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The Importance of Nutrient Management for Potato Production Part I: Plant Nutrition and Yield

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Abstract
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 fertilisation for potato yield formation and yield security is addressed by taking advantage of the results of field trials and existing literature. The most important roles of the macronutrients nitrogen, phosphorous, potassium, magnesium, calcium and sulphur in the plant and their importance for yield formation in potato are reviewed. Fertilisation practices in potato production are discussed. Due to their various functions in plant metabolism, the impact of plant nutrients on potato yield is complex. Therefore, interactions with abiotic and biotic factors, for instance interactions between two different plant nutrients in the soil and the plant, are taken into account.

Keywords Magnesium · Nitrogen · Phosphorous · Potassium · Potato · Productivity · Yield

Introduction

Potato (*Solanum tuberosum* L.) is a highly attractive crop in agricultural production systems since it combines an extraordinarily high yield potential with a high nutritional value. However, while countries with a high-input agriculture, such as the USA, France and Germany, can reach average potato yields of more than 45 t ha^{-1} (Table 1), the average yields of most other countries are considerably lower leading to average potato yields of 20 t ha^{-1} worldwide (Table 1). Potatoes are a good source of energy, minerals,

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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 1997 and 2017

Country	Harvest area (ha)*		Quantity (t)*		Average yield (t/ha)*		
	1997	2017	1997	2017	1997	2017	
Russia[1]	3,154,351	1,889,208	35,137,578	29,589,976	11.1	15.7	Europe
Ukraine	1,577,400	1,323,200	16,700,800	22,208,220	10.6	16.8	
Germany	303,584	250,500	11,659,284	11,720,000	38.4	46.8	
Poland	1,306,442	329,323	20,775,644	9,171,733	15.5	27.9	
Netherlands	179,900	160,791	7,973,000	7,391,881	44.3	46.0	
Total	9,163,046	5,365,045	141,542,970	121,761,565	15.4	22.7	
USA[2]	547,780	415,010	21,186,890	20,017,350	38.7	48.2	America
Peru	248,546	310,400	2,403,510	4,776,294	9.7	15.4	
Canada	375,900	342,218	4,179,818	4,410,829	11.1	12.9	
Brazil	174,830	118,030	2,670,493	3,656,846	15.3	31.0	
Colombia	166,765	149,060	2,716,997	2,819,026	16.3	18.9	
Total	2,014,575	1,797,479	40,998,690	44,173,458	20.4	24.6	
China[3]	3,823,960	5,765,144	57,207,500	99,147,000	15.0	17.2	Asia
India	1,248,800	2,179,000	24,215,900	48,605,000	19.4	22.3	
Bangladesh	133,971	499,725	1,507,860	10,215,957	11.3	20.4	
Iran	157,811	160,902	3,284,106	5,102,342	20.8	31.7	
Turkey	210,900	142,851	5,100,000	4,800,000	24.2	33.6	
Total	6,663,374	10,209,139	106,284,490	195,668,682	16.0	19.2	
Algeria	67,180	148,692	947,518	4,606,403	14.1	31.0	Africa
Egypt	82,561	163,939	1,802,761	4,325,478	21.8	26.4	
South Africa	55,973	67,746	1,579,021	2,450,541	28.2	36.2	
Morocco	66,400	64,293	1,186,610	1,924,871	17.9	30.0	
Tanzania	74,557	211,927	545,200	1,749,213	7.3	8.3	
Total	906,231	1,892,633	10,514,203	25,011,823	11.6	13.2	
World	18,798,740	19,302,642	301,079,129	388,190,674	16.0	20.1	

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

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

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 utilisation possibilities, which makes their production even more attractive.

The yield of a potato crop is mainly determined by its specific genetic background (Evans and Fischer 1999). There is a gap between the actual yield and the yield potential (Van Keulen and Stol 1995; Michel et al. 2015). According to the yield potential concept, the potential yield is never fully reached in natural production systems as biotic and abiotic factors interfere with the potato crop negatively and affect plant growth and tuber development. Important biotic stress factors in potato production include late blight (*Phytophthora infestans*) (Nowicki et al. 2012) and fungal infections, such as early blight (*Alternari solani*), silver scurf (*Helminthosporium solani*) and black scurf (*Rhizoctonia solani*), as well as *Fusarium* and *Verticillium* wilt (Rich 1983). Furthermore, other kinds of pathogens such as plant parasitic nematodes can affect potato yield and production. The white potato cyst nematode (*Globodera pallida*) and the yellow potato cyst nematode (*Globodera rostochiensis*) are the main economically important nematode species (Eves-van den Akker et al. 2016). Besides, various bacterial and viral diseases affect potato yield and production (Rich 1983). The abiotic stresses that reduce yield include high radiation (Jansen 2002), heat stress (Herman et al. 2017), cold stress (Oufir et al. 2008) and air pollutants such as nitrogen dioxide and ozone (Bahl and Kahl 1995). The most important abiotic factor affecting yield and quality is drought stress (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, a further important agronomic measure for potato production is adequate nutrient management (Table 2). A sufficient supply of mineral nutrients (1) can fortify the potato plant against adverse growth conditions, (2) is crucial for achieving high yield and (3) is essential for producing potatoes that meet the desired quality requirements.

