble sugars accumulated in K- and especially in Mg-deficient fully expanded leaves

The total soluble sugar concentrations showed a sharp increase in the leaves of Mg-depleted plants compared to Mg-adequate plants (Fig. 5a). Similarly, K-deficient plants also showed increased concentrations of soluble sugars in their leaves, but the results were less severe than found under Mg-deficiency. The reason for the significant differences in total soluble sugar concentrations on 69 DAP but not yet on 41 DAP might be related to increased tuber sink demand due to a progressed tuber development stage on 69 DAP (approximately 50% of full tuber development), as shown, for instance, by Kolbe and Stephan-Beckmann (1997). On 41 DAP, there could be a lower need for sucrose export to tubers for starch synthesis, which resulted in overall higher soluble sugar concentrations in leaves and, therefore, no significant differences in the sugar concentrations across the differently treated plants. Furthermore, plants with low Mg showed an accumulation of soluble sugars in leaves before any reduction of the CO_2 net assimilation occurred. These observations strengthen the idea that during Mg-deficiency the translocation of assimilates to sink organs is adversely affected prior to photosynthesis (Hermans et al. 2004; Cakmak and Kirkby 2008).

A possible impairment of phloem export could mark the origin of sucrose accumulation and subsequent hydrolysis into glucose and fructose (Fig. 5a). Indeed, Huber (1984) indicated that the accumulation of hexoses in K-deficient leaves was linked to increased INV activity. Recently, Farhat et al. (2016) showed that INV activity is affected in *Sulla carnosa* plants and concentrations of hexose sugars increased in source leaves through Mg-deficiency. Mg-sufficient plants exhibited comparably higher INV activity in the shoots while low-Mg plants showed increased INV activity in source leaves, possibly due to impaired loading of the phloem as a result of Mg-deficiency.

K- and Mg-deficiency caused sugar accumulations in different cell compartments and thus differentially affected the gene expression of sucrose transport systems

The transcript levels of *StSUT1* and *StSUT4*, both genes encoding H^+/sucrose symporters, were more abundant in leaves during K-deficiency (K1+Mg) compared to control plants (K2+Mg) (Fig. 5b). Concomitantly, sucrose accumulated in these leaves (Fig. 5a), possibly leading to—besides a breakdown into hexose units—increased gene expression of the H^+/sucrose symporter *StSUT1* and *StSUT4*. The transcript level increase, in particular *StSUT1*, was not as marked during Mg-deficiency as during K-deficiency (Fig. 5c). Nonetheless, sugar accumulation was more pronounced in source leaves of Mg-deficient than of K-deficient plants (Fig. 5a). Therefore, we assume that the accumulation of sucrose and the following breakdown into hexose sugar units by INV occurred in different leaf compartments under the situation of K- or Mg-deficiency. Magnesium is required by H^+-ATPases, which are pumping protons across the plasma membrane into the apoplasm. Under Mg-deficiency, this proton extrusion may be hampered. Thus, we argue that fewer protons are pumped into the apoplasm and in consequence less sucrose is loaded into the companion cell-sieve element complex. Following our initial assumption, this would result in an accumulation of sucrose in the apoplasm affecting the relative transcript abundance of H^+/sucrose symporters. However, as an alternative scenario, it is feasible that an impaired function of H^+-ATPases already affects an earlier step of sucrose transport, namely the efflux of sucrose from mesophyll cells into the apoplasm what is carried out *via* SWEET transporters (Manck-Götzenberger and Requena 2016). We hypothesize that these SWEET transporters are forced to reduce the export of sucrose from the mesophyll into the apoplasm as a consequence of a reduced activity of H^+/sucrose symporters due to a decreased loading of protons by H^+-ATPases into the apoplasm caused by Mg-deficiency. Sucrose would then accumulate mainly in mesophyll cells. Meanwhile, the increased transcript abundance of the sucrose cotransporter *StSUT4* on 69 DAP could be a later response of the plant to a decreased import of sucrose into sink organs.

The major role of K in the partitioning of photoassimilates can be referred to establish an osmotic potential within the phloem which helps to translocate sucrose from source to sink tissues (Hayashi and Chino 1990; Cakmak 2005). Therefore, under K-deficiency sucrose translocation from source to sink organs might be restricted and sucrose may accumulate in the apoplasm or in cells of the companion cell-sieve element complex. Since sugars accumulate in the close vicinity of H^+/sucrose symporters in the case of K-deficiency, it is likely that this results in a more pronounced increase of the transcript abundance of the H^+/sucrose symporters *StSUT1* and *StSUT4*. Moreover, the expression levels

of *StSUT4* were more abundant than those of *StSUT1*. This fits to the assumption made by Weise et al. (2000) that *StSUT4* is a low-affinity transporter, being mainly active at higher sucrose concentrations.

Finally, the increased expression levels of the sucrose cotransporters in high K supplied plants (K3+Mg) (Fig. 5b and c) could be due to comparatively higher sugar concentrations in these leaves (Fig. 5a). It is conceivable that the plant produced temporally more sugars *via* photosynthesis under K luxury supply than actually needed by the plant´s sink organs what in turn could have led to a slight accumulation of sucrose in source leaves.

K- and Mg-deficiency decreased tuber starch and sugar yield but not starch and sugar concentrations

The tuber sugar and starch yields per plant (amount of sugar and starch per plant) revealed clear differences due to the various K and Mg treatments. Plants with deficient K (K1+Mg) and Mg (K2 and K3-Mg) supply showed significant lower sugar and starch yields compared to plants with sufficient K and Mg (K2 and K3+Mg) supply (Fig. 6a and b). Contrary to the initial expectations that an impairment of photosynthesis and photoassimilate translocation due to K- or Mg-deficiency would adversely affect tuber sugar and starch concentrations, no significant influence of K- or Mg-deficiency on tuber sugar and starch concentrations was detectable (SM_5b and SM_5c). With respect to tuber sugar concentrations, the present findings are in agreement with the results of Stanley and Jewell (1989), who also could not find a significant change in hexose sugar concentrations under conditions of varying K supply in potato. However, Gerendás et al. (2007) determined a decrease in the level of hexose sugars with increasing K supply in potato. The present results coincide only in tendency with the findings of Gerendás et al. (2007) (SM_5b). The significant differences in tuber starch and sugar yields may be a reference to the significant effects of treatments on the tuber yield (Fig. 2f).

Author contributions

E.P. obtained funding. I.C., C.H. and M.K designed the experiment. M.B. and M.K. performed the experiments and collected and evaluated the data. J.B. and M.N. helped with the experimental work and data evaluation. E.P., M.N., I.C., C.H. and I.S. supervised the experiment and data evaluation. All authors have contributed to, read and approved the manuscript.

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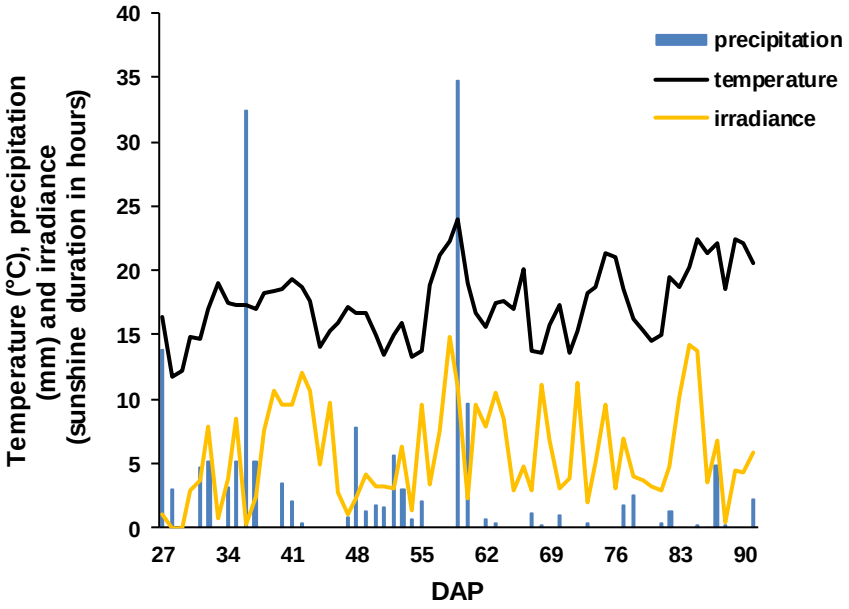
Supplementary material



SM_1: Mean temperature, precipitation, and irradiance over the vegetation period (outdoor installation).

SM_2: Applied amounts (in mg kg^{-1} soil) and used form of nutrients besides K and Mg.

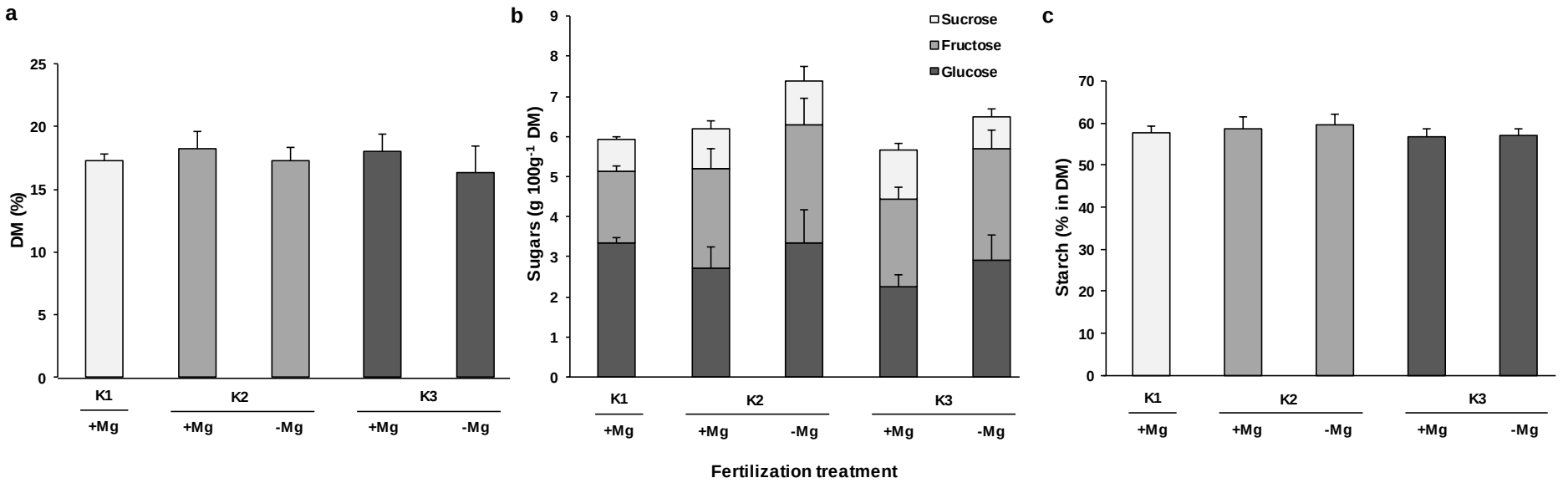
Element	Applied amount of salt	Salt formulation
Nitrogen	300	$Ca(NO)_3$
Phosphorus	100	$Ca(PO_4)_2 . H_2O$
Calcium	1,300	$CaCO_3$
Boron	2	H_3BO_3
Zinc	2	$ZnSO_4 . 7H_2O$
Molybdenum	0.01	$Na_2MoO_4 . 2 H_2O$
Copper	2	$CuSO_4 . 5H_2O$
Manganese	6	$MnSO_4 . H_2O$
Iron	3	Fe(III) EDTA (13% Fe)

SM_3: Gene short names, PCR primer sequences (forward and reverse), Genbank accession numbers, amplicon sizes (bp), and PCR efficiencies (%) with R^2 of PCR efficiency.

Gene	Forward primer	Reverse primer	Accession no.	Amplicon size	PCR efficiency	R^2 PCR efficiency
StSUT1	CAT GGG ATG ATT TGT TTG GA	TGG CAA CAT TGT GAG TGC TA	X69165	98	98.4	0.973
StSUT4	GCA GCC TCT AGA TCC CAG TC	CAG GAT CAC CCA AAC AAC AC	NM_001288141 XM_006364904	139	111.4	0.987
StUBIQUITIN	CAC CAA GCC AAA GAA GAT CA	TCA GCA TTA GGG CAC TCC TT	Z11669 S45502	120	94.5	0.966

SM_4: Thermal cycling protocol.

Initial denaturation	Amplification Denaturation	Amplification Annealing	Amplification Extension	Cycles	Melting curve analysis
98°C for 30 sec	95°C for 10 sec	55°C for 15 sec	72°C for 15 sec	44	65°C to 95°C, 0.5°C, 5 sec/step



SM_5: Tuber DM and sugar (glucose, fructose and sucrose) and starch concentrations of all five fertilization treatments at harvest (n = 8—10). Mean ± SE values. Treatments had no significant effect.

SM_6: Calcium (Ca) concentrations (mg g^{-1} DM) in fully expanded leaves on five sampling dates from day 34 until day 69 after planting (n = 4—5). Mean ± SE values. Capitals = significant differences between differing K treatments of +Mg plants. Small letters = significant differences between differing Mg treatments in K2 plants. No indication = not significant.

Ca

	Fertilization treatment									
DAP*	**K1+Mg**		**K2+Mg**		**K2-Mg**		**K3+Mg**		**K3-Mg**	
34	19.69 ± 3.07	C	10.65 ± 0.73	B	11.92 ± 2.21		8.46 ± 0.42	A	10.18 ± 2.59	
41	15.64 ± 1.93	B	7.65 ± 1.09	Aa	10.31 ± 0.61	b	6.62 ± 0.46	A	8.16 ± 0.89	
48	33.74 ± 2.26	B	13.18 ± 1.48	A	16.01 ± 1.49		10.07 ± 1.55	A	11.75 ± 2.99	
55	21.37 ± 1.68	C	12.73 ± 2.08	B	16.12 ± 1.76		8.52 ± 0.82	A	10.64 ± 1.92	
69	38.04 ± 2.51	C	21.13 ± 1.96	B	25.89 ± 2.37		14.69 ± 2.50	A	17.91 ± 1.79	

* DAP = days after planting.

Chapter 5

Effect of magnesium deficiency and magnesium complementary fertilization on potato (*Solanum tuberosum* L.) root growth

Mirjam Koch, Marcel Naumann and Elke Pawelzik

Effect of magnesium deficiency and magnesium complementary fertilization on potato (*Solanum tuberosum* L.) root growth

Mirjam Koch, Marcel Naumann and Elke Pawelzik

Department for Crop Sciences, Division Quality of Plant Products, Carl-Sprengel-Weg 1, 37075 Göttingen, University of Göttingen.

Abstract

Potato roots have a shallower and less extended root system compared to other crops what makes them less efficient in the acquisition of water and nutrients. As the ability for water and nutrient acquisition is mainly determined by root morphological characteristics such as root length, optimal root growth is of high importance for potato plants. The development and growth of plant roots can be affected by various factors. One of these factors is the supply of the plant with nutrients. Based on the pivotal roles of magnesium (Mg) for photosynthesis and the partitioning of photoassimilates within the plant, Mg is expected having a pivotal influence on the development of plant roots. A negative impact of Mg deficiency on root growth has been demonstrated in other plants. To our knowledge, the effect of Mg deficiency on root growth in potato (*Solanum tuberosum* L.) has never been investigated as well as the effect of a resupply of Mg to Mg-deficient potato plants. A hydroponic culture system with potato plants was conducted with three levels of Mg supply ('Mg low', 'Mg med', 'Mg high') in order to identify a dose that is sufficient for ensuring appropriate root growth and two Mg complementary fertilization treatments (Mg foliar application or increase of Mg concentrations via addition into the nutrient solution). 'Mg low' plants exhibited a sharp decrease in root biomass and root length whereas 'Mg med' and 'Mg high' plants developed twice as much root biomass and doubled root length. Besides, an accumulation of soluble sugars occurred in source leaves of 'Mg low' treated plants. This is indicative for a restricted phloem loading which is supposed having negative effects on root growth. On the other hand, a restricted sink demand due to reduced root growth may lead to an accumulation of soluble sugars in source leaves. The results indicate that the Mg supply of 'Mg med' plants represented already a sufficient supply of Mg for potato with respect to root growth. The Mg foliar application demonstrated only negligible effects on potato root growth, whereas the rise of the Mg nutrient solution concentrations of 'Mg low' plants showed more distinct effects, especially in form of an increased Mg nutrient status and increased root length development.

Keywords

Root length, root-to-shoot ratio, Mg foliar application, Mg resupply, chlorophyll, phloem loading, hydroponic culture system

Introduction

Plant roots are crucial for the acquisition of water and nutrients and thus, determine plant growth and performance (Gruber et al. 2013). The ability of plant roots for acquisition of nutrients mainly is affected by the size of absorbing surface and the ability to explore the soil for nutrients (Sattelmacher et al. 1993; Sattelmacher et al. 1994). Hence, root morphological characteristics such root length, diameter and number highly determine a plant´s nutrient efficiency (Sattelmacher et al. 1994). However, potato roots are known to have a shallower and less extended root system compared to other crops and are classified as poor rooting efficient (Hopkins et al. 2014). Tanner et al. (1982) found that 90 % of potato root length is located in the upper 25 cm of the soil. This might contribute to the fact that potato is a very sensitive crop for water shortages and can be (in comparison with other crops) classified as inefficient in the acquisition of nutrients (van Loon 1981; Hopkins et al. 2014). Therefore, ensuring an unrestricted and optimal root growth of potato gains high importance, especially for nutrients which are mainly taken up by the plant via mass flow such as nitrogen and magnesium (Mg) (Strebel and Duynisveld 1989; Barber 1995). The development and architecture of plant roots can be affected by various reasons. Several studies demonstrated a positive relation between the plant´s mineral nutrition and root growth (Sattelmacher et al. 1993; López-Bucio et al. 2003; Gruber et al. 2013). However, studies related to the impact of mineral nutrition on root growth in potato are rare.

Mg is one of the essential elements in plants and is involved in several physiological and biochemical processes of plant development and growth. For instance, Mg is the central atom of the light harvesting pigments chlorophyll (Braumann et al. 2014). In addition, Mg is needed for the activation and function of several enzymes (Senbayram et al. 2015) - for example for the activation of the CO_2 fixing enzyme ribulose-1,5-bisphosphate (RuBP) carboxylase (Belknap and Portis 1986). The earliest response of Mg deficiency is reported to be an accumulation of sucrose in Mg deficient source leaves (Cakmak and Kirkby 2008), as has been shown in sugar beet (*Beta vulgaris* L. cv. Adonis) (Hermans et al. 2004). This sucrose accumulation can be referred to an impaired phloem loading process and thus, a restricted translocation of photoassimilates from source to sink organs. Mg interacts with ATP of H^+-ATPases which balance charges and are providing energy and therefore are needed by H^+/sucrose symporters, which are loading the phloem with sucrose (Hermans et al. 2005). Marschner et al. (1996) stated that the extent, to which a nutrient is affecting the root growth and development, is mainly dependent on translocation processes of the needed minerals and photoassimilates within the plant. Based on the presented roles of Mg in photosynthesis and for the partitioning of photoassimilates, a strong impact of Mg on the root development can be expected as roots are important sink organs for photoassimilates.

