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The Importance of Nutrient Management for Potato Production Part II: Plant Nutrition and Tuber Quality

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Abstract
The term 'quality' is a complex parameter in the field of potato production, and the desired quality traits depend on the intended use. Important internal quality traits for potatoes are tuber flesh discolouration, dry matter, and starch content. External quality traits include tuber size and shape as well as resistance against mechanical stress during and after harvest. These quality traits are closely interrelated and genetically controlled. It has been demonstrated that all these parameters are also linked to the nutrient status of the plant and/or the tubers. For instance, the susceptibility of tubers for discolouration of both fresh market and processed cultivars is closely related not only to the nutrient supply but also to post-harvest treatment. Besides, the potential to form carcinogenic compounds like acrylamide from precursors during the deep-frying of potato products and the accumulation of toxic substances like glycoalkaloids are important quality criteria in terms of food safety. The influence of the supply of nutrients on potato tuber quality depends initially on their physiological functions, but the ratio to other nutrient needs should also be taken into account.

Keywords Discolouration · Fresh market · Nutrient management · Potato quality parameters · Processing quality

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Introduction

The potato is a nutritionally valuable staple food. It is used for fresh consumption, processing into French fries and chips (crisps), as well as for the production of dry products and starch extraction. Thus, there are specific quality requirements for each use. The nutritional composition and other quality traits of potato tubers are influenced by the supply and availability of both macro- and micronutrients. However, the impact of the nutrients on potato quality is influenced or overlapped by many other factors, such as cultivar, soil, and climate conditions (Bártová et al. 2013; Lombardo et al. 2013; Brazinskiene et al. 2014). The aim of the present review is to evaluate the current state of knowledge about the functions of macronutrients like potassium (K), magnesium (Mg), nitrogen (N), calcium (Ca), phosphorous (P), and sulfur (S) in plant physiology. The focus is on potato quality but not in relation to interactions with other environmental factors.

Important Potato Quality Traits

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; Gerendás 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. This, 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 if they are produced for further processing, such as for French fries or crisps. High dry matter content within the tuber ensures lower oil absorption. This results in a higher yield per unit of oil and improves the texture and shape of the processed product (Kita 2014). In addition to the various internal quality traits described here, the tendency of potatoes to form undesirable discolourations 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 discolouration 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 are then transformed into the dark pigment melanin (McGarry et al. 1996).

Figure 1 shows a schematic illustration of these processes. The same reaction occurs during the processing of raw potatoes and is called raw pulp discolouration. Besides enzymatic reactions, the discolouration of potato tuber products can be caused non-enzymatically due to Maillard reaction and as after-cooking darkening. The Maillard reaction takes place during frying and baking of potato products (crisps, French fries, baked potatoes). Basically, it happens in processes that involve reducing sugars (glucose, fructose) and amino acids. This non-enzymatic browning reaction influences

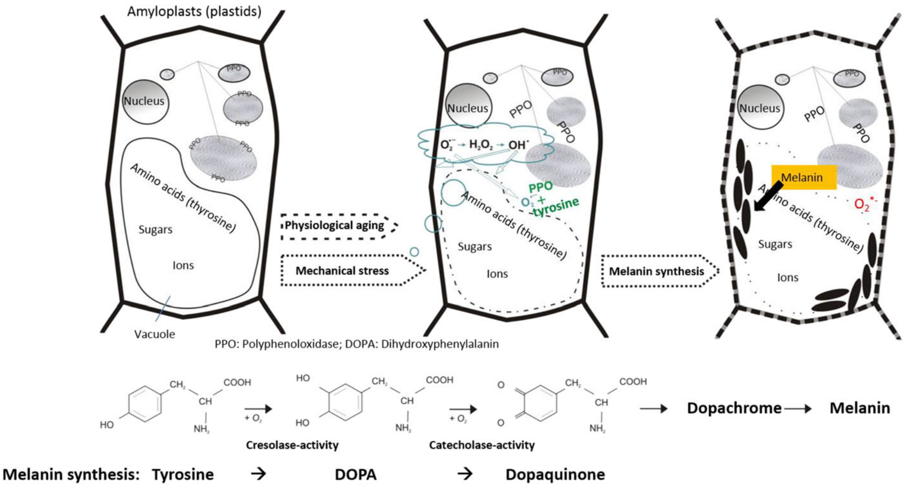

Fig. 1 Mechanism leading to black spot formation (adapted from Ernst et al. (2008))