At the end of the nineteenth century and at the beginning of the twentieth century, a lot of effort was put into investigating the relationships between production factors, such as the nutrient supply of the plant, and the yield of crops (De Wit 1994). The most famous yield-response law originating from this time is the law of the minimum developed by Carl Sprengel and, later, spread by Justus von Liebig in the early nineteenth century. According to the law of the minimum, optimal crop growth can take place only if all required nutrients are at the optimum level (Sprengel 1828; von Liebig 1840, 1855; cited in van der Ploeg et al. 1999). 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 diminishing yield increase formulated first by Eilhard Alfred Mitscherlich (McNall 1933) is of similar importance. This law states that the higher the nutrient supply the lower the yield increase obtained from increase in fertilisation, which means that yield response to fertilisation follows a saturation curve (Spillman 1923). A further law is the law of the optimum formulated by Georg Liebscher. Liebscher stated that the production factor, which is in minimum supply, contributes more to yield (production) increase the closer the other production factors are to their optimum (Liebscher 1895; cited in Nijland et al. 2008). These laws are the basis for modern approaches to develop strategies for efficient resource use in plant production. Based on the emerging challenges in modern agriculture, De Wit (1992) suggested that the laws developed by Liebig, Mitscherlich and Liebscher could be used as particular alternatives in one dynamic model. He concluded that both agriculture and environment should focus towards the minimum of production resources that are necessary for maximum use of other resources (De Wit 1992). Although many studies about the role, the nutrient uptake and the removal of nutrients by cereal crops are available, for the potato crop they rely mainly on data produced decades ago, indicating a need for further studies.

Table 2 Fertilisation 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 fertilisation recommendation system; the procedure applied to develop a fertilisation recommendation differs among regions)

Country/region	Soil type	Recommended fertilisation 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	–
UK (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]	0–1125

[1] Desired value, adaptations are needed according to the site-specific fertilisation 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', fertilisation 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 fertilisation 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 fertilisers together with N or P

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

[6] Fertilisation 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 and 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 fertilisation recommendation range shown here covers cation exchange capacity of me greater and smaller than 6

[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

Nitrogen (N), phosphorous (P) and potassium (K) are the nutrients which are most commonly fertilised in potato production (Davenport et al. 2005). This might explain why most literature is available for these nutrients with respect to potato production, especially in terms of fertilisation strategies and recommendations. Unfortunately, current literature dealing with fertilisation practices of nutrients other than N, P and K is often lacking (Table 2). This review aims to give an overview on the macronutrients N, P, K, magnesium (Mg), calcium (Ca) and sulphur (S) with respect to (1) their most important roles in plant metabolism, (2) their roles for potato yield formation, (3) fertilisation practices (Table 2) and recommendations in potato production, if available, and (4) interactions with abiotic factors influencing the plant availability. A critical review of all essential nutrients in potato growth is beyond the scope of this review. Furthermore, important roles of the nutrients in determining potato quality will only briefly be addressed as this review focuses on the importance of plant nutrients for potato yield.

Roles of Macronutrients in Plant Metabolism, Their Role in Potato Yield Formation and Fertilisation Practices

The nutrients N, P, K, Mg, Ca and S are highlighted successively with respect to their physiological functions in plant metabolism and for tuber yield formation in the following sections of this review. Besides, fertilisation practices will be addressed. Perrenoud (1993) summarised the literature on the uptake of N, P, K, Mg and Ca and their removal by potatoes. The mean values are presented in Fig. 1, giving an overview about the need for these nutrients by the potato crop. From the removal per tonne of tubers, the removal (in kg ha^{-1}) was calculated to give a tuber yield of 40 t ha^{-1}.

Nitrogen

Nitrogen (N) is one of the most crucial macronutrients for plant growth and biomass development. Plants can use N in different forms. Their major sources are ammonium (NH_4^+) and nitrate (NO_3^-) (Silva et al. 2013), albeit the latter one is easily prone to leaching. Mandatory roles of N for plant growth are that it is a component of chlorophyll, amino acids, proteins, nucleic acids, coenzymes and membrane constituents (Andrews et al. 2013; Ahmed et al. 2015). Increasing N supply can increase the proportion of large-sized tubers (Zebarth and Rosen 2007). This has a positive effect on potatoes used for processing. However, large-sized tubers might be unfavourable for potatoes used for fresh consumption or for seed production (Zebarth and Rosen 2007). Besides, N can influence several potato quality determinants such as the nitrate (Bélanger et al. 2002) or acrylamide content (Gerendás et al. 2007) of tubers. The second part of this review will discuss these relations between N and tuber quality in more detail.