This study focused on the impact of Mg deficiency on the root growth of potato plants (*Solanum tuberosum* L.). Due to the indispensable functions of Mg for the production and partitioning of photoassimilates in plants, it is hypothesized that Mg deficiency will lead to a significant reduction of root biomass and total root length, what is regarded as an important morphological parameter for nutrient acquisition (Sattelmacher et al. 1994). Thus, it is aimed to screen three different Mg supplies to identify a dose that is sufficient to allow appropriate root growth. A further aim of this study is to examine, how a resupply of Mg via the roots and via the leaves, respectively, may affect an existing deficiency of Mg and related symptoms such as depressed root growth. Beside root growth, leaf sugar concentrations were determined as indicator for a potential impaired phloem loading process.

Material and methods

Experimental design and growth conditions

Potato plants (*Solanum tuberosum* L.) of the variety 'Laura' were grown in nutrient solution in a climate chamber for a period of 60 days. The plants grew under an alternate day/night cycle of 12 hours with a photosynthetic photon flux density of 180 µmol m^{-2} s^{-1} (MASTER Agro 400 W; Philips, Netherlands) during illumination. Average air temperature was 20 °C during the day and 16 °C during the dark period and relative humidity was 60 %. Before onset of the experiment, plants were propagated in a soil culture system under low Mg supply (plants which were later grown under nutrient solution concentrations of 5 or 100 µM Mg) or sufficient Mg supply (plants which were later grown under nutrient solution concentrations of 500 µM Mg) (supplementary material (SM)_1). For planting only potato pieces with a germ bud instead of whole tubers were used to avoid nutrient delivery from the whole tuber. When the plants reached a height of approximately 10 cm, they were transferred into a nutrient solution with stepwise increasing nutrient concentrations (20% - 50% - 100%) over the first seven days. The full nutrient solution concentration was: 2.75 mM $Ca(NO_3)_2.4\ H_2O$, 0.25 mM NH_4NO_3, 2 mM K_2SO_4, 0.25 mM $Ca(H_2PO_4)_2.H_2O$, 0.1 mM Fe(III) EDTA (13% Fe), 10 µM H_3BO_3, 1 µM $ZnSO_4.7\ H_2O$, 1 µM $MnSO_4.H_2O$, 0.2 µM $CuSO_4\ .5\ H_2O$ and 0.14 µM $H_{24}Mo_7N_6O_{24}.4\ H_2O$. Besides, the plants were treated with three different Mg supplies: A low (5 µM Mg), a medium (100 µM Mg) or a high (500 µM Mg) Mg level, following designated as 'Mg low', 'Mg med' and 'Mg high'. Mg was given as $Mg_2SO_4.7\ H_2O$. The low and the medium Mg supply were represented each by 12 plants. The high Mg level was represented by four plants throughout the whole experiment. After nine days after onset of the experiment (DAO) four plants of the low and four plants of the medium Mg level received three times (10, 17 and 24 DAO) a Mg foliar application with $Mg_2SO_4.7\ H_2O$ (together with the wetting agent Silwet® Top (0.1% (v/v); BASF, Austria), following designated as '+ f'. The concentration of the Mg spraying solution was 200 mM $Mg_2SO_4.7\ H_2O$. Each plant received approximately 28 mg Mg by one Mg foliar application.

Plants, which did not receive an foliar application were sprayed only with distilled water plus the wetting agent. Furthermore, four plants of the low and the medium Mg level received an additional Mg supply via the nutrient solution by increasing the Mg nutrient solution concentration from 5 and 100 µM Mg, respectively, to 500 µM Mg, following designated as 'to Mg high'. The schematic experimental setup is shown in figure 1. The plants were grown in 5 liter plastic pots with one plant per pot. The nutrient solution was aerated and changed every 3-5 days in dependence on plant growth and water consumption.

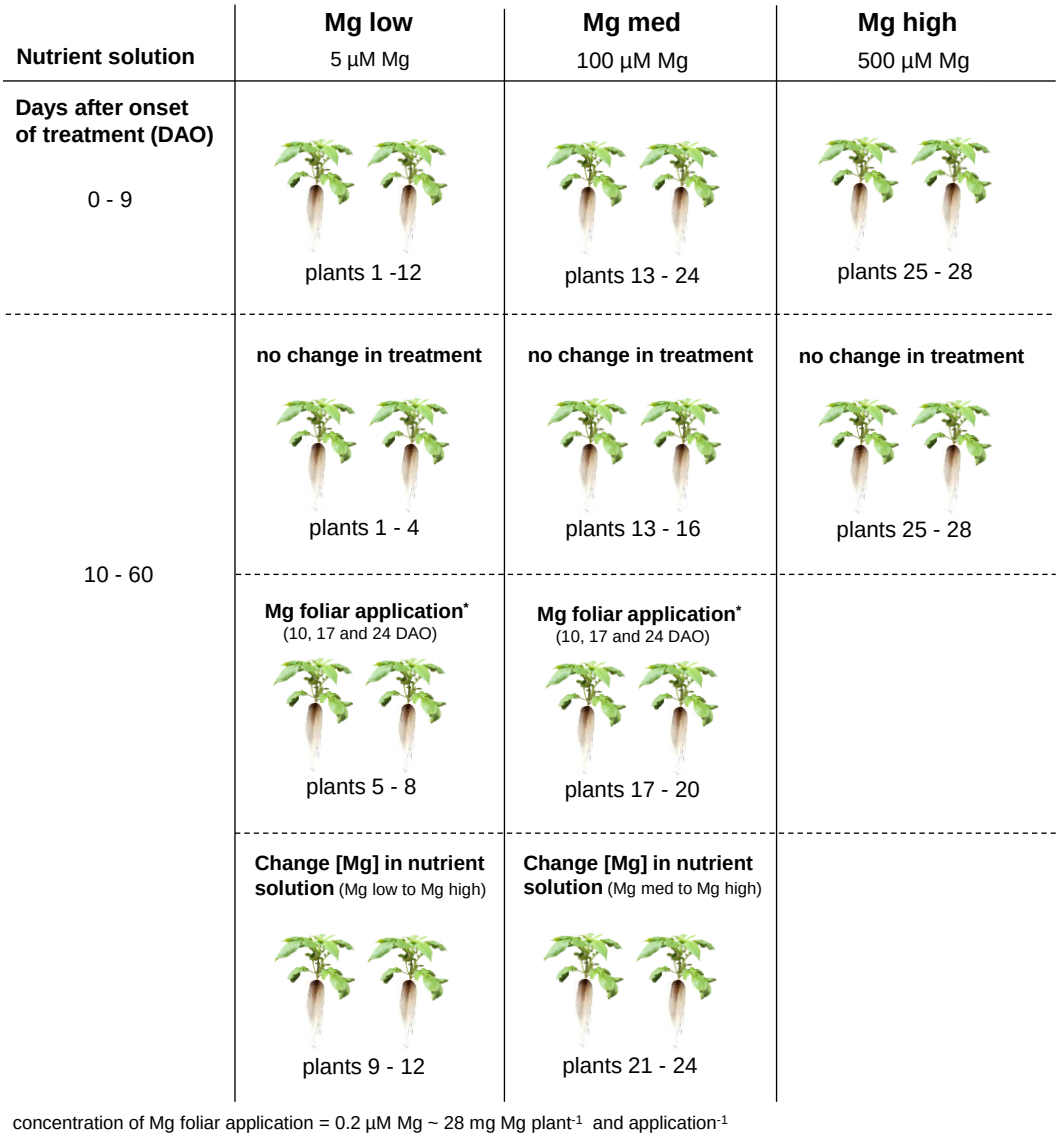


Figure 1: Schematic setup of experiment with three levels of Mg supply ('Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg) and complementary fertilizations (Mg foliar application and change of Mg concentration in nutrient solution from 'Mg low' or 'Mg med', respectively, 'to Mg high'). Plants 1-4 ('Mg low'), 13-16 ('Mg med') and 25-28 ('Mg high') remained unchanged throughout the whole experiment. After 9 DAO plants 5-8 ('Mg low') and 17-20 ('Mg med') received three times an Mg foliar application while plants 9-12 ('Mg low') and plants 21-24 ('Mg med') were raised in their Mg concentration of nutrient solution 'to Mg high'.

Mg determination in fully expanded leaves and roots

Leaf and root samples were dried at 60°C for four days. Afterward, leaves were ground with a mortar and pestle and root samples were ground into 0.5 mm flour in a hammer mill (DFH 48, Culatti, Switzerland). Leaves, which received an Mg foliar application, were washed prior drying to get rid of Mg residues on the leaf surface. Minerals were determined according to an modified method as described by Wheal et al. (2011) and carried out as follows: 100 mg of prepared leaf or root sample was digested with 4 ml of 65% (v/v) nitric acid and 2 ml of 30% (v/v) hydrogen peroxide at 200°C and 40 bar for 75 minutes in a microwave (Ethos 660; MWT AG, Switzerland). The samples were filled up to 25 ml with distilled water and stored in screw cap tubes until analysis. The concentrations of Mg were examined using inductively coupled plasma optical emission spectrometry (Vista-PRO CCD Simultaneous ICP-OES; Varian Inc., USA).

Chlorophyll quantification in fully expanded leaves

Leaves were grounded with mortar and pestle in liquid nitrogen and 20 mg was weighed in 2 ml screw cup micro tubes and stored in liquid nitrogen until further use. The plant material was extracted twice with 80% (v/v) ethanol and a third time with 50% (v/v) ethanol. The samples were shaken in a heat block at 95°C for 30 minutes. After the third extraction step, the supernatants were combined, the pellet discarded, and the samples stored at -20°C until further analysis.

Chlorophyll was examined by preparing a mix of 50 µl ethanolic extract (or 70% (v/v) ethanol as blank) and 120 µl 98% ethanol per well on a 96–well plate. The optical density (OD) was measured at 645 nm and 665 nm in a plate reader (Epoch, 1402203; Biotek, USA), and chlorophyll a and b were calculated according to the following formulas:

$$\text{Chlorophyll a (µg/well)} = 5.48A_{665} - 2.16A_{645.}$$

$$\text{Chlorophyll b (µg/well)} = 9.67A_{645} - 3.04A_{665.}$$

For the results, the sum of chlorophyll a and b was considered.

Soluble sugar determination in fully expanded leaves

The soluble sugars glucose, fructose, and sucrose were determined according to Stitt et al. (1989) (modified as described following). The same ethanolic extract as prepared for chlorophyll extraction was used. The method is based on the conversion of the sugars by the added enzymes Hexokinase (HK) (Roche Diagnostics GmbH,

Germany; Merck, Germany), Phosphoglucose isomerase (PGI) (Roche Diagnostics GmbH, Germany), and Invertase (INV) (Sigma Aldrich, USA). Thereby electrons are released and are transferred to nicotinamide adenine dinucleotide phosphate ($NADP^+$) (Roche Diagnostics GmbH, Germany) forming NADPH + H. For dissolving the enzymes a 100 m*M* hydroxyethylpiperazine-ethanesulfonic acid (HEPES) buffer (Roth, Germany) + 3 m*M* $MgCl_2$ buffer (adjusted with KOH to pH 7) was used. Half of the samples were prepared with HK in suspension (Roche Diagnostics GmbH): 72 µl (108 units) HK was centrifuged three minutes at 11,000 rotations/minute and the pellet was dissolved in 120 µl HEPES-$MgCl_2$ buffer; the other half of the samples was prepared with HK in solid form (Merck, Germany): 0.50 mg was dissolved in 120 µl HEPES-$MgCl_2$ buffer. For preparation of PGI 36 µl (25.2 units) PGI was centrifuged for three minutes at 11,000 rotations/minute and the pellet was dissolved in 120 µl HEPES-$MgCl_2$ buffer. For preparation of INV 8.3 mg (2,500 units) INV was dissolved in 120 µl HEPES-$MgCl_2$ buffer. A further needed enzyme was Glucose-6-phosphat dehydrogenase (G6P-DH) (Roche Diagnostics GmbH, Germany) which was prepared together with 100 m*M* ATP (Sigma-Aldrich, USA) and 45 m*M* NADP to a solution. For this, 85 µl (60 units) G6P-DH were centrifuged for three minutes at 11,000 rotations/minute and the pellet was dissolved in 15.5 ml HEPES + $MgCl_2$ buffer, 480 µl ATP, and 480 µl NADP solution. Next, 50 µl of the ethanolic extract plus 160 µl of the G6P-DH - ATP-NADP solution was added per well on a 96-well plate and shaken for 10 minutes. The converted NADPH was quantified by measuring the OD at 340 nm in a plate reader (Epoch, 1402203; Biotek, USA) after reaching stable values.

NADPH was calculated with the help of Δ OD by using the following formula:

$$\mu M \text{ NADPH} = \Delta \text{ OD}/(2.85*6.22).$$

The calculated values were indicated as:

1 *M* NADPH derived from glucose/fructose = 1 *M* glucose/fructose.

1 *M* NADPH derived from sucrose = 0.5 *M* sucrose (1 mole glucose equivalent).

Phenotype, shoot and root growth and root scanning

The phenotype was documented by taking photos of representative leaflets and roots. Morphological changes of the shoot were recorded by measuring the plant height with a common tapeline and counting the internodes per plant. At harvest the complete shoots were cut off and the total shoot biomasses were assessed. Roots were separated from the shoots and stored at -20°C until root scan analysis. Immediately prior root scanning the roots were thawed, stolons were discarded and the roots were placed in a shell and completely covered with water. Only

the half of each root was used and the total root length was calculated for the whole root on the basis of the determined dry weight of the scanned root part and the non-scanned root part. Root scanning was conducted with a flat-bed scanner (Epson perfection V700 photo, Epson, Germany) and analyzed with the software WinRhizo 2016 (Regent Instruments Inc. Québec City, Canada). Besides, the total root biomasses were examined and based on the dry weights of shoots and roots the shoot-to-root ratios were determined.

Statistics

Statistical analysis were performed using R software version 3.4.0 (R Core Team 2016). All data were checked for normal distribution and homoscedasticity. Then, ANOVA was performed to detect differences between treatments followed by multiple contrast tests. Non-parametric Kruskal-Wallis test was performed if normality and/or homoscedasticity were not given. All tests were performed on a significance level of $p < 0.05$.

Results

Mg status of fully expanded leaves

The 'Mg low' treated plants exhibited the significant lowest Mg concentrations throughout the experiment (Fig. 2a). A complementary fertilization of Mg via Mg foliar application led to increasing Mg leave concentrations of 'Mg low' plants only at the second and third sampling date while an Mg foliar application of 'Mg med' plants only led to significant increasing Mg concentrations at the second sampling date (Fig. 2b). More distinct effects were detected by a complementary fertilization via the nutrient solution: Immediately after change of the Mg concentration in the nutrient solution from 5 and 100 µM Mg, respectively, up to 500 µM Mg (9 DAO), the Mg leave concentrations increased four to five times compared to 'Mg low' treated plants and up to two times compared to 'Mg med' treated plants (Fig. 2b). The significant highest Mg leave concentrations throughout all sampling dates were determined in 'Mg high' treated plants, closely followed by 'Mg low to Mg high' treated plants (Fig. 2a).

Chlorophyll concentrations of fully expanded leaves

The chlorophyll concentrations did not show any significant differences between the treatments, only tendencies can be described (Fig. 3): 14 DAO the highest chlorophyll concentrations were quantified in 'Mg low +f' and 'Mg low to Mg high' treated plants. 35 DAO all treatments showed equal chlorophyll concentrations but with lower values compared to 14 and 56 DAO. At the last sampling date (56 DAO) 'Mg low' treated plants exhibited the highest chlorophyll concentrations.

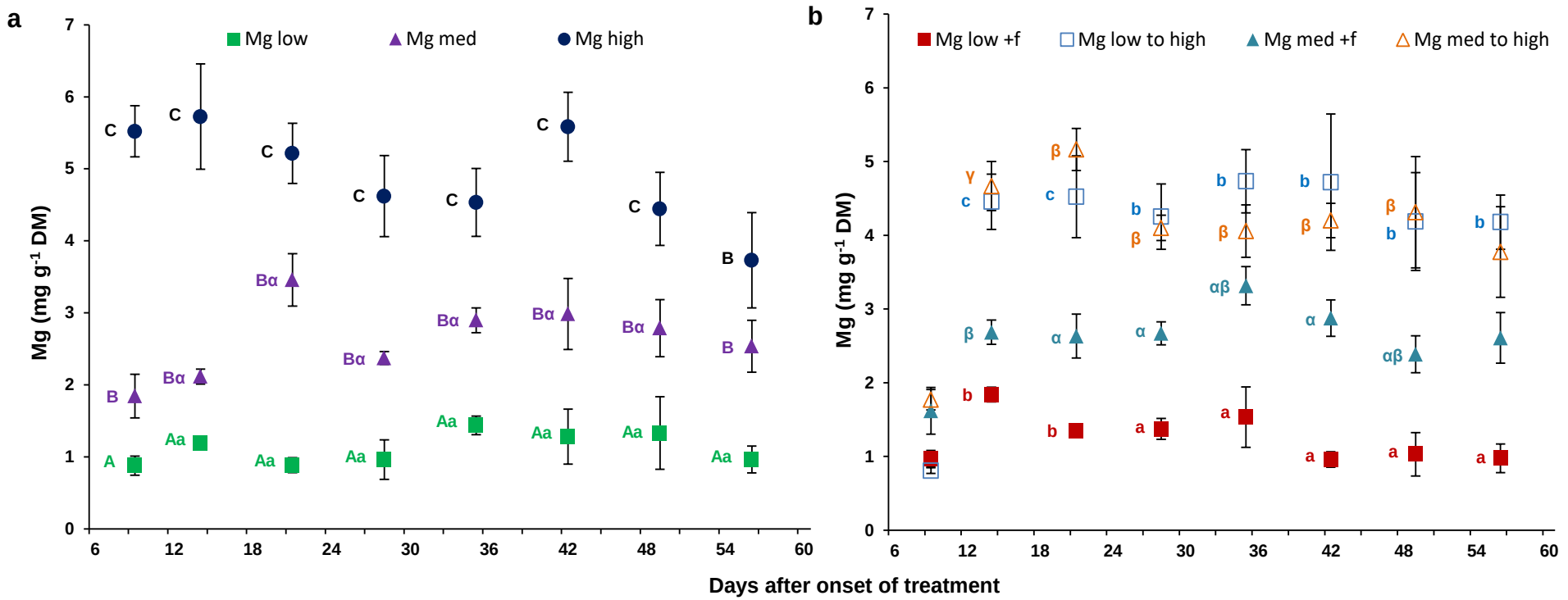


Figure 2: Mg leave concentrations in 'Mg low', 'Mg med' and 'Mg high' treated plants (a) and impact of complementary fertilization treatments ('+f' and 'to Mg high') (n = 4) on Mg leave concentrations (b). 'Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg; '+f' = with Mg foliar application; 'to high' = change of the Mg nutrient solution concentration from 5 or 100, respectively, to 500 µM Mg. Mg foliar application was conducted on 10, 17 and 24 DAO. Mean ± SE values. Capitals = significant differences between 'Mg low', 'Mg med' and 'Mg high' plants. Small letters = significant differences between 'Mg low', 'Mg low +f' and 'Mg low to Mg high' plants. Greek letters = significant differences between 'Mg med', 'Mg med +f' and 'Mg med to Mg high' plants. No indication = no significance.