flavour, colour, 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 posing a significant potential risk to human health (Rice 2005; Vinci et al. 2012). The after-cooking darkening of potato tubers is an undesirable quality trait, which may occur when the 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 the presence of oxygen, leading to a bluish-grey colour (Smith 1977).

The impairment of the internal and external tuber quality is also possible by physiological processes caused or promoted by nutrient deficiency or imbalance (Sowokinos 2007). Internal quality disorders include internal brown spots (IBS), brown centre, and hollow heart. Examples of external quality disorders include tuber malformations, including secondary growth, growth cracks, and thumbnail cracks. IBS occurs mainly in large tubers near both the apical and the basal tuber sections. The initial cause of IBS can be pegged to the on-site shortages in Ca. Combined with other stress conditions (e.g. impaired plant transpiration), the shortage of Ca leads to the loss of cell integrity and subsequent cell death (Palta 2010). This symptom develops mainly in the phloem-rich perimedullary section, whereas necrotic lesions, named here as brown centre, are mainly found in the centre of the tuber (Davies 1998). Brown centre is the result of cell death that may occur during tuber initiation when the temperature is low (Iritani 1981). The combined application of high N rates and intensive irrigation can stimulate fast tuber growth. The enlargement of tubers can lead to the development of hollow hearts from the brown centre (Hiller et al. 1985). Therefore, at specific conditions, both symptoms can be considered different stages of the same defect and are likely to be caused by the same conditions. However, hollow heart may also develop independent of brown centre occurrence in fast growing tubers under changing soil moisture conditions and imbalanced N/Ca supply (Bussan 2007).

External tuber disorders may also be a result of nutrient imbalances. Malformed tubers exhibit different untypical appearances. The causes of interrupted growth are heat and/or moisture stress and/or nutrient stress, e.g. interrupted N supply (Marschner 2012). Growth cracks develop after irregular irrigation of the crop during the tuber enlargement stage. Over-fertilization with N and nutrient imbalances (e.g. boron deficiency) contribute to the occurrence of growth cracks (Hiller et al. 1985; Jefferies and Mackerron 1987). Thumbnail cracks in the tuber periderm appear like thumb nail imprints and are caused by rapid changes in humidity or temperature or from mechanical impact on the tuber during or after harvest (Bohl and Thornton 2006). Ca and Mg contents and their allocation in the tuber can affect the tuber's resistance to mechanical impacts through cell wall stabilizing properties (Koch et al. 2019b). 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 flavour in potatoes (Friedman 2006). Most importantly, as they are toxic for humans (McMillan and Thompson 1979), the recommended safety level for human consumption has been 200 mg/kg FW for 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 causal link between the two processes does not exist (Edwards et al. 1998). The greening of tubers occurs 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). Glycoalkaloid formation can also occur in 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 2 gives a schematic overview about potato tuber properties as affected by important macronutrients. The fertilization strategy has a substantial impact on important potato quality parameters (Marschner 2012). This is especially true for macronutrients like K, Mg, and N. Various studies over the last 40 years have shown a direct impact of K, Mg, and N on potato quality. But the results of these studies usually show varying responses to nutrient supply, as illustrated for Mg in Table 1. The reasons for inconsistent results