N has the greatest impact on potato yield formation among all essential macronutrients (Bucher and Kossmann 2011; Silva et al. 2013). According to De la Morena et al. (1994), potato yield can be divided into the three components: ‘number of stems per square meter’, ‘number of tubers per stem’ and ‘average tuber weight’, whereby N has the greatest impact on the average tuber weight. The need for N of the potato crop is comparatively low within the first 4 to 5 weeks of growth and tuberisation can even be

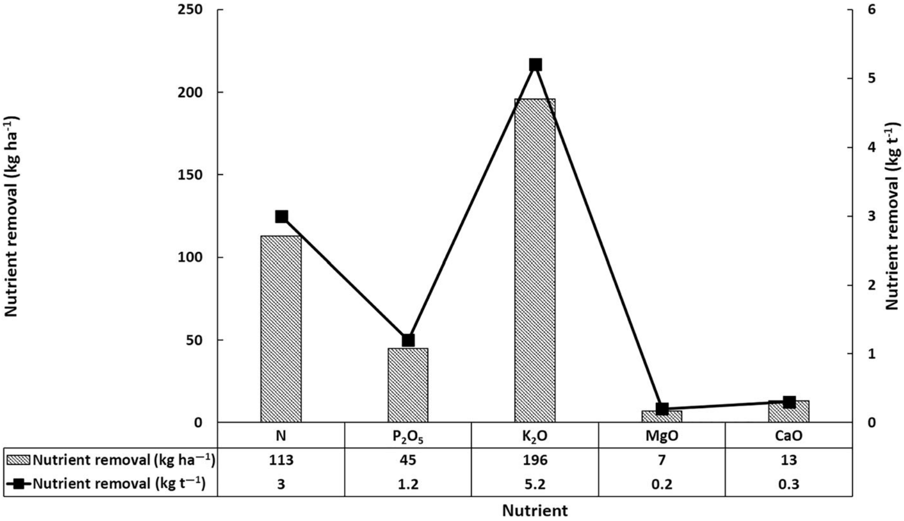

Fig. 1 Removal of N, P_2O_5, K_2O, MgO and CaO by potato tubers. Mean values per tonne of tubers (as shown on the right axis), calculated according to Perrenoud (1993) (and literature cited therein). Calculations on nutrient removal per hectare (as shown on the left axis) were based on a 40 t ha^{-1}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

suppressed or delayed by high N supply (Jackson 1999; Zebarth and Rosen 2007). During this growth period, nitrogen favours stem growth. This reduces the available amount of dry matter for tubers. However, at a later growth stage, the tubers can take benefit from increased aboveground biomass. Here, N has a decisive impact on the number of emerging leaves and the rate of leaf expansion, and, therefore, on the canopy development of the plant (Ospina et al. 2014). 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 dry matter partitioning to the tubers, tuber bulking and, finally, on tuber yield formation (Ahmed et al. 2015). The highest amount of N is needed during tuber bulking. Approximately 58–70% of the total N is taken up during this development stage (Ojala et al. 1990). However, with respect to starch concentrations in tubers, it should be noted that increasing N supply might have a decreasing impact on tuber starch concentrations (% DW) as has been shown by Sharma and Arora (1988). However, the authors found increasing starch yields (kg ha^{-1}). Sharma and Arora (1988) attributed these findings to a dilution effect in which the increasing yield caused by the N application affects the starch concentration.

The tuber dry matter yield per unit of applied nitrogen can be defined as nitrogen use efficiency (NUE) (Tiemens-Hulscher et al. 2014). The NUE of potatoes can be regarded as low compared to other crops. This can be attributed to the shallow rooting system of potatoes that leads to a restricted uptake and, thus, use of N (Iwama 2008). However, strong interactions between the NUE and the maturity group of the respective cultivar have been reported. For instance, compared to early maturity types, later maturity types can profit more from additional available N, especially later in the growing season (Tiemens-Hulscher et al. 2014). Moreover, the water regime can have a significant impact on the NUE. Due to the shallow rooting system of potatoes, they are known not only as inefficient in the use of nutrients such as N but are also very sensitive to water shortages (Liu et al. 2015). Thus, potato crops are usually irrigated under dry conditions although excessively high amounts of water can favour nitrogen leaching. As mentioned previously, given their shallow roots, potatoes are often unable to capture N from deeper soil layers (Cameron et al. 2013). Therefore, the danger of nitrate leaching beyond the rooting zone can increase under excess supply of water (Wolfe et al. 1983). Besides, undesirable N losses can occur via volatilisation as ammonia (NH_3) or via denitrification resulting in nitrous oxide (N_2O) (Vos 2009), both of which are known as greenhouse gases (Petersen and Sommer 2011).