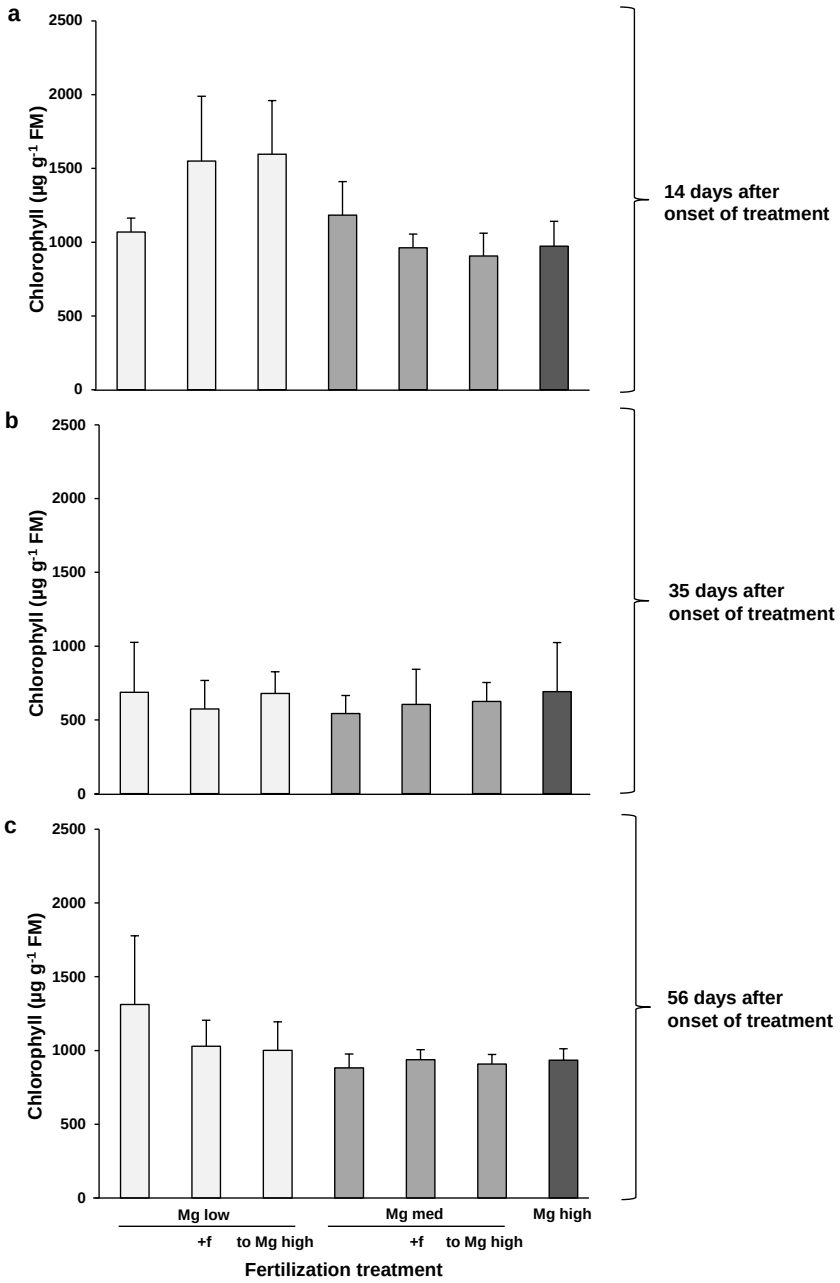


Figure 3: Chlorophyll concentrations in fully expanded leaves of all fertilization treatments at days 14 (a), 35 (b) and 56 (c) after onset of treatment (n = 4). 'Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg; '+f' = with Mg foliar application; 'to high' = change of the Mg nutrient solution concentration from 5 or 100, respectively, to 500 µM Mg. Mean ± SE values. Treatments had no significant effect.

Soluble sugar concentrations in fully expanded leaves

14 and 35 DAO total soluble sugars (glucose, fructose and sucrose) as well as the sum of hexose sugars (glucose and fructose) did not show any significant differences (Fig. 4a and b). But at 35 DAO increasing concentrations of total as well as of hexose sugars became detectable in leaves of 'Mg low' treated plants (Fig. 4b). Meanwhile, plants of all other treatments exhibited up to one third less total soluble sugar concentrations compared to 'Mg low' plants. These differences were not significant at 35 DAO. However, at day 56 DAO similar sugar concentrations

were determined as on 35 DAO: 'Mg low' plants showed significant higher soluble and hexose sugar concentrations compared to 'Mg med' and 'Mg high' plants (Fig. 4c). Moreover, 'Mg low +f' plants exhibited significant lower total soluble sugar concentrations compared to plants which did not receive Mg foliar applications ('Mg low' plants).

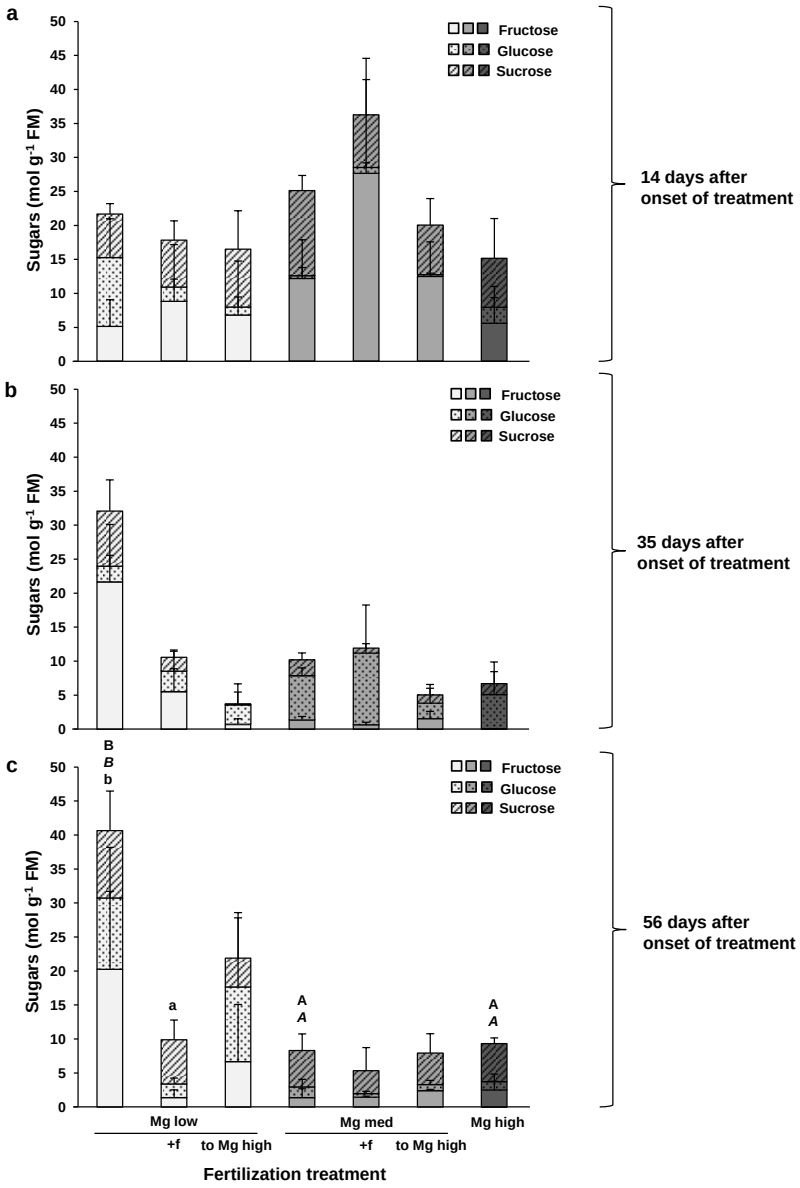


Figure 4: Total soluble and hexose sugar concentrations in fully expanded leaves of all fertilization treatments at days 14 (a), 35 (b) and 56 (c) after onset of treatment (n = 2 - 4). 'Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg; '+f' = with Mg foliar application; 'to high' = change of the Mg nutrient solution concentration from 5 or 100, respectively, to 500 µM Mg. Mean ± SE values. Capitals = significant differences of total sugar sums between 'Mg low', 'Mg med' and 'Mg high' plants. Italic capitals = significant differences of hexose sugars between 'Mg low', 'Mg med' and 'Mg high' plants. Small letters = significant differences of total sugar sums between 'Mg low', 'Mg low +f' and 'Mg low to Mg high' plants. No indication = no significance.

Shoot and root growth

Shoot and root biomass were significantly reduced in 'Mg low' compared to 'Mg med' and 'Mg high' plants (Fig. 5a and b). Additionally, root biomass was more reduced than shoot biomass in 'Mg low' plants what is also reflected in the higher shoot-to-root ratio of 'Mg low' compared to 'Mg high' plants (Fig. 5b). This biomass reduction is pictured in figure 6: Root biomass of 'Mg low' plants appeared smaller compared to roots of 'Mg med' and 'Mg high' treated plants. The complementary fertilization did not affect significantly on shoot as well as on root biomass (Fig. 5 and SM_2), although slight increases due the complementary fertilization treatments of 'Mg low' plants were recorded. 'Mg low' plants showed the lowest quantity of internodes (Fig. 5c) and plant heights (Fig. 5d) but at the last two sampling dates there were no significant differences in quantity of internodes and plant height between 'Mg low', 'Mg med' and 'Mg high' plants.

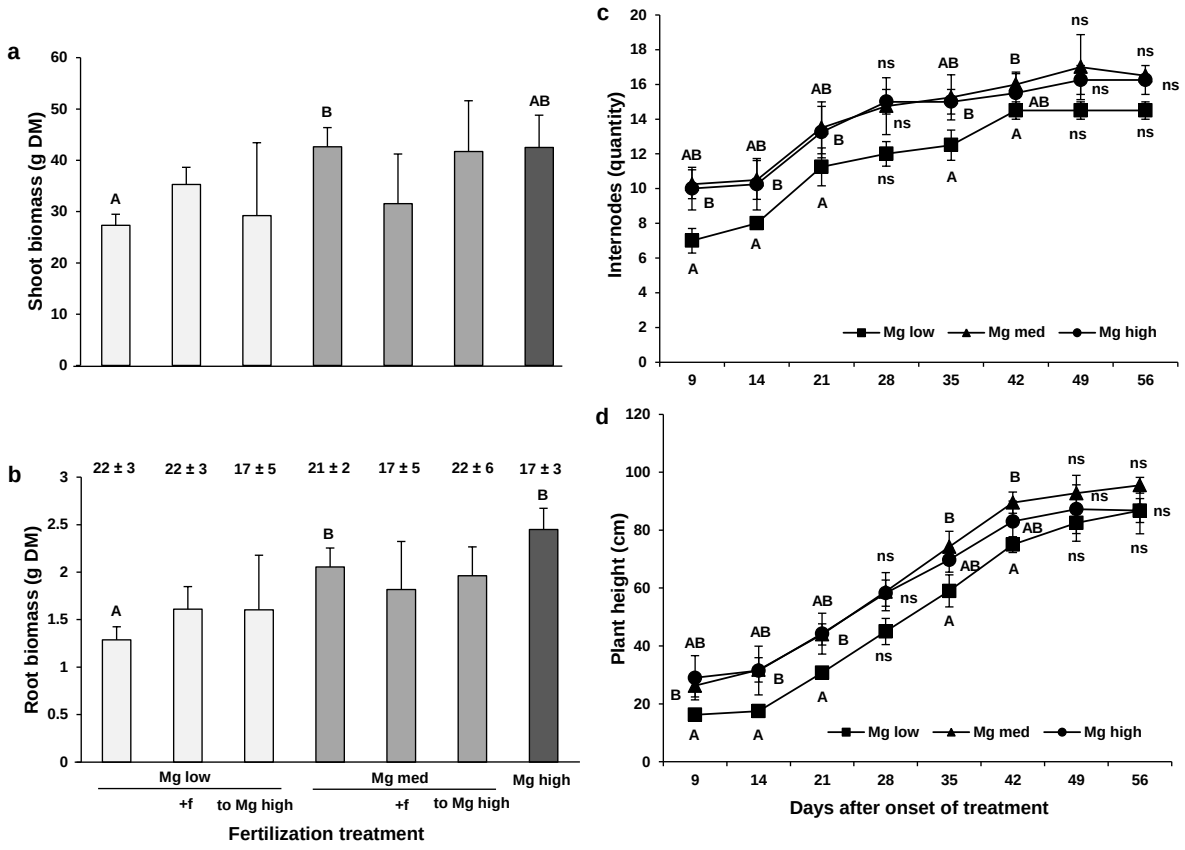


Figure 5: Effect of Mg deficiency ('Mg low') and complementary fertilization of Mg ('+f' and 'to Mg high') on total shoot (a) and total root biomass at harvest with shoot-to-root ratios (mean ± SE values above bar plot) (b), on quantity of internodes (c) and on plant heights (d) at eight various sampling dates (n = 4). 'Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg; '+f' = with Mg foliar application; 'to high' = change of the Mg nutrient solution concentration from 5 or 100, respectively, to 500 µM Mg. Mean ± SE values. Capitals = significant differences between 'Mg low', 'Mg med' and 'Mg high' treated plants. No indication = no significance.

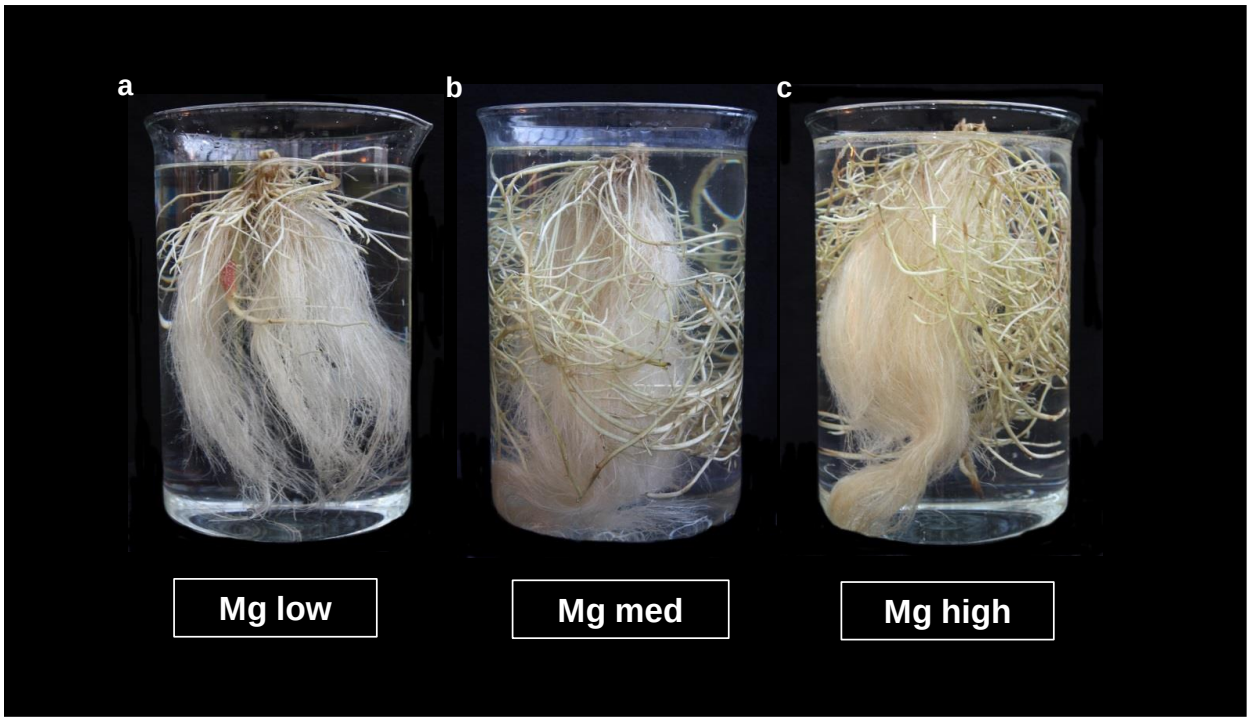


Figure 6: Illustration of potato roots at harvest, which were grown in hydroponic culture systems under low (a), medium (b) and high (c) Mg supply.

Total root length and Mg root status

Total root length was significantly reduced in 'Mg low' compared to 'Mg high' treated plants. 'Mg med' treated plants exhibited comparable total root lengths as 'Mg high' treated plants, but the differences compared to 'Mg low' treated plants were not significant (Fig. 7). Similar results are presented for the Mg root concentrations: The significant lowest Mg concentrations were quantified in roots of 'Mg low' treated plants (Fig. 7). The complementary fertilization treatments did not show a significant impact on the total root length and root Mg concentrations but tendencies can be stated: Total root length increased by rising the Mg nutrient solution concentrations from 5 to 500 µM Mg and the root Mg concentrations increased by rising the Mg nutrient solution concentrations from 5 and 100 µM Mg, respectively, to 500µM Mg. Also an Mg foliar application to 'Mg low' plants could increase total root length, but to a less extent compared to a raise of the Mg nutrient solution concentration.

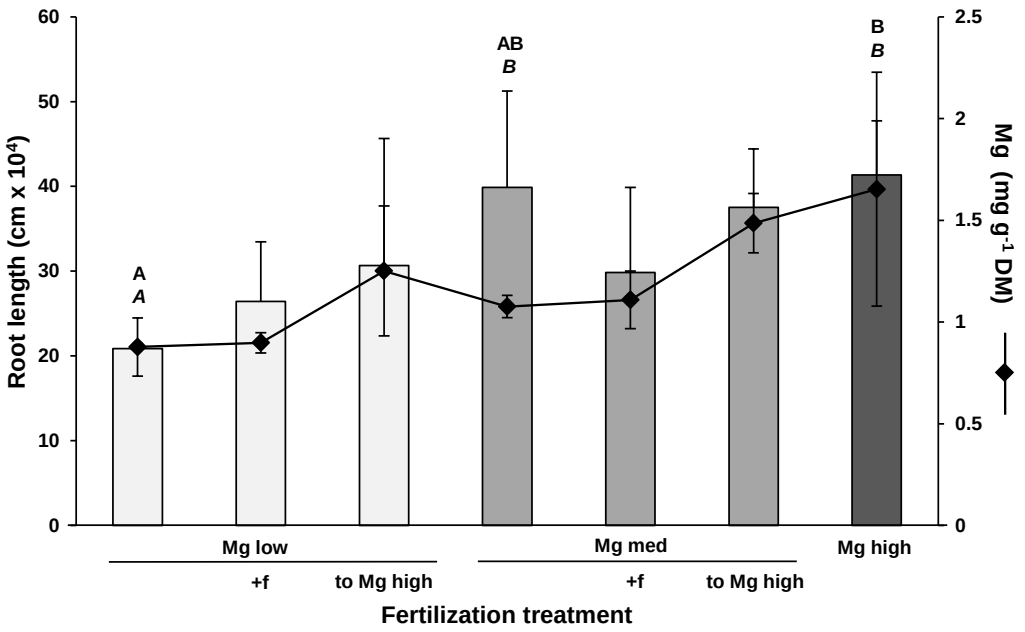


Figure 7: Total root length and root Mg concentrations in 'Mg low', 'Mg med' and 'Mg high' treated plants and impact of complementary fertilization treatments ('+f' and 'to Mg high') (n = 4). 'Mg low' = 5 µM Mg; 'Mg med' = 100 µM Mg; 'Mg high' = 500 µM Mg; '+f' = with Mg foliar application; 'to high' = change of the Mg nutrient solution concentration from 5 or 100, respectively, to 500 µM Mg. Mean ± SE values. Capitals = significant differences of total root length between 'Mg low', 'Mg med' and 'Mg high' plants. Italic capitals = significant differences of Mg root concentrations between 'Mg low', 'Mg med' and 'Mg high' plants. No indication = no significance.

Discussion

Following, first results of the Mg plant status and chlorophyll and sugar leaf concentrations are discussed. Afterwards, in light of these results, the shoot and root growth – with special focus on the root development – is elucidated.