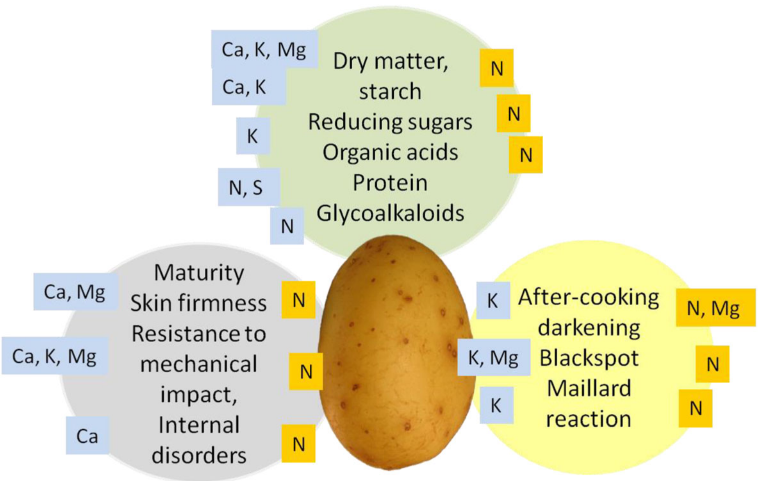

Fig. 2 Potato tuber quality properties as affected by macronutrient supply: traits (grey), main compounds (green), and susceptibility to discolouration (yellow) of tubers and food. Blue: positive effects, orange: negative effects of minerals

Table 1 Contribution of increasing Mg supply to yield, quality formation, and storability of potato tubers shown as relative changes compared with the control; green-red scale represents increase or decrease 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	0—60 kg/ha, (P)	Miča (1979)
	+ (5—8%)	0—100 kg/ha, (F)	Pobereżny and Wszelaczyńska (2011)
	0	0—60 kg/ha, (F)	Miča and Vokal (1983)
	0	0, 130 kg/ha (F)	Koch et al. (2019b)
Starch	0	0—60 kg/ha, (P)	Miča (1979)
	+ (0.5 %)	0—100 kg/ha, (F)	Pobereżny and Wszelaczyńska (2011)
	0	0—60 kg/ha, (F)	Miča and Vokal (1983)
	0	0, 130 kg/ha (F)	Koch et al. (2019b)
Nitrate	- (0.5—10%)	0—75 kg/ha, (F)	Rogozińska et al. (2005)
	0	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	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, 0 no trend

among diverse studies might be different cultivation conditions (e.g. pot versus field experiment), duration of the experiments (long-term versus short-term periods), and choice of the kind and number of cultivars.

The following sections aim to provide an overview of the most crucial impacts of K, Mg, N, Ca, S, and P on potato quality traits while considering results that are either contradictory or have not yet been proven.

Potassium

Potassium (K) has an important impact on tuber quality. It acts as an osmotically active ion. Thus, 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 2012). The positive effect of K supply on the content of organic acids such as ascorbic acid in the tuber is well known (e.g. Hamouz et al. 2009). The average concentration of K 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 supply of K raised the ascorbic acid concentration in tubers (Fig. 3). By increasing the cell turgor in the tuber, the risk of internal enzymatic discolouration (black spot; shown in Fig. 1) caused by mechanical impact stresses potentially