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). Usually, the amount of N applied to potatoes varies between 100 and 300 kg ha^{-1} (Beukema and van der Zaag 1990). There are different methods available for the grower to determine the actual N demand. These can be distinguished as soil-based or plant-based tests (Zebarth and Rosen 2007). The most commonly used soil-based approach is the soil mineral N test (Zebarth and Rosen 2007). Here, soil mineral N (NO_3^- and NH_4^+) is extracted from soil layers from 0 to 60 cm soil depth prior to planting (Vos 2009). Plant-based tests are, for instance, the petiole N test determining the petiole NO_3^- concentration (Porter and Sisson 1991) or the use of a leaf chlorophyll meter as indicator for the N status of the plant (Olivier et al. 2006). Besides, a simple visual diagnosis might be a helpful tool to identify N deficiency during growth. N deficiency symptoms become visible as leaf chlorosis, due to the disturbance of chloroplasts. Usually, chloroses are equally distributed over the whole leaf. These symptoms occur first on younger leaves as those nutrients cannot be translocated within the plant (Mengel and Kirkby 2001). Nonetheless, meeting the actual N demand of the crop and making N fertilisation recommendations remains difficult due to several factors influencing the availability of N in the soil. These include, for example, the amount of available water or temperature throughout the growing season (Vos 2009).

Many growers supply the total or a large amount of N fertiliser pre-planting (Ojala et al. 1990). Due to the aforementioned difficulties in meeting actual N demand of the crop throughout the whole growing season, splitting the N application has become a commonly used approach (Kelling et al. 2015; Rens et al. 2016a). Splitting the N application, first, has the potential to lower the risk of nitrogen leaching, especially in irrigated potato production on sandy soils (Errebhi et al. 1998). Second, it can better meet the actual demand of the potato crop with reference to the respective development stage (Ojala et al. 1990). However, splitting the N application still needs precise management as there are many factors which might affect the efficiency of this process. While excess water availability can favour N leaching, water shortages can result in reduced solubility of the fertiliser and, thus, in reduced N plant availability (Rens et al. 2016b). Therefore, it cannot be generalised that splitting N is advantageous in irrigated or non-irrigated production systems. Furthermore, delaying N supply might delay tuber maturity (Ojala et al. 1990). Therefore, plant development needs to be precisely monitored. Finally, besides the aforementioned N application practices, foliar application of urea might be an efficient measure to overcome unexpected N shortages during crop growth (Qadri et al. 2015).

Phosphorous

Phosphorous (P) is required in relatively high amounts (Fig. 1) by the potato crop as compared to other crops. P serves various functions in plant metabolism. Its most prominent role is cellular energy transfer by dephosphorylation of adenosine triphosphate (ATP) to adenosine diphosphate (ADP). 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 2012; Rosen et al. 2014). Economically speaking, P has a significant impact on the setting of potato tubers, especially in the early growth states (Jenkins and Ali 2000; Hopkins et al. 2014), but also at later growth stages where P enhances tuber maturity (Hopkins et al. 2014; Rosen et al. 2014). There are also reports that P affects tuber size. For instance, a decrease in the yield of large-sized tubers with higher P fertilisation rates has been observed (Jenkins and Ali 2000). Similarly, there are reports which claim that an increase in small-sized tubers is an offset for the decrease of large-sized tubers (Rosen et al. 2014). The potato plant can tolerate moderate P stress without any severe deficiency symptoms until photosynthesis and respiration being reduced to such an extent that carbohydrates 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).