Mg status of the plant

Mg leave concentrations below 2 mg g^{-1} DM are considered critical to ensure optimal plant growth (Bergmann 1993; von Wulffen et al. 2008). Hence, 'Mg low' plants exhibited Mg leave concentrations below values which are presumed to be required for optimal plant growth and development (Fig. 2a). This deficient Mg status of 'Mg low' plants led to the emergence of typical Mg deficiency symptoms on fully expanded leaves of 'Mg low' treated plants: First, moderate and unclear segregated chlorosis became visible (Fig. 8a) which developed into interveinal leave chlorosis and flat spot-like necrosis (Fig. 8b). Usually, Mg deficiency symptoms first occur on older fully expanded leaves, as Mg is phloem mobile and therefore translocated to younger developing leaves under scarcity of Mg (Karley and White 2009), what likewise has been observed in the present study.

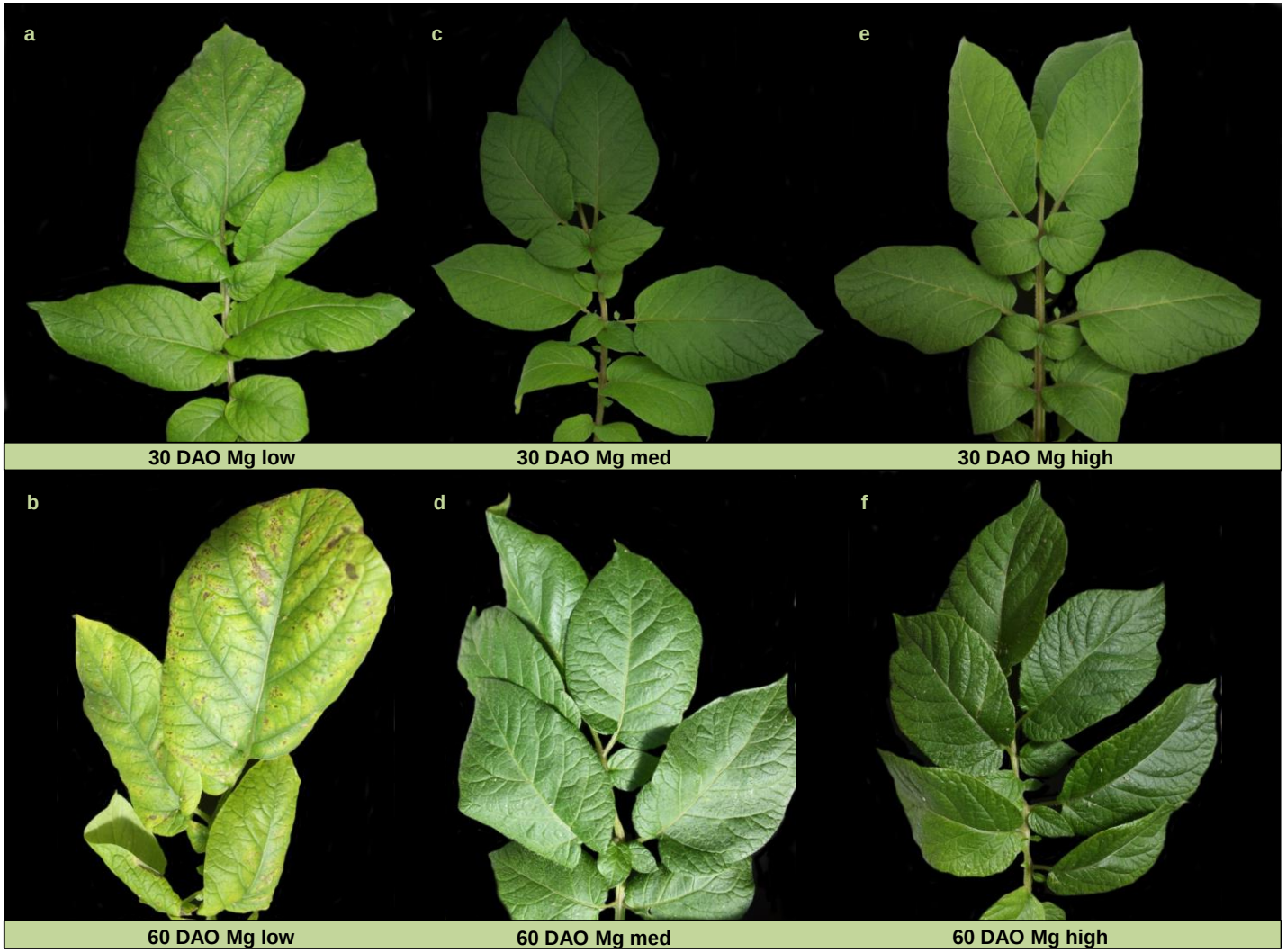


Figure 8: Visual symptoms of Mg deficiency [(a), (b)] of potato leaflets compared to Mg-non-deficient leaflets [(c) – (f)] 30 (above) and 60 (below) days after onset of treatment.

'Mg med' and 'Mg high' treated plants did not show any visible Mg deficiency symptoms (Fig. 8c – f), although at the first two sampling dates also 'Mg med' plants showed Mg leave concentrations in a critical range (Fig. 2a).

An Mg foliar application could not ameliorate a deficient Mg status of the plant, although a short increase of the Mg leave concentrations in 'Mg low' and to a less extend in 'Mg med' plants due to the foliar applications was detectable (Fig. 2b). This effect was significant only after the first and the second Mg foliar application (10 and 17 DAO) in 'Mg low' and only after the first Mg foliar application (10 DAO) in 'Mg med' plants. However, a more efficient effect to restore a limited Mg nutritional status was realized by raising the Mg supply via the nutrient solution. Mg leave concentrations increased up to a level far above values of a critical Mg supply. Furthermore, these Mg leave concentrations remained stable throughout all sampling dates.

Leaf chlorophyll and soluble sugar concentrations under Mg restriction

The actual distribution of Mg in the plant strongly depends on the plant´s Mg supply (Michael 1941). Between 10 to 20% of the total Mg pool is supposed to be bound to chlorophyll (Mayland 1990; Verbruggen and Hermans 2013) while the proportion can be even higher in Mg depleted plants (Scott and Robson 1990). Chlorophyll concentrations of fully expanded leaves did not show any significant differences between the various Mg supplied plants in the present study (Fig. 3). This might be due to the fact that in Mg limited plants an higher proportion of the available Mg was shifted in the synthesis of chlorophyll rather than into other processes or plant structures requiring Mg, as was likewise detected by Scott and Robson (1990) in subterranean clover (*Trifolium subterraneum* L.).

As described earlier and is illustrated in Fig. 8b chlorosis and necrosis appeared in between the leave veins or were spread spot-like over the leaf surface. Therefore, chlorophyll degradation due to Mg deficiency (Cakmak and Kirkby 2008) might be segregated to leaf parts which show clear symptoms of chlorosis and necrosis while leaf parts without these symptoms do not show degradation of chlorophyll. Such an inequality in chlorophyll distribution of leaves might have affected the outcomes of chlorophyll determination.

Beside chlorophyll, soluble sugars in fully expanded leaves were determined. 'Mg low' plants exhibited a distinct accumulation of soluble sugars in leaves with proceeded plant development (Fig. 4b and c). A lack of available Mg might have led to an impaired phloem loading process in these plants what resulted in an accumulation of soluble sugars in source leaves. Moreover, beside an increase in total soluble sugars, we determined an increase of hexose sugars in the same leaves (Fig. 4b and c). This indicates a raised breakdown of sucrose into hexose sugar units. Similar outcomes were recorded by Huber (1984) in soybean plants (*Glycine max* L. *Merr.*) under potassium deficiency. Next

to Mg also potassium is essential for the loading of and the distribution within the phloem of photoassimilates (Cakmak et al. 1994a). Huber (1984) argues the increasing breakdown of sucrose into hexose sugars with an increased activity of the sucrose hydrolyzing enzyme invertase following an accumulation of sucrose. Beside, Farhat et al. (2016) detected an accumulation of sugars in Mg deficient *Sulla carnosa* plants what the authors likewise refer to an increased activity of the enzyme invertase due to an impaired phloem loading process.

The fact, that soluble sugar concentrations did not reveal significant differences between the treatments on 14 DAO (Fig. 4a), can be referred to an less pronounced sink demand of roots at this early growth stage. However, with progressed plant development (35 and 56 DAO) (Fig. 4b and c), an increase of sink demand of developing roots resulted in significant differences between Mg treatments due to the above described reasons.

Root growth as affected by the Mg supply

Root growth showed a more severe reduction compared to shoot growth (Fig. 5a–d). For instance, the shoot growth parameters 'quantity of internodes' and 'plant height' did not show any significant difference compared to the higher Mg supplied plants at the end of the growing period (after 49 DAO) (Fig. 5c and d). While the total root biomass decreased up to 50%, the total shoot biomass was at most reduced up to 35% in 'Mg low' compared to 'Mg med' and 'Mg high' plants (Fig. 5a and b). Also Mengutay et al. (2013) recorded a higher sensitivity of the root compared to the shoot growth in Mg limited maize (*Zea mays*) and wheat plants (*Triticum aestivum*) as well as Neuhaus et al. (2014). A higher sensitivity of the roots compared to the shoots to Mg deficiency is also reflected in the shoot-to-root ratios (Fig. 5b): 'Mg low' plants showed the highest shoot-to-root ratios while 'Mg high' plants exhibited the lowest ratio. However, the shoot-to-root ratio of 'Mg med' plants was similar high as of 'Mg low' plants. This is due to the fact that these plants showed a very high shoot biomass production, even higher than 'Mg high' plants (Fig. 5a). By comparison of our outcomes with other studies, our results are in accordance with Cakmak et al. (1994b) and Mengutay et al. (2013) who both demonstrated a severe reduction of root biomass and an increase of the shoot-to-root ratio under Mg deficiency. Besides, Gruber et al. (2013) found decreased root lengths in Mg deficient Arabidopsis plants. We confirmed these findings for potato in this study: Similar to the total root biomass the total root length showed a reduction up to 50% in 'Mg low' compared to 'Mg med' and 'Mg high' treated plants (Fig. 7). Cakmak et al. (1994b) and Marschner et al. (1996) refer a reduced root growth mainly to a hampered translocation of photoassimilates under Mg deficiency. However, Marschner et al. (1996) supposed that a further reason for a sucrose accumulation in source leaves might be a depressed sink demand. As discussed previously, our results showed a distinct accumulation of

soluble sugars in fully expanded leaves of Mg deficient plants (Fig. 4b and c) what could indicate an impaired loading of the phloem with sucrose and thus, a restricted export of photoassimilates from source (fully expanded leaves) to sink organs (roots). On the other hand, it is possible that a reduced sink demand (reduced root growth), likely because of a reduced production of photoassimilates via photosynthesis due to Mg deficiency, lead to an accumulation of sucrose in source leaves.

Opposite to our findings are the results stated by Hermans and Verbruggen (2005) who intended that Mg deficiency does not markedly reduce the root development. Hermans and Verbruggen (2005) argue their findings with differential distributions of photoassimilates in dependence on the position of the source leave. Based on the outcomes of ^{14}C-labelled sucrose analysis they could draw conclusions about the exact location of source and sink tissue. They illustrated that upper most expanded leaves are mainly translocating sucrose to young developing leaves while older leaves, located closer to the roots, are mainly exporting sucrose to the roots. Furthermore, the upper most expanded leaves were the first plant organs exhibiting symptoms of Mg deficiency while the older leaves with proximity to the roots did not suffer under Mg scarcity yet. Thus, the authors conclude that the latter leaves still were able to export enough photoassimilates to the roots. Explanation for the divergent findings of the mentioned studies might be the different experimental setups. While Cakmak et al. (1994b) as well as Mengutay et al. (2013) grew their plants under Mg deficiency starting at an early growth stage, Hermans and Verbruggen (2005) grew their plants for a period of three weeks under a sufficient supply of Mg, before setting them into a Mg-free nutrient solution. Hence, it is presumable that the Arabidopsis (*Arabidopsis thaliana*) seedlings in the experiment of Hermans and Verbruggen (2005) were able to establish already an adequate root biomass in the first weeks of growing under sufficient Mg supply. Therefore, the above mentioned studies do not oppose each other but results are the outcome of different experimental designs. Moreover, the results presented by Hermans and Verbruggen (2005) may indicate that Mg particularly affects the root development in the first weeks of plant growth.

With view on the previous discussed results, it can be stated that a supply of 100 µM Mg can be considered as sufficient for potato root growth as these plants revealed similar results in root biomass (Fig. 5b), total root length (Fig. 7) and no accumulation of soluble sugars in source leaves (Fig. 4b and c) as did plants with 500 µM Mg supply.

The complementary fertilization treatments ('+f' as well as 'to high') did not show significant impacts on the root development, although a clear tendency became evident that an additional Mg supply via the nutrient solution to 'Mg low' plants increased Mg leaf and root concentrations and total root lengths (Fig. 2b and 7). An Mg foliar application led, compared to an Mg complementary fertilization via the roots, to an only slight and temporally restricted increase

of Mg leaf concentrations and of the total root length (Fig. 2b and 7). This indicates that an Mg foliar application is not an effective tool to restore an Mg deficient nutrient status and depressed root growth of Mg deficient plants. By comparison, Neuhaus et al. (2014) showed more distinct effects by an Mg foliar application on Mg leaf concentrations and demonstrated a significant increase on root biomass. However, similarly to our findings, a raised supply of Mg via the nutrient solution resulted in a significant higher root biomass development compared to an Mg supply via leaves (Neuhaus et al. 2014).

Conclusions

Mg deficient plants revealed significant reduced root biomass and total root lengths. This might be referred to an hampered translocation of photoassimilates from source (leaves) to sink organs (roots) due to Mg deficiency as Mg deficient plants exhibited a sucrose accumulation in source leaves, what indicated an impaired loading of the phloem with sucrose. On the other hand, it is presumable that a reduced root growth due to Mg deficiency resulted in a decreased sink demand what in turn may shift the direction of sugar fluxes within the plant and results in an accumulation of soluble sugars in source leaves. Furthermore, our results demonstrated that an Mg supply of 100µM Mg represents a sufficient supply of Mg for potato root growth. The Mg complementary fertilization treatments in form of Mg foliar applications or Mg resupply via the nutrient solution did not show significant impacts on potato root growth. However, an additional Mg supply via the nutrient solution resulted in a clear increase of Mg leaf and root concentrations and of the total root lengths. Thus, an Mg resupply via the nutrient solution can partly represent an appropriate tool to ameliorate an Mg deficient nutrient status and reduced root growth due to Mg deficiency in potato.

Acknowledgements

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Supplementary material

SM_1: Used form and applied amounts (mg kg^{-1} soil) of nutrients under low and sufficient Mg supply of the soil culture system for plant propagation before transfer into nutrient solution.

Nutrient [Form of nutrient]	Applied amounts low Mg supply	Applied amounts sufficient Mg supply
Magnesium [Mg_2SO_4 x 7 H_2O]	5	100
Potassium [K_2SO_4]	300	300
Nitrogen [$Ca(NO)_3$]	300	300
Phosphorus [$Ca(PO_4)_2$ x H_2O]	100	100
Calcium [$CaCO_3$]	1300	1300
Boron [H_3BO_3]	2	2
Zinc [$ZnSO_4$ x 7H_2O]	2	2
Molybdenum [Na_2MoO_4 x 2 H_2O]	0.01	0.01
Copper [$CuSO_4$ x 5H_2O]	2	2
Manganese [$MnSO_4$ x H_2O]	6	6
Iron [Fe(III) EDTA (13% Fe)]	3	3

SM_2: Effect of Mg complementary fertilizations ('+f' and 'to Mg high') on quantity of internodes and on plant heights in cm at eight various sampling dates (n = 4). Mean ± SE values. Treatments had no significant effect.

Internodes

Days after treatment	Mg low +f	Mg low to Mg high	Mg med +f	Mg med to Mg high
9	7 ± 1	9 ± 1	9 ± 1	9 ± 1
14	8 ± 1	9 ± 1	10 ± 2	10 ± 1
21	11 ± 1	11 ± 1	12 ± 2	12 ± 1
28	13 ± 2	12 ± 0	15 ± 2	14 ± 1
35	13 ± 2	13 ± 0	15 ± 2	15 ± 1
42	15 ± 1	14 ± 1	15 ± 1	16 ± 0
49	15 ± 1	14 ± 1	15 ± 1	16 ± 0
56	15 ± 1	14 ± 1	17 ± 2	16 ± 0

Plant heights

9	16 ± 2	18 ± 1	22 ± 1	21 ± 2
14	18 ± 1	19 ± 1	29 ± 5	25 ± 4
21	35 ± 2	29 ± 3	37 ± 5	38 ± 2
28	53 ± 3	48 ± 8	52 ± 5	53 ± 3
35	66 ± 3	61 ± 7	68 ± 6	65 ± 3
42	80 ± 3	76 ± 12	83 ± 7	82 ± 2
49	87 ± 2	80 ± 22	91 ± 9	91 ± 2
56	88 ± 4	80 ± 22	91 ± 5	90 ± 2

Chapter 6

Cracking and Fracture Properties of Potato (Solanum tuberosum L.) Tubers and their Relation to Dry Matter, Starch and Mineral Distribution

Mirjam Koch, Marcel Naumann and Elke Pawelzik

Submitted

Cracking and Fracture Properties of Potato (*Solanum tuberosum* L.) Tubers and their Relation to Dry Matter, Starch and Mineral Distribution

Mirjam Koch*, Marcel Naumann and Elke Pawelzik

Department for Crop Sciences, Division Quality of Plant Products, Carl-Sprengel-Weg 1, 37075 Göttingen, University of Göttingen, Germany.

* Correspondence to: Mirjam Koch, Department for Crop Sciences, Division Quality of Plant Products, Carl-Sprengel-Weg 1, 37075 Göttingen, University of Göttingen, Germany. Tel.: 49(0)551-39-25568. Fax: 49(0)551/39-25570. Email: mirjam.koch@agr.uni-goettingen.de.

Running title: Cracking and fracture properties of potato tubers (*Solanum tuberosum* L.)

Abstract

BACKGROUND: Potato disorders lead to significant reductions of yield and quality of marketable tubers. Thumbnail cracks are non-infectious physiological disorders of the skin of tubers, which can significantly reduce the tuber appearance and hence, the overall quality. Next to thumbnail cracks, we aimed to characterize fracture properties of the tuber skin. Knowledge regarding physiological reasons that influence the susceptibility of potato tubers towards mechanical impacts and thus towards cracking and fracturing is limited. Tuber dry matter (DM) and starch content were demonstrated to correlate with the rheological properties of tubers, which, in turn, might affect the susceptibility of the tuber towards cracking and fracturing. Aside from this, divalent cations, such as calcium (Ca) and magnesium (Mg), and their distribution in the tuber, might affect the tuber susceptibility for mechanical impacts via cell wall stabilizing properties.

RESULTS: Tubers with higher DM, starch and Ca concentrations, respectively, exhibited the highest resistances against mechanical impacts.

CONCLUSIONS: The reason for the increased resistance of tubers against mechanical impacts with higher DM and starch concentrations is assumed to be related to a certain cell structure of these tubers, why a higher strength is needed to damage cell structures. Besides, the relation between higher Ca concentrations and the improved resistance of tubers against mechanical impacts is supposed to be linked with the role of Ca for linking cell wall polymers and thus stabilizing the cell wall.