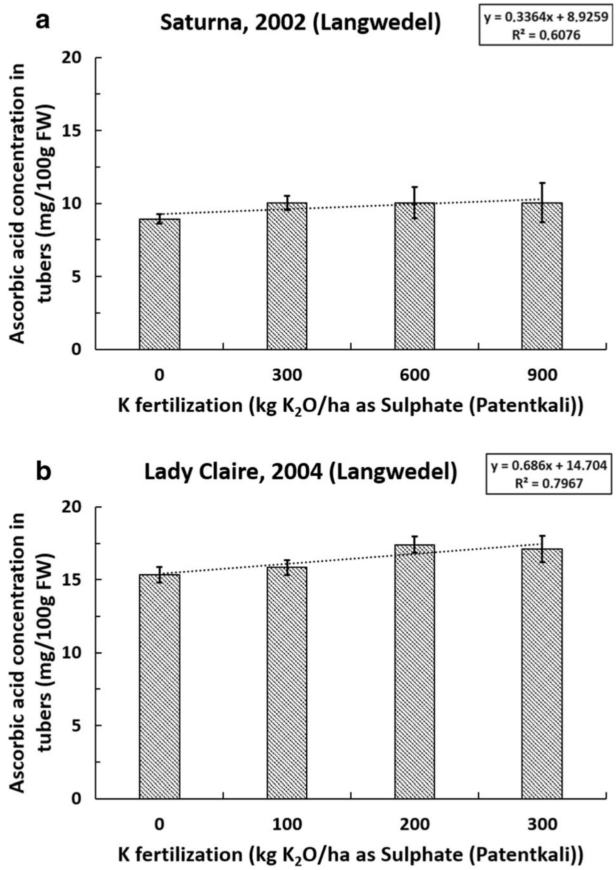

Fig. 3 Effect of increasing K supply on the ascorbic acid content of potato tubers. **a** Cultivar: Saturna; year of cultivation: 2002; experimental site: Langwedel (Lowery Saxony, Germany); **b** Cultivar: Lady Claire; year of cultivation: 2004; experimental site: Langwedel (Lowery Saxony, Germany)

decreases (Praeger et al. 2009; Fig. 4). 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 content in potato tubers can be regarded as a positive quality trait. This is because of its antioxidative capacity, which in turn has a positive impact on human health (Delgado et al. 2001). Increasing the K concentration in tubers, generated by K supply, leads to a lowering of reducing sugars (Fig. 5). These are important precursors of acrylamide formation during the Maillard reaction (Matthäus and Haase 2014). The cause of the after-cooking darkening can be countered through high contents of citric acid. Citric acid competes with the phenolic compound chlorogenic acid to bind ferric ions (in fact, citric acid acts as a transporter of Fe in plants) (Wang-Pruski and Nowak 2004). Indeed, in potato, a positive correlation between the K content in tubers and citric acid content was also found in field trials in 2002 and 2004 (Fig. 6).

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, including soluble sugars, organic acids, or amino acids, and decrease the

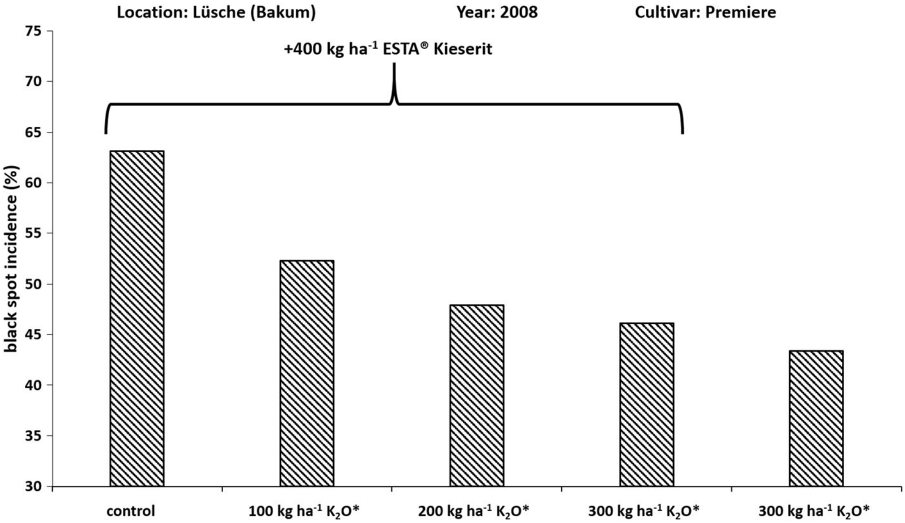

Fig. 4 Effect of combined K and Mg fertilization on black spot incidence. The experimental site was Lüsche (Bakum), Northwest Germany, predominantly characterized by silty sand. Soil analysis showed 13.6 mg K_2O 100 g^{-1} soil after calcium acetate lactate (CAL) extraction and 3.2 mg Mg/100 g^{-1} soil 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)