Similar to N, the need for P is rather low in the first weeks of growth but, contrary to N, P is also taken up in comparatively large amounts after tuber bulking during the maturity phase of tubers. Most P is taken up between 40 and 60 days after emergence (Horneck and Rosen 2008; Rosen et al. 2014). There are several P fertiliser management strategies with respect to the rate, placement or timing (Hopkins 2013). With regard to the P fertiliser rate, soil P levels should be examined first via soil testing, e.g. with the help of the Mehlich III method (Pote et al. 1996). Usually, lower amounts of fertiliser P are needed under high soil test P levels. However, differences have been reported between different soil types: while non-sandy soils, such as loams, still show yield responses at high soil test P levels, these yield responses were found to be lower in sandy soils (Rosen et al. 2014). With regard to placement, a primary distinction can be made between broadcast and band P fertiliser application. Due to the shallow root system of potatoes, band application can be advantageous in terms of P use efficiency as the band is usually placed in close vicinity to the majority of the roots (Hopkins et al. 2014). Moreover, under broadcast application higher P fertiliser rates are often needed: this increases the risk of runoff losses. Therefore, under broadcast application, P fertiliser should be incorporated into the soil (Rosen et al. 2014). Similar to the application practices for N, there exist also for P the possibility for an in-season fertiliser application beside pre-planting P fertiliser application. Although there are several studies which investigate the effect of an in-season P fertiliser application versus a pre-planting P fertiliser application, none could be found which showed an increase in P use efficiency due to splitting of the P application (e.g. Hopkins et al. 2010; Stark and Hopkins 2015). However, P petiole tests during crop growth are still recommended to identify possible P limitations for crop growth (Rosen et al. 2014).

Compared to N, P is very immobile in soils as it is only poorly soluble. Thus, plant roots need to grow in the direction of P for its uptake. As only a few roots develop during the first growth period, it is a typical time for P deficiency to occur in potato

(Hopkins 2013). However, the P use efficiency of potato is rather low even at a later growth stage, similar to that for N (Hopkins 2013). This might, likewise, be attributed to the shallow and inefficient rooting system of potato (Hopkins et al. 2014). Moreover, restricted P availability can additionally reduce root growth due to its role in cell division (Rosen et al. 2014). Soil pH can have a decisive impact on P fertiliser solubility. A neutral pH of 6.0 to 7.5 is assumed to be in the best range in terms of P solubility. However, pH values in the acid as well as in the alkaline range can both adversely affect P availability (Hopkins 2013; Rosen et al. 2014). Under acidic soil conditions, P tends to build poorly soluble mineral precipitates with aluminium, iron or manganese, while under alkaline soil conditions a similar reaction occurs with magnesium or calcium (Hopkins 2013). Due to the high need of potato for P on the one hand and due to rather low P use efficiency on the other, P is often applied in excess amounts (Hopkins et al. 2010). The applied amounts range from 100 to 400 kg P ha^{-1} (Maier et al. 2002; Hopkins et al. 2014). This is a main reason why P, besides N, often contributes to the pollution of surface and groundwater (Davenport et al. 2005) as it directly dissolves into the water or enters the water attached to colloids and particles via soil erosion (Withers and Haygarth 2007). Usually, the water bodies (e.g. lakes) where these P sources enter are limited in P. Thus, the arrival of P can result in immense algae blooms leading, finally, to eutrophication of the water body (Withers and Haygarth 2007; Hopkins et al. 2010).

Potassium

Out of all the macronutrients, potassium (K) has the highest concentrations in potato tubers. It accounts 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). It is also the most abundant inorganic cation in the remaining plant tissues, in potato leaves at 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 (Fig. 1).

The major functions of K in plants are controlling enzyme activity, cation–anion homeostasis and membrane polarisation. These are based on its osmotic nature, which is why it is needed for cell extension, turgor regulation and 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's enzyme functions is stimulating the starch synthase for starch synthesis (Hawker et al. 1979). A sufficient supply of K is also needed for high biomass production and leaf area development. Under K deficiency, there can be a decrease in the 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 aforementioned 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). Koch et al. (2019a) could demonstrate in pot experiments with potato plants that K-deficient plants exhibit a significantly reduced CO_2 net assimilation rate. 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 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 has been found in potato plants (Koch et al. 2019a). The accumulation of sucrose in the leaves of K-deficient plants occurs due to impaired phloem loading and transport of sucrose in phloem. K is also needed for stabilising a specified pH value for energy-providing ATP production for phloem loading, whereas for distribution of sucrose within the phloem, K establishes the needed osmotic pressure (Cakmak et al. 1994a). Based on the aforementioned roles of K in enzyme regulation, photosynthesis and partitioning of carbohydrates within the plant, it can be assumed that K has a central relevance in the potato crop for establishing desired tuber and starch yields. Indeed, Koch et al. (2019a) could show that K-deficient potato plants exhibited significant tuber yield and starch yield (g starch plant^{-1}) reductions. However, the starch concentrations (% in DW) did not show significant reductions upon K deficiency. With respect to other potato quality determinants, K is a nutrient with several important functions. Besides dry matter, starch content and specific gravity, K can affect the content of reducing sugars, which are precursors for acrylamide formation in processed potato products (Panique et al. 1997; Gerendás et al. 2007). Furthermore, K can lower black spot bruise (McNabnay et al. 1999) and after-cooking darkening (Wang-Pruski and Nowak 2004) due to an increase in organic acids upon K application. For more on the roles of K in determining potato quality, please refer to the second part of this review.