Keywords: thumbnail cracks, fracturability, mineral distributions, dry matter, potato

Introduction

A majority of the world´s potato production is used for fresh consumption; however, in industrial nations there has been a decrease in the consumption of fresh potatoes in recent years (Camire et al. 2009; Lange et al. 2014). At the same time, the demand for a high quality of food products, including vegetables and fruits, has sharply increased (Ali et al. 2010). Visual appearance is a major sensory quality attribute of fruits and vegetables (Zhang et al. 2014). It has been shown that the external appearance of potato tubers is one of the most important factors that influences consumer preferences (Fiers et al. 2010). A symptom that is likely to negatively impact consumer´s purchase behavior is the 'thumbnail crack', which is a small curved and few millimeter deep crack of the tuber skin (Fig. 1). These small injuries can significantly decrease the appeal of tubers (Hiller et al. 1985; Bohl and Thornton 2006). Furthermore, such small damage areas can serve as entrance points for secondary infections (Hide et al. 1992) and hence might additionally reduce the quality and quantity of marketable tubers (Šaøec et al. 2006). Thumbnail cracks are classified as non-infectious physiological disorders as they are caused by abiotic factors like unfavorable environmental conditions—for instance, a rapid change of humidity or temperature, or inappropriate agricultural practices causing mechanical impacts during or after harvest (Sparks 1970; Dean and Thornton 1989).

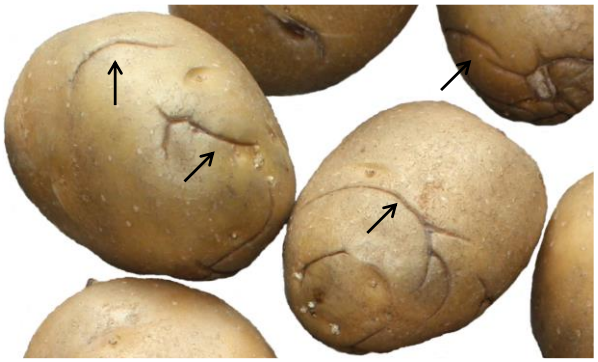

Figure 1: Typical occurrence of the 'thumbnail crack' symptom.

Aside from the tuber´s susceptibility for thumbnail cracking, the further characterization of rheological properties of the tuber skin, especially its fracturability due to an applied force was focused in the present study. Determinants of the rheological properties, which, in turn, might affect the susceptibility for cracking or fracturing of the tuber skin are the cultivar (Peters 1996; Kaur et al. 2007), storage conditions (Kaur et al. 2007), soil type (Hesen et al. 1960), or the status of nutrient supply (Hesen et al. 1960; Peters 1996; McNabnay et al. 1999). However, knowledge with respect to the physiological reasons that affect the susceptibly of potato tubers cracking and fracturing is rare. There are indications that the tuber dry matter (DM) and starch concentrations are determinants

that are correlated with the tuber´s rheological properties (Bordoloi et al. 2012). The tuber´s DM and starch concentrations may vary considerably between cultivars (Vakis 1978; Jansen et al. 2001). Furthermore, the potassium (K) and magnesium (Mg) status of the plant are both known to affect on the tuber´s DM and starch concentrations—but with divergent outcomes (Laughlin 1966; Miča 1979; Panique et al. 1997; Poberezny et al. 2011). To our knowledge, the impact of K and Mg nutrition on the tuber´s DM and starch concentrations in relation to the formation of thumbnail cracks and fracture properties of the tuber skin has never been investigated.

Moreover, the stability of cell wall and thus of the tissue that forms the tuber periderm, can be affected by divalent cations, such as Ca and Mg. These divalent cations are supposed to stabilize the cell wall via cross-linking cell wall polymers (Pooviah 1986; Andersson et al. 1994; Weiler and Nover 2008), which might affect the susceptibility of tubers towards cracking or to fracture. In addition, the distribution patterns of DM, starch, and minerals within the tubers themselves might affect the susceptibility of tubers towards forming thumbnail cracks or fractures.

The assumptions of the present study are as follows:

First, a hypothesis is drawn that the tuber´s susceptibility to form thumbnail cracks and to fracture will correlate with the tuber DM and starch concentrations, which are, in turn influenced by the K and Mg supply and the cultivar. Second, based on the relations between Ca, and likely also Mg, and the cell wall stability, a decreasing susceptibility of the tubers to form thumbnail cracks and to fracture with increasing Ca and Mg tuber concentrations are expected. Finally, it is assumed, that distinct distribution patterns of DM, starch, and minerals within the tuber can correlate to the occurrence of thumbnail cracks and on the susceptibility to fracture.

Material and Methods

Plant Growth Conditions

In 2015, a field trial with two sites (Müncheberg and Uedem, Germany), four different K and Mg fertilization treatments (Table 1), and two cultivars, Omega and Laura, was conducted. Both cultivars are assigned to a medium-early maturity group, but are different in their intended use, cooking type, and tuber shape. While Omega is used as a table potato and a crisp potato, falling under the mealy cooking type with a round–oval tuber shape, Laura is only used as a table potato, with a waxy cooking type and an oval tuber shape (Europlant 2014; Federal Plant Variety Office 2016). Each combination of the fertilization treatment and cultivar was replicated four times. The trial at the site in Müncheberg (following designated as 'Müncheberg') was conducted in a completely randomized block design, while at the trial of the site Uedem (following designated as 'Uedem') two cultivars were grown in two separated blocks, which were themselves completely randomized. The different K and Mg supplies

(F1–F3, control = Ctr) are shown in Table 1. 'F1' represents a fertilization regime without K and without Mg. The fertilization treatment 'F2' was supplied with K, but without Mg. The fertilization treatment 'F3' received Mg, but no K. The 'Ctr' treatment was supplied with K as well as with Mg, according to common agricultural practice. K was applied as K_2O via potassium sulphate (50% K_2O; 45 %SO_3) and Mg was applied as MgO via kieserite (25% MgO; 50% SO_3). All the other nutrients were provided as shown in Table 1.

Further field trials were performed in 2016 with the two cultivars Omega and Laura, and four different K and Mg fertilization treatments at three sites (Müncheberg and Uedem, Germany; Kościan, Poland). The experimental design for the sites 'Müncheberg' and 'Uedem' were the same as the trials conducted in 2015 and the design of the trial at the site Kościan (following designated as 'Kościan') was the same as the design employed in 'Müncheberg' in 2015 and 2016. The climate conditions throughout the vegetation periods (supplementary material (SM), SM_1) and the soil types and the K and Mg soil status (SM_2) were documented for all three sites.

Table 1: Nutrient supply (in kg ha^{-1}) of the four fertilization treatments (F1, F2, F3, and Control).

	K_2O	**MgO**	**SO_3**	**N**	**P_2O_5**
F1	x	x	535	x	120
F2	300	x	266	92	120
F3	x	130	271	90	120
Control	300	130	x	185	120

Tuber Handling after Harvest and Assignment of Analyses

After harvest, the tubers were stored at 4°C and 70% relative humidity. All the analyses were conducted across a period of eight weeks after harvest. In 2015, only whole tubers were analyzed. Aside from this, the evaluation of the thumbnail cracks was performed only with tubers from 'Müncheberg', while fracturability was assessed only with tubers from 'Uedem'. DM, starch, K, Mg and Ca concentrations were assessed in tubers from both trials. In 2016, evaluations for the thumbnail crack occurrence were performed with tubers from 'Müncheberg' and 'Kościan'. The determination of fracturability were performed with whole tubers from 'Müncheberg', 'Uedem', and 'Kościan' and with bud- and the stem-ends with tubers from 'Müncheberg' and 'Kościan'. Dry matter, starch, K, Mg, and Calcium (Ca) concentrations and their distributions were assessed in whole tubers from 'Müncheberg', 'Uedem', and 'Kościan' and with the tuber segments bud-end, stem-end, middle, flesh, and skin with tubers from 'Müncheberg' and 'Kościan'.

Dry Matter and Starch Concentrations

For DM and starch analyses, an average of 3–5 tubers or tuber segments of 3–5 tubers per treatment was formed. The used tuber quantity was chosen on the basis of tuber size, e.g., three bigger tubers or five smaller tubers. For DM determination, tubers were cut into pieces and the fresh sample weight of the subsample was determined. Afterwards, the sample was dried at 60°C for 24 hours and, subsequently, at 105°C for four hours and the dry weight was determined.

For starch analysis, tubers were cut into pieces and the samples were freeze-dried for four days in a freeze-dryer (EPSILON 2-40, Christ, Germany). Afterwards, the tubers were grinded to 0.5 mm of flour in a hammer mill (DFH 48, Culatti, Switzerland). Following this step, the residual moisture was assessed by determining the weight of a subsample of freeze-dried potato flour before and after drying for 12 hours at 105°C. Starch was quantified according to ICC standard no. 123 (modified). In 100 ml flasks, 25 ml of hydrochloric acid was added twice to 1 g of potato flour and placed for 15 minutes in a scalding water bath (Memmert, Germany); it was then shaken for the first eight minutes. The flasks were filled up to 90 ml with distilled water and cooled to room temperature. Following this, 5 ml of tungstophosphoric acid ($H_3PW_{12}O_{40}$) was added and panned. Finally, the flasks were filled up to 100 ml with distilled water and the optical rotation was examined in a polarimeter (Kreipo 0.05, Zeiss, Germany) at 589 nm.

Mineral Concentrations

Prior analyses, samples were prepared as described for starch determinations. The tuber skin was peeled with a common peeler with an average thickness of peel of 1.2 mm. In 2016, the tubers of the four biological replicates per fertilization treatment were pooled to form three technical replicates when enough tubers were not available. The minerals were assessed following an adjusted method as described by Wheal et al. (2011). From each sample, 100 mg was digested in 4 ml of 65% (v/v) nitric acid and 2 ml of 30% (v/v) hydrogen peroxide for 75 minutes at 200°C and 40 bar in a microwave (Ethos 660; MWT AG, Switzerland). Subsequently, the samples were filled up to 25 ml with distilled water. The concentrations of K, Mg, and Ca were examined by using inductively coupled plasma optical emission spectrometry (Vista-PRO CCD Simultaneous ICP-OES; Varian Inc., USA).

Thumbnail Crack Evaluation

To evaluate the susceptibility to form thumbnail cracks, the tubers were damaged in a controlled way with the help of a drum (Flottwerk H. J. Dames GmbH & Co. KG, Rotenburg an der Fulda, Germany). Here, the mechanical impacts on the potato tubers were simulated, which might also occur during or after harvest. Each sample was

assessed to a volume of 6 liters and damaged in the drum for 50 seconds. A continuous tuber temperature of 4°C was preserved throughout the analysis. Subsequently, the tubers were stored for five days at room temperature, followed by an evaluation of the thumbnail cracks with grades ranging from 1–9 (1 = very severe occurrence; 3 = severe occurrence; 5 = medium occurrence; 7 = slight occurrence; 9 = almost no occurrence) according to a standard procedure as has been described by Meyer et al. (2014). The thumbnail cracks were only analyzed on tubers from 'Müncheberg' in both the experimental years and, furthermore, as shown in the supporting information in 2016 from 'Kościan'.

Tuber Skin Fracturability Measured by Penetration Test

Fracturability of the tuber skin was assessed by using a texture analyzer (Stable Micro Systems Ltd., TA.XT.plus, UK). 'Fracturability' is defined as the complete loss of resistance of the tuber skin due to a certain applied force that causes a destruction of the potato peel and the subjacent soft tissue (SM_3). The measurement was carried out at a speed of 2 mm per second and a 5-kg measuring cell was used. A stamp of 5 mm Ø penetrated the potato tuber with a depth of 10 mm. To preserve a tuber temperature of approximately 4°C throughout the measurement, the tubers were stored in a freezer cabinet immediately after removal from the storage device prior to analysis for one hour (at most).

For assessment of fracturability of the whole potato, at least 20 tubers per treatment were considered for the analyzed potato bud- and the stem-ends of at least 12 tubers were taken. Furthermore, in 2016, the tubers of the four biological replicates per fertilization treatment were pooled into three technical replicates due to the restricted availability of tubers per treatment.

Statistics

The statistical software R (R Core Team 2016) was used to evaluate the data. The data evaluation was split into two main steps. In a first step, the values from 2015 were considered. Here, the focus was set on the effect of the fertilization treatment and the cultivar. A statistical mixed model was separately defined for each site with fertilization treatment and the cultivars, and the interaction of fertilization treatment and cultivar as fixed effects. The splitting, according to the sites, was necessary because of further influence factors, which were not orthogonal for all sites. The block and the plots (nested in block) were regarded as random factors. The data were assumed to be normally distributed and heteroscedastic due to the different sites. These assumptions are based on graphical residual analyses. Based on these models, Pseudo R^2 was calculated and the analyses of variances (ANOVA) were conducted, followed by multiple contrast tests in order to compare the several fertilization treatments and the

cultivars, respectively. In the second step, the values from 2016 were considered, with a focus on the cultivar and the tuber segment. Only the fertilization treatment 'Ctr' was investigated. The statistical procedure and the assumptions about the data were the same as in the first step. All tests were performed at a significance level of $p < 0.05$.

Results

Tuber Cracking and Fracturability and DM, Starch, and Mineral Concentrations based on the Fertilization Treatment and the Cultivar (2015)

The fertilization regime and the cultivar did not show any impact on the occurrence of thumbnail cracks (SM_4a). The fracturability was not influenced by the fertilization treatment as well, but it was significantly different in the cultivars in form of a higher fracturability in Omega compared to Laura (SM_4b).

The fertilization treatment did not affect the DM and starch concentrations in the present study (Table 2). However, there was a significant impact of the cultivar on DM: Tubers of the cultivar Omega from 'Müncheberg' revealed a significantly higher DM in comparison to Laura (Table 2). Similar findings were assessed in tubers from 'Uedem' (Table 2).

Likewise, for the DM and starch concentrations, the fertilization treatment did not cause a significant variation in the tuber K as well as in the tuber Ca concentrations. The fertilization treatment 'F1', however, exhibited significantly lower Mg concentrations in comparison to the 'Ctr' fertilization treatment in tubers from 'Müncheberg' (Table 2). Moreover, Omega showed significantly lower Mg concentrations in comparison to Laura in tubers from this site (Table 2). According to the ANOVA test, there was a significant influence of the cultivar on the Ca concentrations in tubers from both trials (Table 2, below Table). However, the results of multiple contrast tests revealed significantly higher Ca concentrations only in tubers of the fertilization treatment 'F2' from 'Uedem' (Table 2).

Table 2: Dry matter (%), starch (% in DM), K, Mg, and Ca (mg g^{-1} DM) concentrations of the whole tubers of the cultivars Omega and Laura from 'Müncheberg' and 'Uedem' under different K- and Mg-fertilization treatments (F1, F2, F3, and Ctr) in 2015. Mean ± SE values (n = 3−4). Levels of significance for cultivar, fertilization, and its interaction tested via the ANOVA test are shown below the table with *, **, and *** for $p < 0.05$, 0.01, and 0.001, respectively. ns = not significant. Capitals = significant differences between the cultivars of one fertilization treatment, small letters = significant differences between the fertilization treatments, and no indication = no significant differences.

Müncheberg

Omega	F1		F2		F3		Ctr	
DM	24.03 ± 0.39	B	23.69 ± 1.23	B	23.67 ± 1.77	B	24.30 ± 0.88	B
Starch	63.96 ± 1.92		66.06 ± 2.36		65.45 ± 1.09		63.88 ± 2.31	
K	23.29 ± 1.86		25.29 ± 0.95		24.52 ± 2.15		26.16 ± 1.60	
Mg	0.90 ± 0.07	Aa	1.03 ± 0.03	Aab	1.05 ± 0.12	Aab	1.07 ± 0.03	Ab
Ca	0.29 ± 0.06		0.23 ± 0.03		0.26 ± 0.05		0.27 ± 0.07	
Laura								
DM	20.85 ± 1.01	A	20.39 ± 1.09	A	20.46 ± 0.53	A	19.90 ± 0.99	A
Starch	61.18 ± 1.94		61.87 ± 3.76		62.23 ± 1.64		65.47 ± 2.62	
K	25.05 ± 2.60		27.66 ± 1.72		24.87 ± 1.15		27.29 ± 0.94	
Mg	1.18 ± 0.13	B	1.25 ± 0.03	B	1.21 ± 0.01	B	1.21 ± 0.04	B
Ca	0.21 ± 0.06		0.25 ± 0.11		0.19 ± 0.05		0.20 ± 0.05	

Uedem

Omega								
DM	20.64 ± 1.94		21.14 ± 2.28		23.12 ± 1.65	B	21.69 ± 0.68	
Starch	68.19 ± 2.05		67.91 ± 2.44		69.88 ± 1.02		69.05 ± 2.46	
K	27.17 ± 2.86		29.23 ± 6.75		25.96 ± 0.62		26.76 ± 1.10	
Mg	1.11 ± 0.08		1.27 ± 0.23		1.17 ± 0.05		1.21 ± 0.04	
Ca	0.47 ± 0.03		0.56 ± 0.15	B	0.45 ± 0.08		0.45 ± 0.06	
Laura								
DM	18.75 ± 1.23		19.06 ± 0.40		19.35 ± 1.72	A	18.31 ± 0.76	
Starch	65.56 ± 1.07		66.42 ± 2.41		66.46 ± 1.26		65.89 ± 1.48	
K	28.53 ± 2.22		27.81 ± 1.13		26.79 ± 2.26		23.76 ± 4.92	
Mg	1.20 ± 0.06		1.20 ± 0.02		1.14 ± 0.07		1.12 ± 0.08	
Ca	0.37 ± 0.03		0.38 ± 0.01	A	0.38 ± 0.05		0.36 ± 0.01	

DM Müncheberg: Cultivar ***, fertilization ns, cultivar x fertilization ns; Starch Müncheberg: Cultivar **, fertilization ns, cultivar x fertilization ns; K Müncheberg: Cultivar *, fertilization **, cultivar x fertilization ns; Mg Müncheberg: Cultivar ***, fertilization *, cultivar x fertilization ns; Ca Müncheberg: Cultivar *, fertilization ns, cultivar x fertilization ns; DM Uedem: Cultivar **, fertilization ns, cultivar x fertilization ns; Starch Uedem: Cultivar *, fretilization ns, cultivar x fertilization ns; K Uedem: Cultivar ns, fertilization ns, cultivar x fertilization ns; Mg Uedem: Cultivar ns, fertilization ns, cultivar x fertilization ns; Ca Uedem: Cultivar **, fertilization ns, cultivar x fertilization ns.

Tuber Cracking and Fracturability and DM, Starch, and Mineral Concentrations based on the Fertilization Treatment (2016)

Likewise as in the experimental year 2015, in 2016, there was no impact of fertilization treatment on the investigated parameters. Therefore, in 2016, the focus was set on the impact of the cultivar and of the different tuber segments. Here, unless otherwise mentioned, tubers from 'Kościan' (SM_5 and 6) showed negligible deviation in comparison to tubers from 'Müncheberg' and 'Uedem'. Thus, the following results focus on analyses done with tubers from 'Uedem' and 'Müncheberg'.

Tuber Cracking and Fracturability and DM, Starch, and Mineral Concentrations based on the Cultivar and their Distribution in the Tuber (Müncheberg, 2016)

The influence factors cultivar and tuber segment, respectively, did not affect the occurrence of thumbnail cracks, although there was a tendency for a higher occurrence of thumbnail cracks in the cultivar Laura in comparison to Omega (Fig. 2a). However, the influence factors cultivar and tuber segment demonstrated more distinct effects on fracturability: first, Omega showed significantly higher fracturability in comparison to Laura; second, the stem-ends demonstrated a significantly higher fracturability in comparison to the bud-ends (Fig. 2b).