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 ATP formation and phloem loading of carbohydrates, and also increase the plant respiration (Römheld and Kirkby 2010; Marschner 2012). 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 glycoalkaloids,

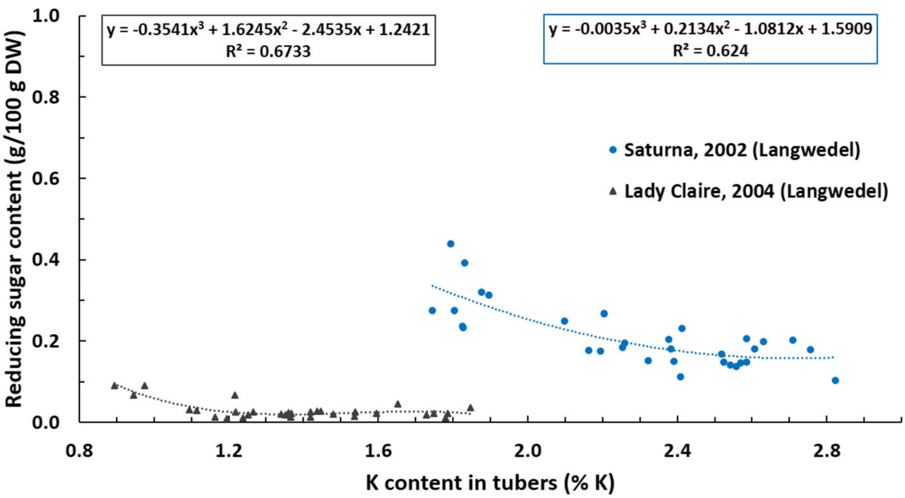

Fig. 5 Effect of increasing K concentration in potato tubers on the reducing sugar content of potato tubers. Data from K+S KALI GmbH, unpublished

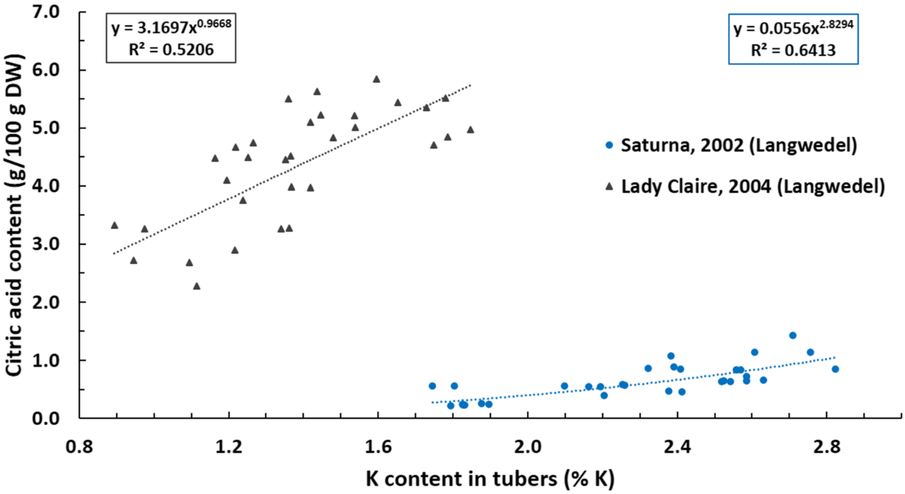

Fig. 6 Effect of increasing K concentration in potato tubers on the citric acid content of potato tubers. Data from K+S KALI GmbH, unpublished

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 positively influenced by K supply. Pobereżny and Wszelaczyńska (2011) showed that intermediate K doses ranging from 0 to 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 6 months.