The potato plant shows maximum uptake of K, similar to N, early in plant development, approximately 30 to 40 days after emergence (Stark et al. 2004; Horneck and Rosen 2008). The previously described roles of K for leaf area development and photosynthesis might be a reason for this. Besides, K has a decisive role in tuber initiation and tuber bulking (Karam et al. 2009). Afterwards, similar to N, the uptake of K drops close to zero during the maturity phase of the tubers (Stark et al. 2004; Horneck and Rosen 2008).

Corresponding to high amounts of K removal and K concentrations of tubers, recommendations for K fertilisation are usually quite high (Panique et al. 1997). However, there are several studies which could not find a positive effect of K fertilisation on tuber yield (Roberts and Beaton 1988; Kang et al. 2014; Koch et al. 2019b). This might be attributed to an already sufficient K status of the respective soils. Tuber yield seems to reach a maximum at a certain available K level, but as has been demonstrated by Kang et al. (2014), an additional supply seems not to have any further effect. Nevertheless, there are indications that the potato crop is able to take up more K than is actually required (Kang et al. 2014). However, especially in sandy soils, the danger of loss of K due to leaching is high because K is very mobile in the soil (Wulff et al. 1998). Thus, applications of K higher than the actual demand are not recommended and K fertilisation decisions should be based on soil K tests. Panique et al. (1997) suggest that soil K values below 104 mg K kg^{-1} for sandy soils and below the range of 100 to 125 mg K kg^{-1} for medium-textured soils, such as silty loams, are critical. K deficiency occurring during crop growth might be identified by petiole testing (Stark et al. 2004) or with help of visual analysis. 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).

Usually, all the K is applied pre-planting (Stark et al. 2004; Horneck and Rosen 2008). In-season split applications have been shown to have no increasing effect on tuber yield (Westermann and Tindall 1995; Kumar et al. 2007). Stark et al. (2004) recommend a broadcast K application at the pre-planting stage as band application might lead to salt stress.

The form of K application, for example as sulphate or chloride, can have tremendous effects on assimilate distribution and, therefore, on yield formation and other 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 by increasing K fertilisation (Panique et al. 1997). However, it is assumed that, compared to the sulphate form, fertilisation of K in chloride form leads to higher osmotic potential in the crops as 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, lead to increased competition for assimilates between shoot and tuber, as the shoot is a strong sink for such assimilates. In addition, chloride-induced high growth rates of the shoot as a result of increased water uptake lead to 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). However, recently, Hütsch et al. (2018) could demonstrate in pot experiments with the two cultivars Marabel and Désirée that both cultivars were not chloride sensitive and did not show any tuber yield or quality reductions. Thus, the authors argue, potatoes are not necessarily chloride sensitive, although it needs to be noted that both the cultivars used, Marabel and Désirée, are potatoes for fresh consumption (FPVO 2018), i.e. these tubers are usually characterised by lower starch contents as compared to cultivars for chips, fries or starch production. Kumar et al. (2007) investigated the impact of K_2SO_4 versus KCl on dry matter percentage and crispiness of two processing cultivars and found them to be superior when they received K as K_2SO_4 instead of KCl. Moreover, Marabel belongs to the early maturity group and Désirée to the medium-early maturity group (FPVO 2018). The usage type and maturity group might both have tremendous effect on the amount of assimilates needed for translocation to the tubers. Therefore, it is feasible that different cultivars and maturity groups respond differently in terms of chlorine sensitivity.

Magnesium

Magnesium (Mg) can be designated as ‘the forgotten element in crop production’ (Cakmak and Yazici 2010) as its supply and the need for it 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). Along with K, Mg serves as a cation 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 RuBP (Woodrow and Berry 1988; Yuguan et al. 2009). Moreover, Mg specifically binds to RuBP and thereby enhances its catalytical activity (Belknap and Portis 1986). Besides RuBP, 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 their 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. Although Koch et al. (2019a) could not find any reduction in the CO_2 net assimilation rate in Mg-deficient potato plants, Mg-deficient plants revealed significant accumulations of soluble sugars in source leaves, indicating a restricted phloem-loading process in these plants. Moreover, the authors could determine significant tuber yield and starch yield (g starch plant^{-1}) reductions. However, as described for K, the starch concentrations (% in DW) did not differ between Mg deficient and sufficient supplied plants.