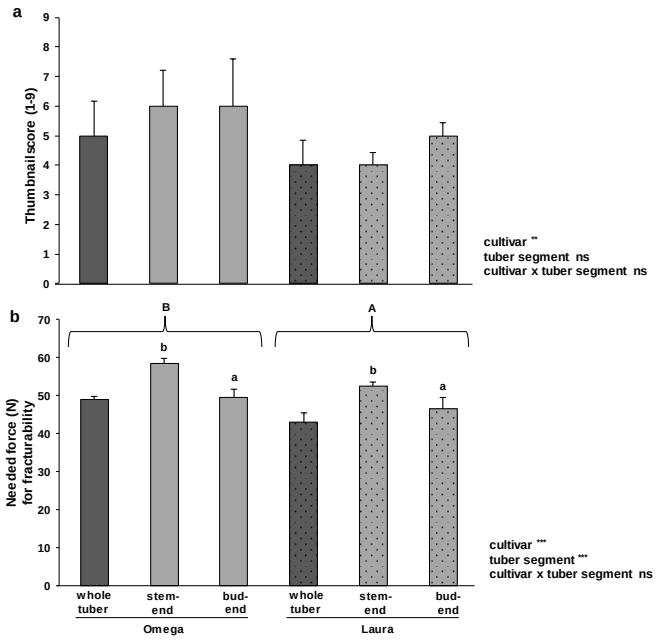

Figure 2: Thumbnail crack occurrence of whole tubers, tuber stem, and bud-ends of the cultivars Omega and Laura from 'Müncheberg' for the control fertilization treatment in 2016 (n = 4) (a). Thumbnail score: 1 = very severe occurrence, 3 = severe occurrence, 5 = medium occurrence, 7 = slight occurrence, and 9 = almost no occurrence. Fracturability of whole tubers, the tuber stem, and bud-ends of the cultivars Omega and Laura from 'Müncheberg' for the control fertilization treatment in 2016 (n = 3) (b). Mean ± SE values. Levels of significance tested via the ANOVA test are shown in the right lower corner with ** and *** for $p < 0.01$ and 0.001, respectively. ns = not significant. Capitals = significant differences between the cultivars of one tuber segment, small letters = significant differences between tuber segments of one cultivar and the storage period, and no indication = no significant differences.

Tubers revealed significantly higher DM and starch concentrations in Omega in comparison to Laura when the DM and starch concentrations were averaged over all the tuber segments of one cultivar (Table 3). The significant lowest DM as well as starch concentrations were examined in the tuber skin (Table 3). There was a tendency of ascertainable lower DM in the bud- in comparison to the stem-ends of the tubers (Table 3).

Opposite to the DM and starch concentrations, the significant highest K, Mg, and Ca concentrations were assessed in the tuber skin (Table 3). Furthermore, K showed higher concentrations in the bud- in comparison to the stem-ends (Table 3). Omega revealed in tendency higher Ca concentrations than Laura, however, these differences were not significant: For instance, the Ca concentrations were up to one-third higher in the tuber skin of Omega in comparison to Laura (Table 3); Due to significant interactions of the influence factors cultivar and the tuber segment, a statistical contrast test between the cultivars of the averaged Ca concentrations over all the tuber parts was unfeasible. Nevertheless, according to the ANOVA test, the cultivar exhibited a significant impact on the Ca concentrations (Table 3, below Table). However, tubers from 'Kościan' revealed significantly higher Ca concentrations in Omega in comparison to Laura when the Ca concentrations were averaged over all the tuber segments of one cultivar (SM_5), as there were no significant interactions between the influence factors cultivar and tuber segment in tubers from this site (SM_5, below Table).

Table 3: Dry matter (%), starch (% in DM), K, Mg, and Ca (mg g^{-1} DM) concentrations of whole tubers and the tuber segments stem- and bud-end, middle, skin, and flesh of the cultivars Omega and Laura from 'Müncheberg' during control fertilization treatment in 2016. Mean ± SE values (n = 3–4). Levels of significance tested via the ANOVA test are shown below the table with *, **, and *** for $p < 0.05$, 0.01, and 0.001, respectively. ns = not significant. Capitals = significant differences between cultivars, and small letters = significant differences between tuber segments of one cultivar.

	whole tuber	stem-end		middle		bud-end		skin		flesh		Average over tuber segments	
Omega													
DM	24.65 ± 0.49	24.45 ± 0.71	b	24.49 ± 1.29	b	22.54 ± 0.46	ab	17.99 ± 0.47	a	23.80 ± 1.88	b	22.65 ± 2.73	B
Starch	68.79 ± 2.15	70.28 ± 2.34	b	72.52 ± 3.03	b	68.76 ± 2.67	b	46.18 ± 3.35	a	74.27 ± 1.66	b	64.43 ± 11.49	B
K	26.04 ± 0.61	21.17 ± 0.72	a	23.09 ± 0.62	ab	28.16 ± 1.39	b	35.62 ± 1.45	c	22.04 ± 0.83	ab	26.02 ± 6.01	
Mg	1.19 ± 0.08	0.96 ± 0.05	a	1.02 ± 0.05	a	1.12 ± 0.01	ab	1.37 ± 0.03	b	0.97 ± 0.01	a	1.09 ± 0.17	
Ca	0.24 ± 0.01	0.28 ± 0.04	a	0.20 ± 0.01	a	0.30 ± 0.01	a	0.93 ± 0.07	b	0.13 ± 0.01	a	0.37 ± 0.32	
Laura													
DM	23.66 ± 5.71	20.93 ± 1.17	bc	18.96 ± 1.23	abc	17.23 ± 0.98	ab	14.75 ± 0.91	a	20.59 ± 0.29	b	18.49 ± 2.56	A
Starch	58.90 ± 1.06	64.37 ± 1.16	bc	62.59 ± 0.18	bc	60.88 ± 0.89	bc	44.64 ± 3.06	a	68.13 ± 0.11	c	60.12 ± 9.06	A
K	25.93 ± 2.94	20.63 ± 3.31	ab	22.05 ± 1.58	ab	27.08 ± 1.66	b	36.87 ± 1.46	c	19.75 ± 1.27	a	25.28 ± 7.07	
Mg	1.16 ± 0.07	1.14 ± 0.04	ab	1.04 ± 0.04	a	1.07 ± 0.04	a	1.34 ± 0.03	b	1.05 ± 0.07	a	1.13 ± 0.12	
Ca	0.19 ± 0.03	0.27 ± 0.04	a	0.20 ± 0.04	a	0.24 ± 0.04	a	0.63 ± 0.05	b	0.14 ± 0.05	a	0.29 ± 0.19	

DM: Cultivar **, tuber segment ***, cultivar x tuber segment ns; Starch: Cultivar *, tuber segment ***, cultivar x tuber segment ns; K: Cultivar ns, tuber segment ***, cultivar x tuber segment ns; Mg: Cultivar ns, tuber segment ***, cultivar x tuber segment **; Ca: Cultivar *, tuber segment ***, cultivar x tuber segment ***.

Fracturability and DM, Starch, and Mineral Concentrations based on the Cultivar (Uedem, 2016)

Omega demonstrated a significant higher fracturability as well as significant higher DM and Ca concentrations in comparison to Laura (Figs. 3a, 3e, and 3f). Aside from this, there was an impact of the cultivar on the starch concentrations that was detected by the ANOVA test, but without the significant effects put forward by a detailed contrast test.

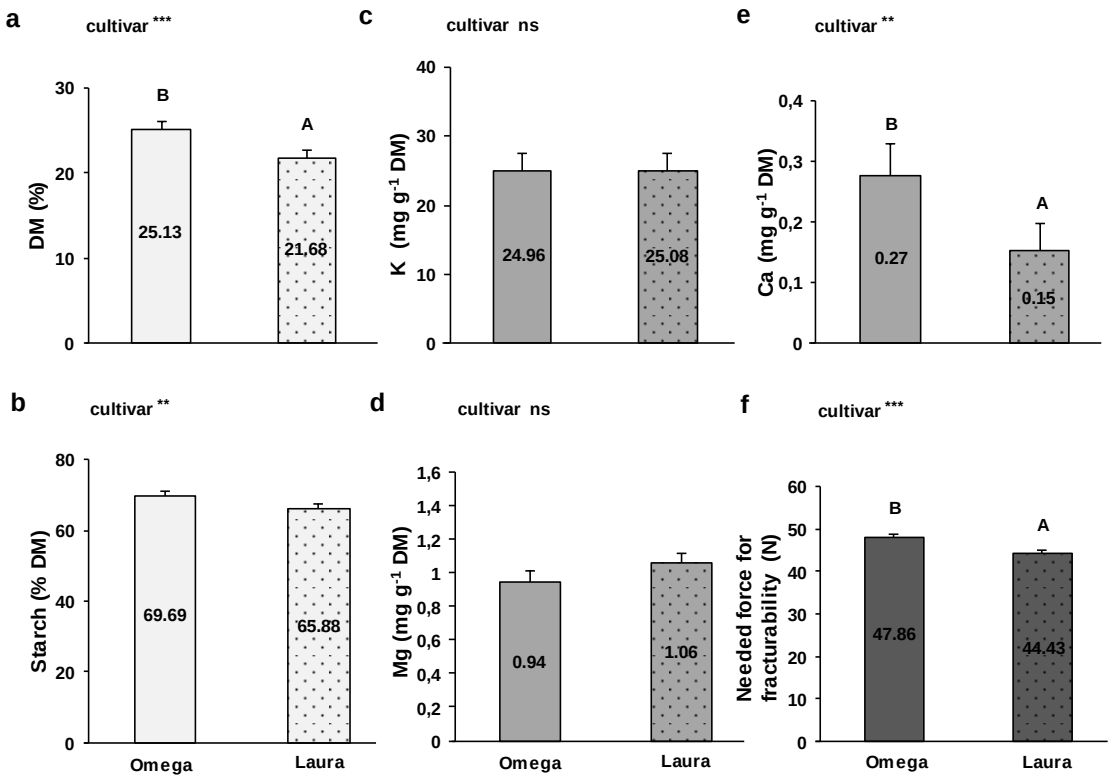

Figure 3: Dry matter (a), starch (b), K (c), Mg (d), and Ca (e) concentrations in relation to the tuber´s fracturability (f) of whole tubers of the cultivars Omega and Laura from 'Uedem' with respect to control fertilization treatment in 2016. Mean (shown inside the bars) ± SE values (n = 4). Levels of significance tested via the ANOVA test are shown in the left upper corner with *, **, and *** for $p < 0.05$, 0.01, and 0.001, respectively. ns = not significant. Capitals = significant differences between the cultivars, and no indication = no significant differences.

Discussion

Effect of Fertilization Treatment

The fertilization treatment did not show a clear impact on the occurrence of thumbnail cracks and on the fracturability as well as on the DM, starch, and mineral concentrations in both years of the experiment and at all the three field sites. An already sufficient supply of K and Mg in the soils of the field sites in the present study is probably reasonable for the lack of a response to the fertilizer application (SM_2). This assumption is strengthened by the fact that even the tuber yield remained unaffected by the K and Mg fertilization treatments (SM_7). Therefore, we conclude that a luxury supply of K and Mg, which goes well beyond a sufficient supply, does not

have any impact on the investigated parameters. Consequently, the following discussion focuses on the influence of the cultivar and tuber segments on the occurrence of thumbnail cracks and the fracturability as well as on their relationship to the tuber DM, starch, and mineral concentrations.

Thumbnail Crack Occurrence and Fracturability in Relation to the DM, Starch, and Mineral Concentrations and Distributions

The thumbnail crack evaluations did not show any significant influence by the different treatments, except a slight effect due to the cultivar in form of a higher occurrence of thumbnail cracks in Laura in comparison to Omega (Fig. 2a and SM_6a). The sensitivity of Laura to tuber skin damage may be related to its typical tuber shape, which is long-oval—such a trait is more prone to damage (Šaøec et al. 2006)—Omega is round-oval (Europlant 2014; Federal Plant Variety Office 2016). In contrast to the thumbnail evaluations, more distinct differences due to the cultivar and tuber segment became obvious during fracturability. The tubers of Omega exhibited a higher fracturability in comparison to those of Laura (Figs. 2b, 3f, SM_4b, and SM_6b). This might be related to the higher DM and starch concentrations (Fig. 3a and b, Table 2 and 3, and SM_5) of Omega in comparison to Laura. Singh et al. (2008) explored rheological parameters like the fracturability and hardness of potato tubers based on their DM and starch concentrations. The authors determined the highest fracturability and hardness in the cultivars that also exhibited the highest DM and starch concentrations. Equally, Bordoloi et al. (2012) demonstrated clear differences in textural characteristics, such as hardness and cohesiveness, between mealy and waxy potato cultivars, in which the authors refer to microstructural features such as cell size and structure, which, in turn, were closely related to the cultivars' DM and starch concentrations. They argue that mealy cultivars, possessing higher amounts of DM and starch, show smaller cell sizes and a more well-defined cell structure. Similar results were already published by Hudson (1975), who showed that bruising susceptibility of tubers was highest, which had low specific gravity but large cell sizes. Larger cells are thought to be the ones that are first damaged (Konstankiewicz et al. 2001; 2002), while smaller cells exhibit greater surface area per unit volume and thus may need greater strength to be separated or damaged (Šaøec et al. 2006).

Furthermore, the stem-ends of tubers illustrated a superior fracturability compared to bud-ends (Fig. 2b and SM_6b). Meanwhile, the stem-ends exhibited higher DM concentrations in comparison to the bud-ends (Table 3 and SM_5). This might have led to higher resistances of the stem- in comparison to the bud-ends owing to the previously described reasons.

While our results showed increasing DM from the bud- to the stem-end, it was the opposite for K (Table 3 and SM_5). These outcomes are in accordance with Johnston et al. (1968), who also noted increasing DM, but

decreasing K concentrations, from the bud-end to the stem-end in potato tubers; the work of Westermann et al. (1994) contained the same observations. Likewise, LeRiche et al. (2009) assessed higher K concentrations at the bud-end compared to the stem-end of potato tubers. On the one hand, K is supposed to have an positive effect on tuber DM and starch formation, which can be referred to the roles of K in photosynthesis and the translocation of the assimilates from source, such as photosynthetic active leaves, to sink organs, which are in the case of potato especially roots and tubers. This issue is, for example, described in the reviews by Römheld and Kirkby (2010) or Zörb et al. (2014). On the other hand, K is mainly responsible for regulating the osmotic potential of cell sap, and therefore, of central importance for the maintenance of turgor pressure or cell growth (Mengel and Arneke 1982; Zörb et al. 2014). Thus, we suppose that there is a relationship between decreasing DM, while increasing K concentrations from the stem to the bud-end due to the osmotic properties of K. K can lead to an increase of cell and tuber water content, which, in turn, can result in a reduction of DM (Schippers 1968; Westermann et al. 1994). Apart from higher DM in Omega in comparison to Laura, Omega showed a clear trend of higher Ca concentrations, especially in the tuber skin (Fig. 3e, Table 2 and 3, SM_5). Our findings are in accordance with Subramanian et al. (2011), who also found markedly high Ca concentrations in the tuber´s surface layers in contrast with the tuber´s flesh. The plant cell wall has several main constituents; these include pectin, hemicellulose, and cellulose. With approximately 60%, pectin is the main component of the cell walls of potato (van Dijk et al. 2002; Sila et al. 2009). Pectin mainly consists of a complex mixture of polysaccharides, which are cross-linked by the binding of divalent cations, such as Ca^{2+}, on the free carboxyl groups (Pooviah 1986; Weiler and Nover 2008). Thus, Ca can contribute to improve the cell wall stability of plant-based foods (Pooviah 1986). For instance, Conway et al. (1994) demonstrated increased fruit firmness and reduced decay in apples *(Malus domestics* Borkh.) through postharvest treatment with Ca. Likewise, Glenn and Poovaiah (1990) displayed that Ca-untreated apples *(Malus domestics* Borkh.) showed in the regions of the middle lamella distended or even separated regions, while cell-to-cell contact was maintained in Ca-treated apples during storage. Based on these relations between Ca and cell wall stability, we assume that Omega showed superior cell wall stability in comparison to Laura, which has contributed to the higher resistance of Omega. Aside from Ca, Mg is also supposed to increase cell wall stability via linkage to cell wall polymers (Andersson et al. 1994). However, the results of the present study did not indicate such an effect by Mg.

Conclusions

The occurrence of thumbnail cracks and fracturability of the tuber were investigated based on the (i) varying K and Mg supply, (ii) the cultivar, (iii) the DM and starch, and the (iv) mineral concentrations. Contrary our initial

presumption, no clear effect of the fertilization treatment on the investigated rheological properties and on the DM, starch, and mineral concentrations was detectable, likely due to a sufficient supply of K and Mg in the soils of the field sites in the present study. However, the present study allowed drawing following conclusions:

1. The cultivar 'Omega' and the tuber segment 'stem-end', which both revealed higher DM and starch concentrations, exhibited a higher resistance against the caused mechanical impacts. The relationship of higher DM and starch concentrations and increased resistance against mechanical impacts might be referred to certain cultivar characteristics of mealy cultivars, which are usually accompanied by higher DM and starch concentrations.
2. The cultivar 'Omega', which exhibited higher Ca concentrations, demonstrated a higher resistance against the caused mechanical impacts. This effect due to higher Ca concentrations can be traced to the role of Ca in stabilizing cell walls via linking cell wall polymers. A balanced Ca supply, especially of tubers exhibiting lower Ca concentrations, therefore might be of importance to maintain a higher resistance of tubers against mechanical impacts.