The form of K application, for example as sulfate or chloride, has a significant impact on tuber quality traits. Figure 7 summarizes the effect of different K fertilizers on yield, starch yield, and starch content. Independent of the K-form

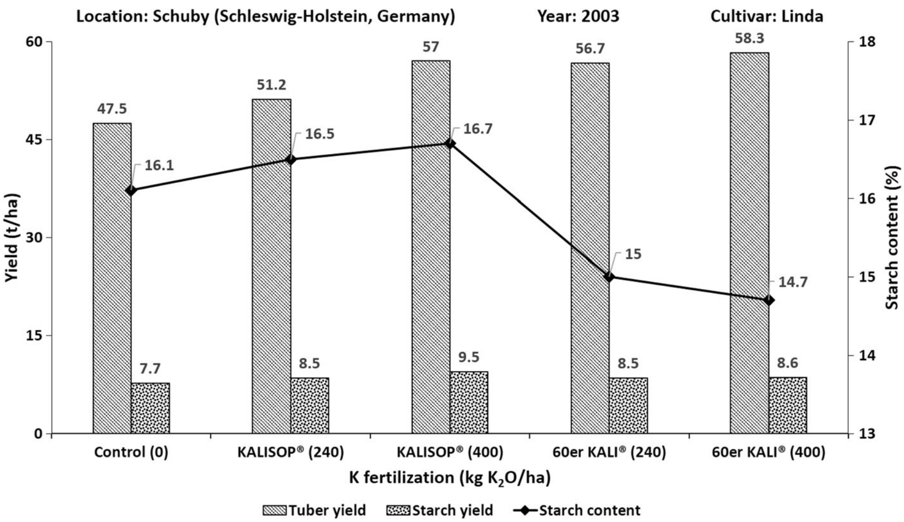

Fig. 7 Effect of increasing K supply either as sulfate or as chloride on yield, starch yield, and starch content of potato; Mg supply in all variants 320 kg ha^{-1} ESTA® Kieserit gran. Data from the Agricultural Chamber of Lower Saxony, Germany, 2003

supplied (either as K_2SO_4 or as 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 sulfate form. What could be the reason for this phenomenon? It is assumed that application of K in chloride form leads, in comparison to the sulfate form, to a lower osmotic potential in crops, as the osmotically active chloride is accumulated in higher amounts than sulfate. This subsequently leads to a higher water uptake and a correspondingly higher vegetative growth. Higher vegetative growth rates, particularly of the above-ground plant parts, lead to an increasing competition for assimilates between shoots and tubers; as the shoot is a strong sink for such assimilates, K is also osmotically active (Marschner 2012). Hence, a very high accumulation of K in tubers leads to an increased uptake of water by the tuber. This can result in a dilution of the starch content independent of the form of K application.

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). It can also be assumed that Mg tends to improve the resistance towards mechanical stress that affect tubers though Koch et al. (2019b) could not verify such an effect. Findings regarding the effect of Mg supply on enzymatic discolouration and the accumulation of minor compounds are not consistent, as reviewed by Gerendás and Führs (2013). For example, Klein et al. (1981) found that fertilization with $MgSO_4$ reduced enzymatic discolouration and the concentration of phenolics, whereas Mondy et al. (1967) showed a positive correlation between them. These contradictory results 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 this concept, increasing citric and/or ascorbic acid in the tubers contributes to the reduction of enzymatic discolourations. The synthesis of ascorbic acid originates from glucose (Marschner 2012). A positive influence of favourable environmental conditions for photosynthesis (e.g. high light intensity) on ascorbic acid concentrations in various crops has been reported (e.g. Noctor and Foyer 1998). The significance of Mg for assimilation and carbohydrate translocation (Koch et al. 2019a) may have a positive effect of increased Mg supply on ascorbic acid formation. However, Mondy and Ponnampalam (1986) did not observe the significant effects of increasing Mg supply on the concentration of ascorbic acid, which agrees with the early reports of Karikka et al. (1944). Gerendás 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 asparagine or acrylamide formation in tubers and processed food, even though an effect can be expected considering the function of Mg in protein biosynthesis and carbohydrate partitioning (Gerendás and Führs 2013). Recent work showed that when there is a deficit of Mg, the content of reducing sugars in the tuber increases, while the tuber yield decreases but the relationship was non-significant. However, the sugar concentration in the tuber remains unaffected because the supposed increase was to be evaluated as a concentration effect (Koch et al. 2019a). 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 1). 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 about the effect of Mg are available. However, in the above-cited study, Pobereżny and Wszelaczyńska (2011) showed that intermediate Mg doses ranging from 0 to 100 kg MgO ha^{-1} (optimum: 60 kg MgO ha^{-1}) reduced fresh weight losses during 6 months of storage. This is similar to what has been noticed in the case of K.