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 their leaves, whereas, simultaneously, the concentration of sucrose in the phloem sap decreased. Evidence was also provided that a re-supply of Mg to Mg-deficient plants for only 1 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 fertilisers 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, 1994b) 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, 1994b) induced Mg deficiency 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 root growth or morphology when they had earlier been sufficiently supplied with Mg. In a more recent study, following the approach by Cakmak et al. (1994a, 1994b) to induce Mg deficiency at a very early growth stage, Koch et al. (2019a) found significant root biomass and total root length reductions upon Mg deficiency in potato plants. It is likely that impaired root growth is a result of hampered assimilate translocation processes (Cakmak et al. 1994a, 1994b; Koch et al. 2019a). Moreover, depending on growth conditions, plants having deficiency of Mg might develop an increased root-to-shoot ratio (Cakmak et al. 1994a, 1994b).

The symptoms of Mg deficiency, such as interveinal chlorosis, and K deficiency can be first observed in older leaves, as Mg can easily be translocated to active growing plant parts (Cakmak and Kirkby 2008; White and Broadley 2009; Gransee and Führs 2013).

Recommendations for the fertilisation of Mg are hard to find in literature. In practice, the applied amounts of K usually determine the respective Mg supply. Thereby, the amounts of K and Mg are applied in a ratio of 3:1. Koch et al. (2019a) investigated the impact of different amounts of K and Mg applications on potato yield and further parameters and found that there is no yield improvement by increasing the K amount in this ratio but a decrease in the concentrations of Mg in leaves. Besides, lowering the K or Mg supply resulted in significant yield decreases. Thus, the authors could demonstrate that an Mg application, based on a ratio of K to Mg of 3:1, is a recommendable fertilisation strategy for Mg.

Potassium–Magnesium Antagonisms

The competition of cations for uptake is a well-known phenomenon (Fageria 2001). One of the most commonly observed phenomena based on cation antagonism is K-induced Mg deficiency. Indeed, Koch et al. (2019a) could find a significant decrease in Mg leaf concentrations with higher K supply in potato plants. Besides, the highest Mg leaf concentrations were determined in plants receiving the lowest K supply (Koch et al. 2019a). These alleged interactions between both nutrients could be the effect of the specificity of K transporters on the one hand and the unspecificity 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 follows typically different mechanisms: while Mg is mainly delivered by mass flow and, to a smaller extent, by interception, K is mainly delivered by diffusion (Strebel and Duynisveld 1989; Barber 1995; Marschner 2012). To ensure delivery to the roots, plants need to decrease 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, delivery to the plant roots is mainly enabled by mass flow (Zhang and George 2002). It may so happen 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. As compared to K, this reduces 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, Mg uptake can be blocked under high plant-available K concentrations in the soil solution even though K uptake can be facilitated by Mg transporters (Gransee and Führs 2013). At the same time, there are very specific K transporters which ensure, depending on the K concentration in the soil solution, K uptake at low (HATS = *H*igh *A*ffinity *T*ransport *S*ystem) as well as at high K concentrations (LATS = *L*ow *A*ffinity *T*ransport *S*ystem) (Britto and Kronzucker 2008).

However, 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 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.

With reference to the described antagonistic effects, it is often wrongly concluded that K and Mg should not be applied together in order to prevent antagonistic effects during uptake. As can be seen in Fig. 2, the yield of the control treatment receiving Mg in the form of 400 kg ha^{-1} as magnesium sulphate (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 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 single K treatment could be expected, finally leading to reduced yield. Only the combination of K and Mg supply revealed the highest yield.

Calcium

Calcium (Ca) is essential for the potato crop, mainly due to its role in cell wall and membrane stabilisation (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 2012) and as a second messenger in intracellular signal transduction processes (Pottosin and Schonknecht 2007). Ca has extremely low cytosolic concentrations of less than 1 μM. A major part of Ca is present in bound form. 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;