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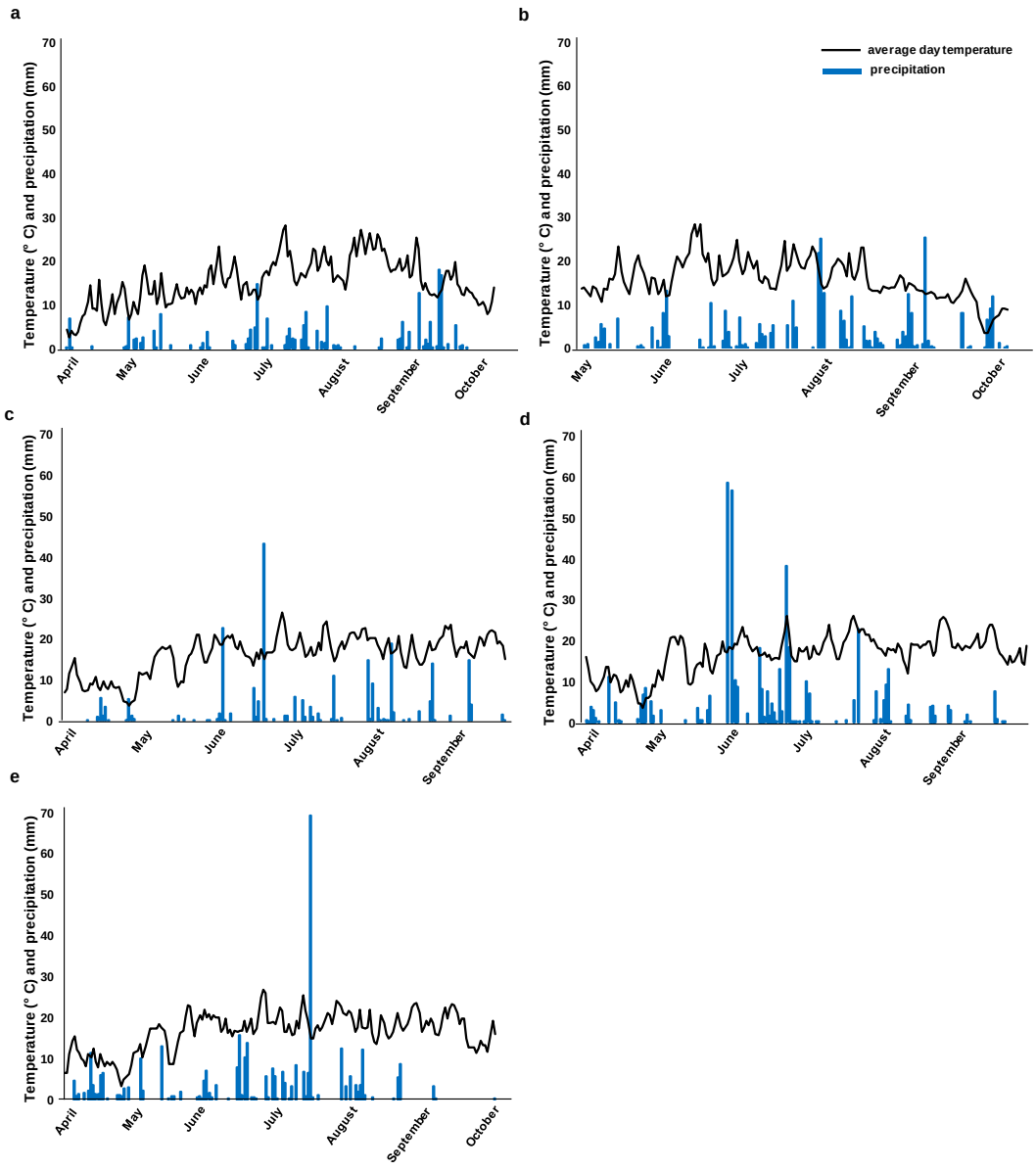
Supplementary material

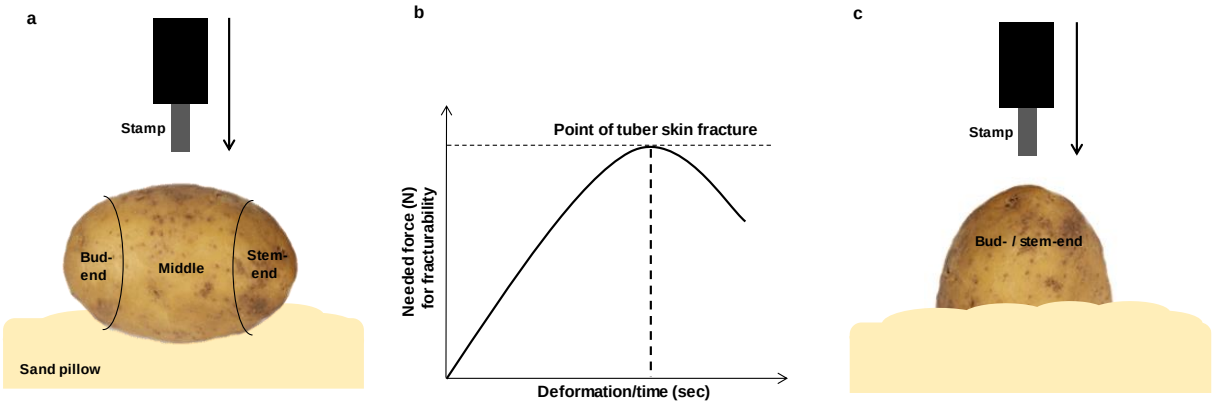


SM_1: Climate conditions (average day temperature in °C and precipitation in mm) of the sites Müncheberg (a) and Uedem (b) throughout the vegetation period in 2015 and of the sites Müncheberg (c), Uedem (d), and Kościan (e) throughout the vegetation period in 2016.

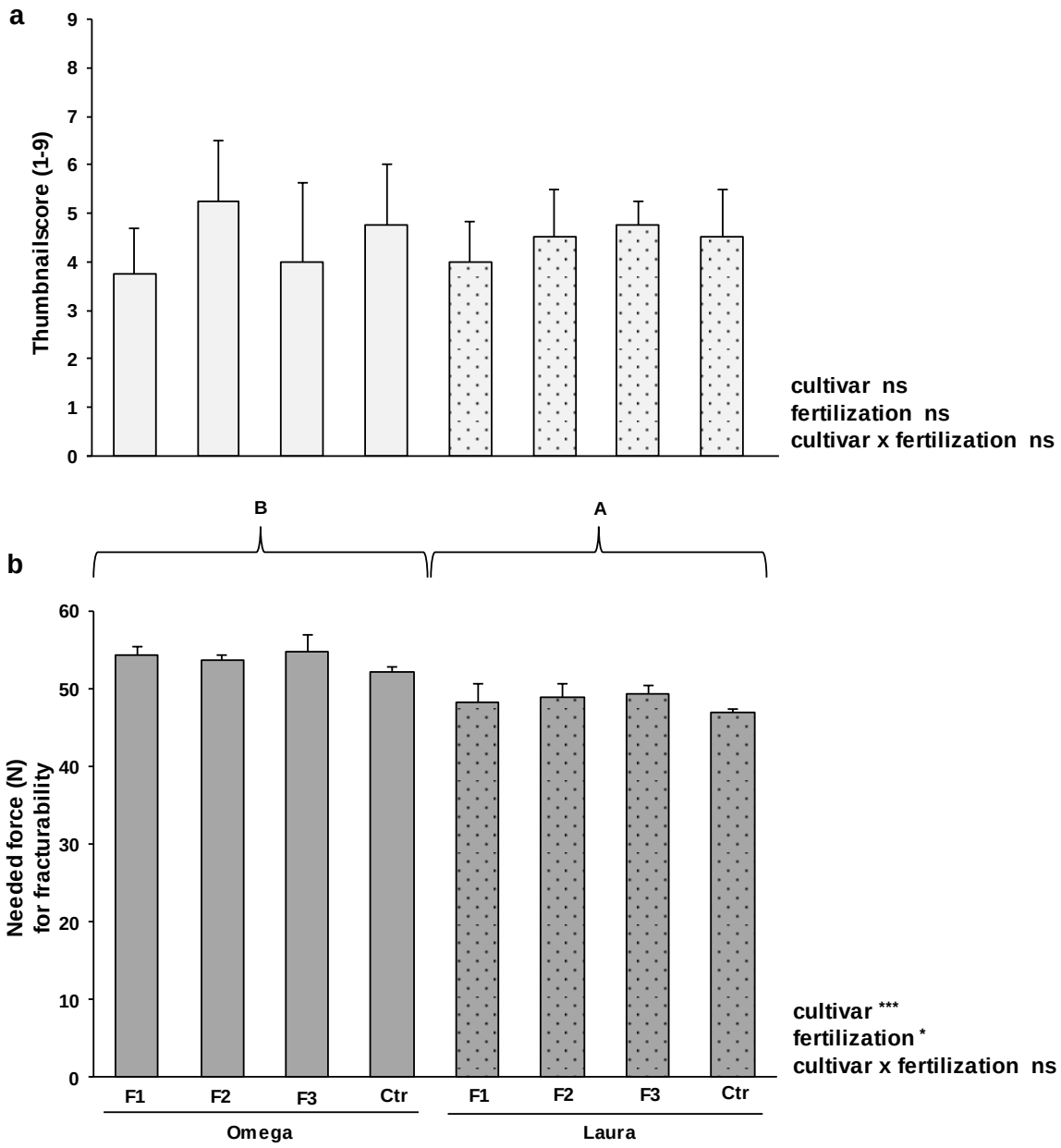
SM_2: Soil type and soil nutrient status of K and Mg (in mg 100 g^{-1} soil) in the field sites before fertilization treatments.

	Müncheberg †	Uedem ‡	Kościan §
Soil type	loamy sand	sandy clay	luvisol
K	11.7	11.0	12.5
Mg	3.8	6.5	7.4

Date of soil sampling: † February 2015; ‡ April 2015; § August 2016



SM_3: Schemes for the conduction of tuber skin penetration analyses and of used tuber parts for determination of fracturability, and DM, starch, and mineral analyses. During penetration of the potato tuber (a), the needed force (N) for fracturability is recorded. This is the point of the highest force (N) on a force-deformation curve (point of tuber skin fracture, b), which is characterized by a subsequent decline of force. A sand pillow was placed below the tuber or tuber segment, respectively, which served as a counter bearing. For the measurements of the whole tuber, the stamp penetrated in the middle of the tuber (a). For measurements of the tuber bud- and stem-ends, the tubers were cut the middle and each half of the tuber was placed with its sliced side on the sand pillow, while the stamp penetrated the opposite bud- or stem-end, respectively (c).

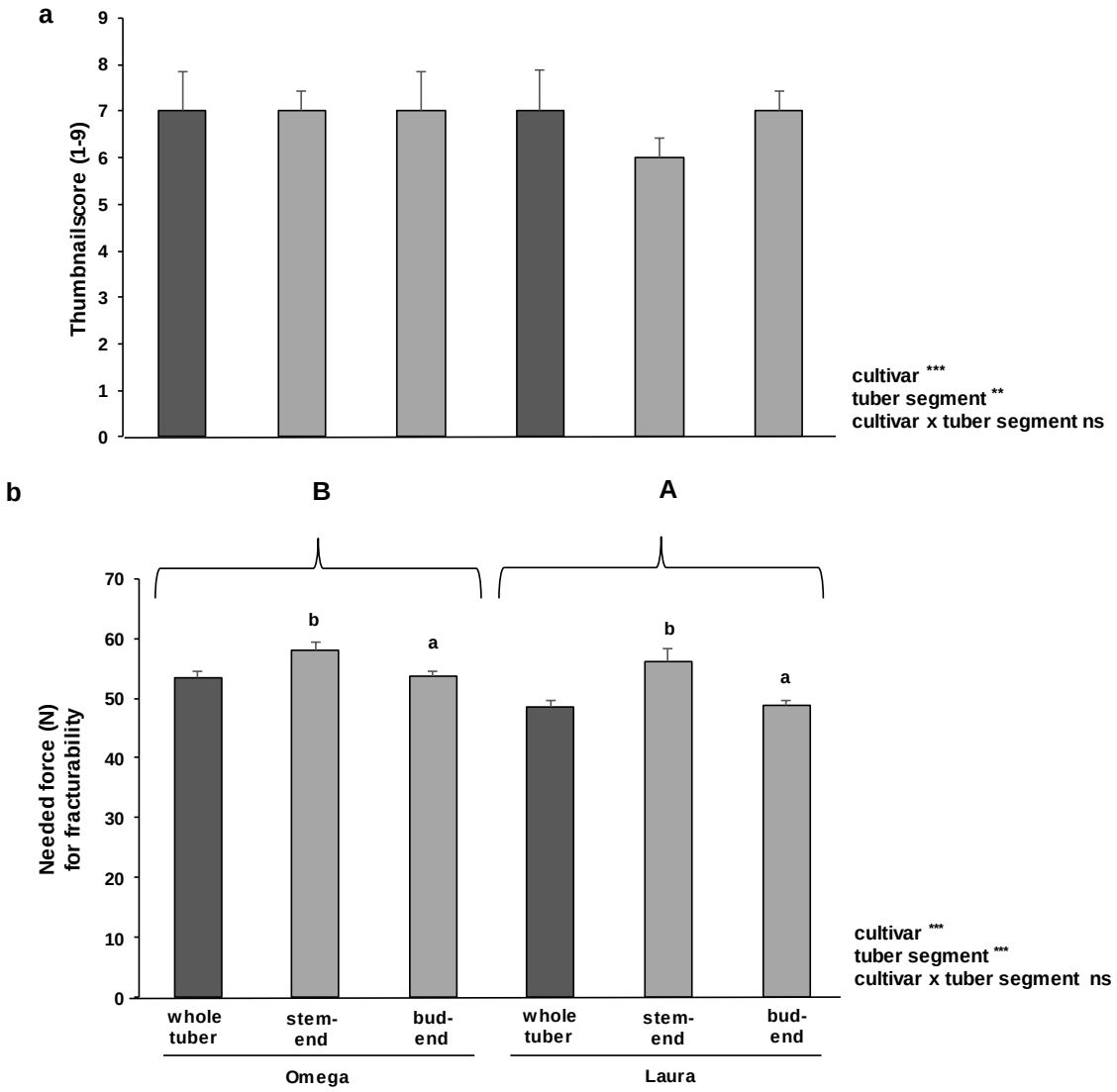


SM_4: Thumbnail crack occurrence of whole tubers of the cultivars Omega and Laura from 'Müncheberg' (a) and the fracturability of whole tubers of the cultivars Omega and Laura from 'Uedem' (b) under different K and Mg fertilization treatments in 2015. Mean ± SE values (n = 4). Levels of significance tested via ANOVA are shown in the right lower corner with * and *** for $p < 0.05$ and 0.001, respectively. ns = not significant. Capitals = significant differences between the cultivars of one fertilization treatment, and no indication = no significant differences.

SM_5: Dry matter (%), starch (% in DM), K, Mg, and Ca (mg g^{-1} DM) concentrations of whole tubers and the tuber segments stem- and bud-end, middle, skin, and flesh of the cultivars Omega and Laura from 'Kościan' during control fertilization treatment in 2016. Mean ± SE values (n = 3–4). Levels of significance tested via the ANOVA test are shown below the table with *, **, and *** for $p < 0.05$, 0.01, and 0.001, respectively. ns = not significant. Capitals = significant differences between cultivars, and small letters = significant differences between tuber segments of one cultivar.

	whole tuber	stem-end		middle		bud-end		skin		flesh		Average over tuber segments	
Omega													
DM	23.61 ± 1.19	26.89 ± 0.73	b	24.41 ± 1.14	ab	24.01 ± 1.43	ab	20.63 ± 0.79	a	26.11 ± 0.95	b	24.41 ± 2.42	B
Starch	68.77 ± 1.41	70.02 ± 0.86	b	69.95 ± 1.83	b	65.37 ± 2.38	b	46.64 ± 1.06	a	66.68 ± 8.88	b	63.74 ± 9.78	B
K	22.97 ± 1.39	19.12 ± 1.32	a	21.98 ± 3.52	ab	25.49 ± 2.96	b	33.30 ± 2.09	c	21.27 ± 0.97	ab	24.23 ± 5.56	
Mg	1.24 ± 0.14	1.18 ± 0.07	a	1.14 ± 0.07	a	1.16 ± 0.07	a	1.48 ± 0.06	b	1.12 ± 0.06	a	1.21 ± 0.15	
Ca	0.32 ± 0.03	0.36 ± 0.08	a	0.34 ± 0.07	a	0.41 ± 0.03	a	0.93 ± 0.12	b	0.27 ± 0.01	a	0.46 ± 0.27	B
Laura													
DM	21.65 ± 1.49	22.69 ± 1.24	b	20.43 ± 1.17	ab	20.37 ± 1.34	ab	16.68 ± 0.62	a	21.96 ± 1.27	b	20.43 ± 2.32	A
Starch	63.89 ± 2.73	66.21 ± 2.13	b	65.08 ± 2.28	b	64.89 ± 2.12	b	46.20 ± 1.18	a	70.06 ± 1.53	b	62.49 ± 9.34	A
K	19.99 ± 1.55	16.01 ± 1.14	a	21.55 ± 2.51	bc	24.66 ± 1.99	c	37.35 ± 4.55	d	19.21 ± 2.02	b	23.76 ± 8.23	
Mg	1.09 ± 0.06	1.20 ± 0.07	a	1.12 ± 0.01	a	1.17 ± 0.05	a	1.52 ± 0.07	b	1.06 ± 0.02	a	1.21 ± 0.18	
Ca	0.23 ± 0.03	0.27 ± 0.01	a	0.20 ± 0.02	a	0.26 ± 0.04	a	0.68 ± 0.15	b	0.17 ± 0.04	a	0.32 ± 0.21	A

DM: Cultivar ***, tuber segment ***, cultivar x tuber segment ns; Starch: Cultivar **, tuber segment ***, cultivar x tuber segment ns; K: Cultivar ns, tuber segment ***, cultivar x tuber segment **; Mg: Cultivar ns, tuber segment ***, cultivar x tuber segment **; Ca: Cultivar *, tuber segment ***, cultivar x tuber segment ns.



SM_6: Thumbnail crack occurrence of whole tubers, tuber stem- and bud-ends of the cultivars Omega and Laura from 'Kościan' in 2016 (n = 4) (a). Thumbnail score: 1 = very severe occurrence, 3 = severe occurrence, 5 = medium occurrence, 7 = slight occurrence, and 9 = almost no occurrence. Fracturability of whole tubers and tuber stem and bud ends of the cultivars Omega and Laura from 'Kościan' the trial at the site in Kościan in 2016 (n = 3) (b). Mean ± SE values. Levels of significance tested via the ANOVA test are shown in the right lower corner with ** and *** for $p < 0.01$ and 0.001, respectively. ns = not significant. Capitals = significant differences between the cultivars of one tuber segment, small letters = significant differences between stem- and bud end, and no indication = no significant differences.

SM_7: Effect of fertilization on the tuber yield (dt ha^{-1}) of all the fertilization treatments from 'Müncheberg' and 'Uedem' in 2015 and 'Müncheberg', 'Uedem', and 'Kościan' in 2016. Mean ± SE values (n = 4). The treatments had no significant effect.

		2015							
		F1		**F2**		**F3**		**Ctr**	
Müncheberg	**Omega**	293.1 ± 51.6	ns	307.6 ± 52.3	ns	299.5 ± 52.9	ns	307.2 ± 49.1	ns
	Laura	318.3 ± 20.1	ns	325.9 ± 11.9	ns	318.9 ± 17.2	ns	331.7 ± 22.1	ns
Uedem	**Omega**	431.9 ± 79.5	ns	456.9 ± 45.8	ns	467.9 ± 36.6	ns	451.0 ± 38.9	ns
	Laura	544.6 ± 23.4	ns	556.3 ± 4.5	ns	536.7 ± 41.9	ns	537.4 ± 84.2	ns
		2016							
Müncheberg	**Omega**	331.8 ± 51.6	ns	348.5 ± 37.5	ns	313.4 ± 36.6	ns	371.2 ± 58.9	ns
	Laura	340.3 ± 55.3	ns	370.0 ± 52.3	ns	351.7 ± 44.6	ns	362.3 ± 43.8	ns
Kościan	**Omega**	497.4 ± 45.2	ns	267.5 ± 12.7	ns	519.3 ± 48.1	ns	558.5 ± 28.1	ns
	Laura	553.2 ± 38.7	ns	186.3 ± 59.6	ns	545.8 ± 53.8	ns	617.2 ± 54.7	ns
Uedem	**Omega**	270.4 ± 27.4	ns	267.5 ± 12.7	ns	234.6 ± 31.1	ns	253.3 ± 22.5	ns
	Laura	183.2 ± 47.0	ns	186.3 ± 59.6	ns	217.4 ± 74.9	ns	158.4 ± 62.9	ns

Chapter 7

General discussion

General discussion

A central factor of influence on potato development and quality is the supply of the plant with nutrients (Westermann 2005). The presented research aimed to investigate the effect of various K and Mg supply on potato plant development and quality-related tuber attributes. With regard to this, four research objectives were stated (see chapter 1, section 1.8) whose outcomes are discussed following.