Nitrogen

Nitrogen (N) is essential for many physiological functions in the cell and consequently for plant growth and yield formation (see part I of the review). However, many quality traits can be affected adversely by N supply (Fig. 2). Plants are able to take up N from different sources, such as ammonium, nitrate, and nitrite. Ammonium is the dominant form in acidic or anaerobic soils, and nitrate is prevalent in well-aerated soils, whereas nitrite availability is generally lower and dependent on nitrification and denitrification in soils (Hachiya and Sakakibara 2016). The nitrate content in potato tubers depends on the cultivar, abiotic factors, the used cultivation system (conventional/organic) (Lachman et al. 2005), and the supply of other nutrients. An increase in the nitrate content as a result of increasing N rates can be reduced by simultaneous addition of increasing Mg rates (Rogozińska et al. 2005). Mg contributes along with micronutrients such as copper and manganese to the activation of nitrate reductases (Rogozińska et al. 2001). Depending on the cultivation conditions, the nitrate content in potato tubers can vary from 34 mg/kg FW (Lachman et al. 2005) to 843 mg/kg FW (Cieslik and Sikora 1998), whereas the content of nitrite is generally lower (0.4–5.73 mg/kg FW). Furthermore, the distribution of nitrate in the tuber is very diverse (Fig. 8). Naumann et al. (2019) showed that the nitrate content in the skin (peel thickness 2–3 mm) is about 6.5 times more than that in the medulla. Qsaki et al. (1995) have found in their studies that nitrate is able to stimulate the branching of stolons and increase stem and shoot growth, which might be one reason for the unequal distribution of nitrate in the tuber. It is

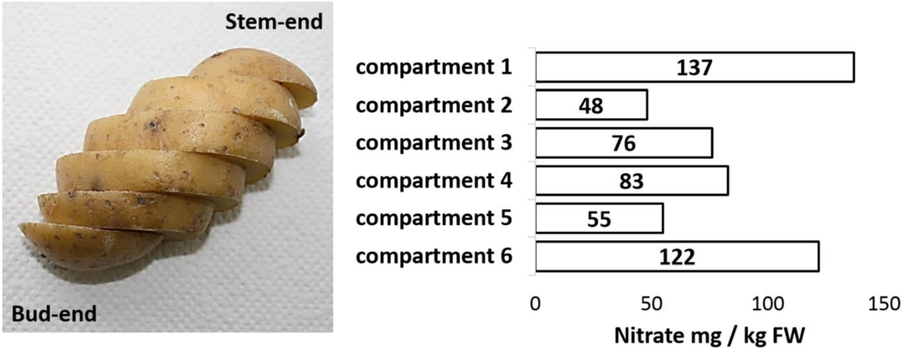

Fig. 8 Nitrate distribution in potatoes (exemplary presentation; adapted from (Naumann et al. 2019))

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). Thus, the amino acid pattern is typically characterized by high amide contents which are 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 asparagine, in particular, as a response to high N supply has been observed. This is typically referred to as the favourable 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). In contrast to the effect of increased N supply on asparagine accumulation, a lower N supply can lead to an increase in reducing sugars of 60 up to 100% in tuber dry matter (De Wilde et al. 2006). Therefore, the formation of acrylamide also depends heavily on the N nutrition (De Wilde et al. 2006). This is particularly true when there is a K deficiency. This is because not only the production of amides is increased as a result of 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).