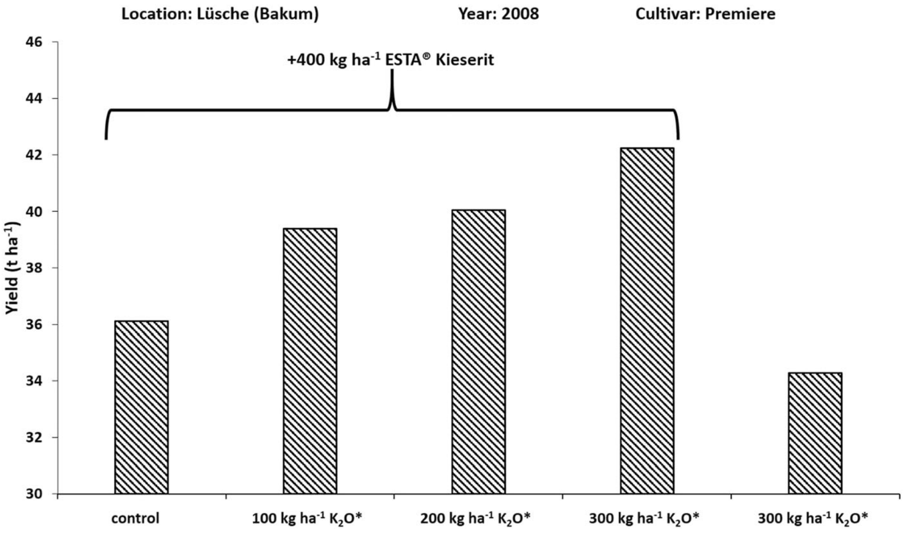

Fig. 2 Effect of combined K and Mg fertilisation on yield of potato. The experimental site was Lüsche (Bakum), Northwest Germany, predominantly characterised by silty sand. Soil analysis showed 13.6 mg K_2O 100 g^{-1} soil after calcium acetate lactate (CAL) extraction and 3.2 mg Mg/100 g^{-1} soil after $CaCl_2$ 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)

Marschner 2012). 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).

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 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).

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 indicated Ca concentrations also in phloem sap but without further transport (Clarkson 1984). Clarkson (1984) argues that these observations, together with the fact that Ca easily interacts with macromolecules, means 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 in 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 hardly transpire. The most Ca is distributed in the above-ground parts of the plant (Ozgen et al. 2006; Kärenlampi and White 2009). Kratzke and Palta (1985) demonstrated that Ca uptake and subsequent transport within the potato plant needs to be distinguished between different root types. First, there are the main roots, transporting water mainly to the aboveground parts of the plant. Second, there are the stolon roots arising from the stolons and the tuber roots arising directly from the base of the buds on the tuber. These latter root types could be shown to transport water mainly to the tubers (Kratzke and Palta 1985). As Ca and water are usually transported together, a follow-up study was conducted: it was demonstrated that a Ca application in the area surrounding tubers and stolons could cause a threefold increase of the Ca concentrations in tubers (Palta 2010). Thus, stolon and tuber roots may have a decisive role in the supply of Ca to the tubers.

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; Lazarević et al. 2014). Although liming can usually increase potato yields, people often refrain from liming these soils as soils with higher pH values could favour the development of common scab (*Streptomyces* spp.) (van Lierop et al. 1982; Waterer 2002). However, other severe problems related to low soil pH conditions may arise: these make it 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 aluminium (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 and $Ca(OH)_2$ can not only improve the supply of Ca but also neutralise the soil pH and reduce the risk of Al or Mn toxicity in the plant (Mengel and Kirkby 2001; Lazarević et al. 2014). On the other hand, when pH is raised, it is possible that essential plant nutrients like phosphorous and zinc can be less available to plants (Haynes 1990).

Sulphur

Sulphur (S) is essential for many cellular metabolites and, therefore, can be a 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 essential building blocks of proteins (De Kok et al. 2005; Galili and Amir 2013). Eppendorfer and Eggum (1994) found severe reductions of these amino acids in potatoes suffering S deficiency. Sharma et al. (2011) found increase in dry matter, specific gravity and starch content with increase in S supply. However, the authors determined the highest values with an S supply of 45 kg ha^{-1}. S levels above 45 kg ha^{-1} did not show any further effect on the investigated parameters. Compared to other crops, like the *Brassica* species, potato has a comparatively low demand for S (Barczak and Nowak 2015), but several high-yielding years might remove considerable amounts of S from the soil. S fertilisation has been shown to increase the resistance of potato against *Streptomyces scabies*, which is probably caused by a decrease of soil pH due to S supply (Klikocka et al. 2005). Moreover, S supply could cause a reduction in the infection rate with *Rhizoctonia solani* (Klikocka et al. 2005).

Plants with S deficiency develop a yellowish phenotype similar to conditions caused by N deficiency. Both are based on a loss of chlorophyll. Although under S deficiency there is no direct impact on chlorophyll, S deficiency inhibits the synthesis of thylakoid membranes and, therefore, promotes chlorophyll deficiency (Imsande 1998). S can be translocated within the plant both via 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 in younger leaves (Mengel and Kirkby 2001). However, as potatoes are usually fertilised with K_2SO_4 instead of KCl, it can be expected that the need of potatoes for S should usually be covered via an application of K_2SO_4.

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 few years in USA, Canada and Central and Western Europe, there has been a two- or threefold increase in emissions in Africa, China, Australia and New Zealand.

Conclusion

Beside other agronomic strategies, 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, as a first step, important to understand individual physiological functions of each nutrient. Moreover, resulting features such as nutrient antagonism or site-specific effects providing varying abiotic and biotic environmental conditions need to be taken into account as well. Based on this fundamental knowledge, a potato grower may decide the accurate choice of type, time and amount of fertiliser application.

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