Effect of K and Mg deficiency on (i) production and partitioning of photoassimilates, (ii) above and belowground biomass development, and (iii) tuber quality of potato

The roles of K and Mg for photosynthesis and the translocation of photoassimilates from source to sink organs have been demonstrated in various crop species (Dreyer et al. 2017; Farhat et al. 2016; Jákli et al. 2017; Tränkner et al. 2016). However, the impact of a K and Mg deficiency on photosynthesis and the partitioning of photoassimilates in potato were unclear. It could be shown that K deficiency in potato significantly reduced shoot biomass (what equals a decrease in photosynthetic active biomass), CO_2 net assimilation rate, and leave chlorophyll concentrations (Chapter 4, Fig. 1a, 2a and 4b; Chapter 7, Fig. 1) and thus severely impaired photosynthesis. Meanwhile, Mg deficiency did not significantly reduced shoot growth (and thus photosynthetic active biomass), CO_2 net assimilation rate (at an early growth stage) nor decreased chlorophyll concentrations. Lastly, it did not severely impair photosynthesis (Chapter 4, Fig. 1c and e, 2a and 4c; Chapter 7, Fig. 1).

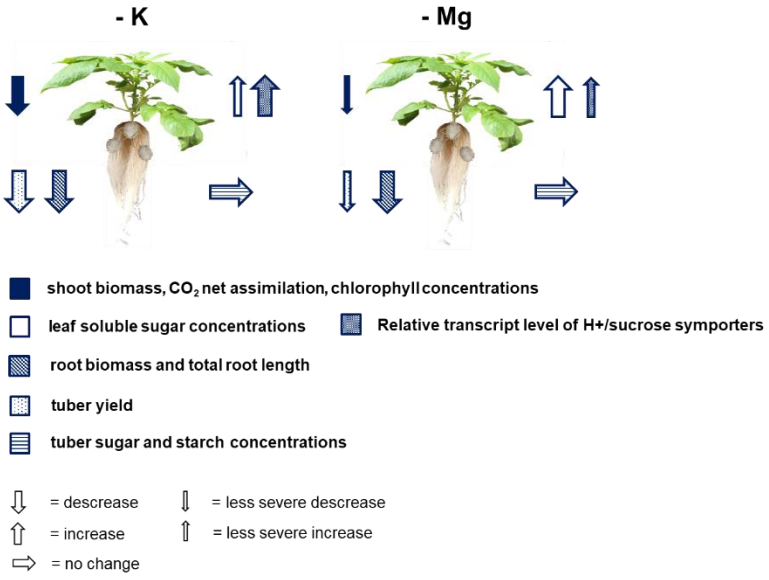


Figure 1: Scheme summarizing the impact of K (- K) and Mg (- Mg) deficiency on photosynthesis, translocation of photoassimilates, root biomass, total root length and tuber yield and quality in potato.

Besides, both K and Mg deficiency lead to a significant increase of soluble sugars and to an increased transcript level of H^+/sucrose symporters in fully expanded leaves, which indicated a hampered allocation of photoassimilates from source to sink organs (Chapter 4, Fig. 5; Chapter 7, Fig. 1). Thereby, the increase of soluble sugars was much more pronounced in Mg- compared to K-deficient plants. However, the transcript levels of H^+/sucrose symporters were less increased under Mg-deficiency. The latter case probably was caused by an impaired sucrose transport due to Mg-deficiency already at an earlier step, namely the efflux of sucrose from mesophyll cells into the apoplast, what is carried out via SWEET transporters (Manck-Götzenberger and Requena 2016). Thus, it is assumed that K-deficiency lead to a sucrose accumulation in the apoplast resulting in an increased transcript level of H^+/sucrose symporters. Meanwhile, Mg-deficiency caused sugar accumulation in mesophyll cells, why Mg-deficient plants did not show pronounced increases of transcript levels of H^+/sucrose symporters but likely affected another sugar transport system.

Furthermore, it has been shown that the partitioning of photoassimilates was hampered before any impact on photosynthesis under Mg deficiency (Chapter 4). This is in compliance with results shown e.g. by Hermans et al. (2004). Furthermore, the latter assumption may lead to the presumption that Mg is of higher relevance for the translocation of photoassimilates rather than for the production of photoassimilates via photosynthesis.

K and Mg deficiency caused a reduction of root biomass and total root length (Chapter 4, Fig. 2b and c; Chapter 5, Fig. 5b and 7). This coincided with a significant increase of soluble sugars in source leaves of K and especially Mg deficient plants (Chapter 4, Fig. 5a; Chapter 5, Fig. 4b and c), indicating a restricted translocation of photoassimilates from source leaves to sink organs (roots in this case). Thus, a relation between the translocation of photoassimilates and root growth is assumed, as plants, which exhibited a distinct sugar accumulation in source leaves also revealed decreased root growth. Moreover, both studies (Chapter 4 and 5) imply a higher sensitivity of root compared to shoot growth under Mg deficiency whereas K deficiency led to an equivalent reduction of root as well as of shoot growth (Chapter 7, Fig. 1). It is likely, that this also can be referred to the previous made assumption that Mg is of greater relevance for the translocation of photoassimilates rather than for photosynthesis while it is the opposite for K.

Another aim of this thesis was to test whether a resupply of Mg (via leaves or roots) can ameliorate deficiency symptoms such as depressed root growth or lack in Mg. A Mg foliar application led to a very temporally increase of Mg leave concentrations with a subsequent decrease to equal Mg concentrations as before the application of Mg deficient plants (Chapter 5, Fig. 2b). Shoot and root biomass and total root length revealed also a very slight increase upon Mg foliar application (Chapter 5, Fig. 5a, b, and 7). Meanwhile, a complementary fertilization of Mg via the roots exhibited much more pronounced effects, especially in form of increased Mg leaf (Chapter 5, Fig. 2b) and root

concentrations (Chapter 5, Fig. 7) and in form of an increase of the total root length compared to the Mg deficient plants (Chapter 5, Fig. 7). By comparison, Jezek et al. (2015) demonstrated that an Mg foliar application sufficiently improved the Mg status of the plant but the authors did not investigate root growth. Though, Neuhaus et al. (2014) could show an significant increase of a Mg foliar application on root biomass. However, a rise of the Mg supply via the nutrient solution exhibited much more distinct effects – similarly to our findings.

K deficient plants showed a more severe reduction of tuber yield compared to Mg deficient plants (Chapter 4, Fig. 2f; Chapter 7, Fig. 1) and a greater reduction of photosynthesis compared to the partitioning of photoassimilates, while it was the opposite for Mg deficient plants. This indicates that a hampered photosynthesis impairs tuber yield more severe compared to the translocation of photoassimilates. However, it is also conceivable that not a decrease of photosynthesis resulted in reduced sink growth but a decreased sink demand in form of reduced tuber yield and/or root growth resulted in a decrease of photosynthesis as has been argued by Marschner et al. (1996).

Surprisingly, with respect to our initial expectation that K and Mg deficiency will negatively affect tuber quality, we could not determine significant differences in tuber sugar and starch concentrations of various K and Mg supplied plants (Chapter 4, SM_5b and c). Only a slight tendency in form of a decrease of hexose sugars (glucose and fructose) was revealed in plants with high K and sufficient Mg supply (Chapter 4, SM_5b, K3+Mg plants). However, the total amount of tuber sugar and starch per plant showed significant differences: Medium and high K supplied plants showed significant higher sugar and starch yields per plant compared to low K supplied plants and Mg sufficient supplied plants (K2 and K3+Mg) exhibited significant higher starch yields compared to Mg deficient supplied plants (K2 and K3-Mg) (Chapter 4, Fig. 6). These findings can be referred to the significant reduction of tuber yields due to K and Mg deficiency, respectively (Chapter 4, Fig. 2f).

Influence of K and Mg interactive effects on K and Mg concentrations of different plant tissues and biomass development

Nutrient interactions between ions often have been research issue – however with contradictory outcomes. With respect to interactions between K and Mg there have been reports about antagonistic (Hossner and Doll 1970), synergistic (Ding et al. 2006) and neutral (Allison et al. 2002) interactive effects. One aim of the present study was to clarify the nature of interactive effects between K and Mg in potato. Antagonism between K and Mg usually is referred to competitive uptake mechanism of K and Mg from the soil solution. While Mg transporters are highly unspecific and take up other cations than Mg, K transporters are very specific (with the expectation of sodium as has been shown by

Castillo et al. (2015)) and the uptake of K is ensured under low as well as under high K concentrations in the soil solution (Britto and Kronzucker 2008; Karley and White 2009; Mayland 1990). Indeed, our results demonstrated significant decreased Mg concentrations in leaves with increasing K supply (Chapter 4, Table 2), indicating an antagonistic effect of K on Mg. However, tubers and roots exhibited significant higher Mg concentrations with higher K supply (Chapter 4, Fig. 3b), indicating a synergistic effect of K on the tuber and root Mg concentrations. These outcomes can be argued by the following reasons. Usually, plants show higher K concentrations in the shoot compared to the roots (Karley and White 2009; White 1997) what likewise is reflected in our results (Chapter 4, Fig. 3a). As the plant strives to preserve a balance between cations and anions (Kirkby and Mengel 1967), it is likely that the higher K concentrations in the shoot led to lower Mg concentrations while lower K concentrations in roots and tubers led to higher Mg concentrations. Likewise, the significant highest Mg concentrations were determined in leaves of plants with the lowest K supply (Chapter 4, Table 2; K1+Mg plants). Moreover, it is feasible that an antagonistic interaction mechanism is located in the translocation from root to shoot (and probably not in the uptake from soil solution into the roots) as has been suggested by Ohno and Grunes (1985). This antagonistic interaction mechanism may have led to a depletion of Mg in leaves whereas Mg enriched in roots and tubers compared to leaves. Lastly, it cannot be validated an overall antagonistic effect between K and Mg in potato. Likewise, although increasing K supply revealed a synergistic effect on the tuber and root Mg concentrations, it cannot be confirmed an overall synergistic effect of K on Mg in potato.

Relation between tuber DM and mineral concentrations and distributions on the one hand and resistance of the tuber skin against mechanical impacts on the other hand

Inappropriate agricultural practices causing mechanical impacts during or after harvest or adverse environmental conditions can result e.g. in cracking of tuber skin (Dean and Thornton 1989; Sparks 1970). Such cracks can significantly reduce the quality of the tubers and the appeal to consumers (Bohl and Thornton 2006). Beside those abiotic reasons which might cause tuber cracking, further causes can be, for instance, the cultivar, the soil type or storage conditions. However, there is only little information about physiological parameters which affect the tuber resistance against mechanical impacts and thus their susceptibility for cracking. In the present thesis (Chapter 6), a focus was set on the elucidation of factors that correlate with the symptom 'thumbnail crack' what is a few millimeter deep crack of the tuber skin. Besides, the fracturability of the tuber skin was investigated in order to further characterize the susceptibility of the tuber skin against mechanical impacts. The results suggest that DM and starch concentrations

might be associated with the resistance against mechanical impacts. The higher the DM and starch concentrations, the higher was the resistance of the tuber skin towards mechanical impacts (e.g. Chapter 6, Fig. 3). A relation between DM and starch on the one hand and rheological parameters in form of increasing values for fracturability, hardness and cohesiveness (meaning improved resistance against mechanical impacts) on the other hand also has been reported by Bordoloi et al. (2012) and Singh et al. (2008). Bordoloi et al. (2012) elucidate this relation by the observation that tubers which exhibit higher DM and starch concentrations showed smaller cell sizes and a more advantageous cell structure. Larger cells are the first to be damaged whereas smaller cells show a greater surface area per unit volume why a greater strength would be needed to separate or damage smaller compared to larger cells (Konstankiewicz et al. 2002; Šaøec et al. 2006).

A further parameter which positively correlated with the resistance against mechanical impacts on the tuber skin was the tuber Ca concentration. Divalent cations like Ca are known to improve cell wall stability as they are binding to cell wall polymers and thus stabilize the cell walls (Poovaiah 1986; Weiler and Nover 2008). This relation between Ca and cell wall stability has been well proven in apple, for example (Conway et al. 1994; Glenn and Poovaiah 1990). Beside Ca, likewise for Mg an improving impact on the cell wall stability is discussed (Andersson et al. 1994). However, our outcomes (Chapter 6) cannot confirm such a contribution of Mg.

Another research objective of the present thesis was to test how K and Mg supply might affect physiological parameters which in turn affect the resistance of the tuber against mechanical impacts (Chapter 6). Various studies reported about an impact of the K and Mg supply on DM and starch of potato tubers (Miča 1979; Panique et al. 1997; Poberezny and Wszelaczynska 2011; Westermann et al. 1994). In the field trials there was no influence of different K and Mg treatments on the DM and starch concentrations (e.g. Chapter 6, Table 2). Besides, there was no impact of the different K and Mg treatments on the tuber yield in the field trials (Chapter 6, SM_7). Likewise, in the pot experiment presented in chapter 4, no impact of different K and Mg supply on the DM and starch concentrations were assessed (Chapter 4, SM_5a). Though, significant higher tuber starch amounts per plant with increasing K and Mg supply were examined in this study (Chapter 4, Fig. 6). However, these differences in tuber starch yield can be rather referred to the differences of tuber yield resulted from the different treatments of K and Mg (Chapter 4, Fig. 2f), as discussed previously in section 7.1, than to a direct effect of K and Mg supply on starch. The reason for no effect of the different K and Mg supply on tuber yield in the field trials (Chapter 6) but for an effect in the pot experiment (Chapter 4) can be referred to an already sufficient soil K and Mg status of the field sites soils (Chapter 6, SM_2) compared to a deficient soil K and Mg status of the soil used in the pot experiment (Chapter 4).

Clear relations between DM and the cultivar and the tuber segment have been identified: The cultivar Omega revealed a significant higher resistance against mechanical impacts on the tuber skin compared to Laura (Chapter 6, e.g. Fig. 2 and 3) while Omega exhibited significant higher DM compared to Laura (Chapter 6, e.g. Fig. 3 and Table 3). Besides, the tuber segment 'stem end' showed a higher resistance against mechanical impacts compared to the 'bud end' (Chapter 6, e.g. Fig. 2) with coincident higher DM in the stem compared to the bud end (Chapter 6, e.g. Table 3). The higher DM in stem ends might be related with the distribution pattern of K within the tuber that was lower in the stem compared to the bud end (Chapter 6, e.g. Table 3). K is known for its osmotic properties (Mengel and Arneke 1982) why decreasing K concentrations may lead to an decrease of cell and tuber water content while DM is increasing (Schippers 1968; Westermann et al. 1994). This might explain why the bud ends were more prone for damages. As mentioned before, Omega revealed a higher resistance against mechanical impacts compared to Laura. A similar relation as for DM and the cultivar Omega with respect to the tuber resistance against mechanical impacts was examined between Ca and the cultivar Omega: Next to higher DM, Omega revealed higher Ca concentrations (Chapter 6, e.g. Fig. 3 and Table 3).

Appropriate K and Mg supply for the potato crop

A search of the ISI web of Science (see chapter 1, section 1.5) demonstrated that there is little awareness about both the importance of Mg supply and about a suitable combined supply of K and Mg for potato plant development and tuber quality. The present research contributes to improve the current knowledge regarding the roles of K and Mg for potato plant development and tuber quality formation. While for Mg a higher importance for the partitioning of photoassimilates within the plant was indicated, K showed a higher relevance for the production of photoassimilates (Fig. 1). But only under sufficient supply of both nutrients an appropriate tuber and starch yield and root development was realized (e.g. Chapter 4, Fig. 2a, b, c and f, and 6b). Results of the present study could not examine a definite antagonistic or synergistic effect between K and Mg. However, it is likely that the antagonistic effect is also causing a synergistic effect (as described in section 7.2) and thus, both effects are related with each other. Nevertheless, although plants with the highest K supply (K3+Mg, Chapter 4) showed the lowest Mg concentrations in leaves (Chapter 4, Table 2), there was no indication for an adverse effect on plant development (e.g. shoot and root biomass, total root length and tuber yield; Chapter 4, Fig. 2). Based on the outcomes of this study it can be concluded that an appropriate combined supply of K and Mg for potato production and tuber quality is reflected in a ratio of K and Mg of 3 : 1 (300 mg K kg^{-1} soil : 100 mg Mg kg^{-1} soil). This ratio was, for instance, represented by K2+Mg plants (Chapter 4, Table 1).

The doubled supply of K (K3+Mg plants, representing a K to Mg ratio of 6 : 1) did not exhibit a significant increase in biomass development (including root and shoot biomass, total root length and tuber yield) and no improvement of important tuber quality attributes such as tuber sugar and starch concentrations and yields.

Summary

Knowledge regarding the importance of K and Mg for potato plant development and tuber quality is limited. K and Mg are nutrients, besides other crucial roles, for photosynthesis and the partitioning of photoassimilates within the plant. Hence, a negative effect of a K and Mg deficiency on tuber yield and quality can be expected as tubers are strong sink organs being highly dependent on the production of photoassimilates and its translocation down to the tubers. This thesis aimed to examine the extent to which a K and Mg deficiency may affect potato plant development, tuber yield and tuber quality with view on the roles of K and Mg for photosynthesis and the partitioning of photoassimilates. Both K- and Mg-deficiency lead to reduced CO_2 net assimilation and photosynthetic active biomass production, with stronger reductions in K-compared to Mg-deficient plants. Low K- as well as low Mg supply resulted in accumulation of sugars in source leaves, especially in Mg-deficient plants. This is indicative for a restricted phloem loading. Besides, K and Mg restricted plants exhibited an impaired root length development what is supposed to be a result of a restricted source to sink transport of photoassimilates. However, while low K-deficiency resulted in a sharp increase of transcript levels of H^+/sucrose symporters, which are responsible to load the phloem with sucrose, this was less pronounced under Mg-deficiency. The latter case is probably the result of an impaired sucrose transport due to Mg-deficiency already at an earlier step, namely the efflux of sucrose from mesophyll cells into the apoplast. Therefore, it is assumed that K- and Mg-deficiency caused sugar accumulation in seperated cell compartments of source leaves leading to a different impact on the gene expression of sucrose transport systems. Tuber sugar and starch concentrations, however, remained unaffected under the various treatments. Nevertheless, the total amount of tuber sugar and starch per plant decreased significantly upon K- and Mg-deficiency.

A further research objective of this thesis was the external appearance of potato tubers what is an important quality attribute of potato tubers. The external appearance of potato tubers has been shown to mainly influence the customer´s purchase behavior. Thus, external blemishes, such as cracks of the tuber skin, significantly reduce the quality and the appeal of tubers for consumers. One factor, which is influencing on the development of cracks is the susceptibility of the tuber skin for mechanical impacts. Knowledge regarding physiological parameters which influence the resistance of the tuber skin towards mechanical impacts is rare. The present thesis revealed that tuber DM and starch concentrations can be considered as such parameters. The cultivar, which exhibited higher DM and starch concentrations, demonstrated higher resistance against mechanical impacts. Tuber DM and starch concentration were shown to correlate with the rheological characteristics of tubers due to related characteristics of tubers exhibiting higher

DM and starch concentrations such as smaller cell sizes (as smaller cells need a greater strength to be separated or damaged) and an advantageous cell structure (Bordoloi et al. 2012). Besides, tubers with higher Ca concentrations showed an increased resistance against mechanical impacts. This may be related to the contribution of Ca for cell wall stability. Ca is binding to cell wall polymers of the plant cell wall and thus is stabilizing the cell wall and therefore the tuber periderm that is forming the tuber skin.

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