Calcium

Calcium (Ca) is involved in various functions in the plant cell that are related to the quality of potatoes, such as maintaining structural cell integrity and regulating metabolic responses (Palta 1996; Seling et al. 2000). It is needed for cell wall and membrane stabilization (Hirschi 2004; Palta 2010). In cell walls, Ca contributes to their characteristic structure by bridging galacturonates of pectin via carboxylate groups (Subramanian et al. 2011). On the other hand, 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 (Koch et al. 2019b). Additionally, it also gives 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 Ca concentrations in tubers. However, potato tubers are very low in Ca which can be attributed to the fact that Ca is mainly transported via the xylem (Palta 1996). Ca deficiency can lead to several physiological plant disorders, such as internal brown spots (ITS) and hollow heart (Palta 2010) which can also lead to a decline in the internal potato tuber quality (Clough 1994). Collier et al. (1978) demonstrated that an additional supply of Ca could increase tuber Ca concentrations and reduce the occurrence of ITS. This has also been shown by Ozgen et al. (2006) who proved that there was an inverse relationship between tuber Ca and the occurrence of ITS. Kratzke and Palta (Kratzke and Palta 1985, 1986) and Palta (2010) demonstrated that Ca concentrations in tubers could be increased if Ca is directly applied to the tuber-stolon area.

Phosphorous and Sulfur

The macronutrients phosphorous (P) and sulfur (S) also contribute to the yield of quality potatoes through their physiological functions in the plant. Up to 75% of the potato tuber dry matter is composed of carbohydrates, the main representative of which is starch (McGill et al. 2013). The quality of starch in potatoes is dependent on different physical and chemical characteristics which are mainly determined by the amylose content, granule size, and glucose-6-phosphate content (Christensen and Madsen 1996; Haase and Plate 1996). The bound P in starch, mainly present as glucose-6-phosphate, is responsible for its unique technological properties in view of gelatinization temperatures and cross-linking ability (Christensen and Madsen 1996). An increased availability of P in soil leads to an increase in P concentration in the tuber. This in turn leads to higher amylose content and changed thermal and pasting starch properties (Leonel et al. 2016). A recent study confirmed that increased P availability in soils resulted in tubers with higher dry matter content, lower total sugar content, and higher contents of both starch and proteins (Leonel et al. 2017). Therefore, P is extremely important in the optimal development of quality potato tubers.

Beside N, S also has a decisive impact on amino acid formation and hence protein synthesis. Thus, 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 2012). As described above, acrylamide is formed by reducing sugars reacting with asparagine. Prosser et al. (2001) in their study have compared different crops exposed to S deficiency. They observed that there was an increase in the transport of amino acids glutamine and asparagine. In potato, Elmore et al. (2007) could show a cultivar-dependent increase of acrylamide precursors under S deprivation but no increase of acrylamide itself. They argued that the acrylamide formation depends on separate amounts of amino acid and sugar precursors and that in their study, precursor amino acids were more than precursor sugars which may also react with acrylamide non-precursor amino acids. In addition, an increasing supply of S can improve the absorption of K and P (Klikocka et al. 2015) and thus indirectly support the quality-promoting effects of these macroelements in the tuber.

Conclusion

An adequate and balanced supply of nutrients to potatoes is important for achieving not only a high yield but also the desired quality. The discussed roles of the represented plant nutrients on potato quality traits are diverse and complex. On the one hand, clear relations could be demonstrated between the nutrient supply and physiological processes which are important for potato tuber quality, such as the impact of K on photosynthesis. On the other hand, quality traits, such as the presence of ascorbic acid, which are built up by precursors originating from photosynthesis, did not show clear results with respect to the impact of K supply on ascorbic acid content in potato tubers. This might be related to the fact that the influence of the respective nutrient on a certain quality trait is overlapped by other factors such as climate or specific site conditions. Besides appropriate nutrients and their ratios, even the choice of fertilizer can be of particular relevance. Along with the principles of adequate potato nutrition, other agronomic measures like choice of cultivar and plant protection need to be considered as well.

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