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Nutrient Deficiencies

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Important factors for the success of almost every plant growing system are the control and the adjustment of plant nutrients. No matter whether the system involves a traditional open field or a high-end indoor operation with hydroponics, proper nutrient management can help to optimize yields, costs of production, environmental impacts and the quality of horticultural products. In modern plant nutrition, 17 mineral elements are reported as nutrients (Table 6.1). To be counted among nutrients, an element has to fulfil three conditions. First, it must be needed by plants to complete their life cycle, i.e. a plant would not be able to produce offspring in the absence of this unique element. Second, the nutrient's function cannot be fulfilled by any other element. Specific elements that can replace some nutritional functions are known, but in general, they are not capable of substituting the whole spectrum of functions of the lacking nutrient. Third, a nutritional element has to be directly involved in the plant metabolism. In consequence, a nutrient deficiency leads to malfunctions in the plant's metabolism and, in turn, to a reduction of plant growth and development (Arnon and Stout 1939; Marschner 2012).

Nutrients are grouped into macronutrients or micronutrients (Table 6.1). Micronutrients are needed in a markedly smaller amount compared with macronutrients. On average, the concentration of a specific macronutrient is greater than or equal to 1 g kg^{-1}, whereas micronutrient concentrations only reach levels up to 100 mg kg^{-1} (Marschner 2012). The quantitative need of nutrients, however, can vary from plant species to plant species.

6.1 Nitrogen Deficiency

After carbon, nitrogen (N) accounts for the highest dry matter content (1–5%) of plant material among all established plant nutrients (Marschner 2012). Nitrogen is a constituent of many important molecules such as proteins, nucleic acids and amino acids and of signalling molecules. Nitric oxide (NO), for example, is known to be important for stomatal movement. It also plays a role in apoptosis, germination and many more mechanisms (Baudouin and Hancock 2014). Although the discovery of the Haber-Bosch process made inorganic N fertilizer available and affordable and enabled the intensive local application of large amounts of inorganic N onto fields, N deficiencies still occur during the cultivation of horticultural crop plants. The most common symptom of the N starvation of plants is the uniform chlorosis of the whole leaf blade of older leaves (Fig. 6.1). The green of the affected leaves becomes brighter until the leaves appear yellow. Under ongoing N starvation, the brightening process spreads out to the younger leaves, and the senescence of the older leaves begins (Uchida 2000).) Because N is a structural compound of chlorophyll, the described leaf discolouration is based on the decrease of the chlorophyll concentration in the leaf tissue. Under N deficiency, plants degrade not only chlorophyll but also proteins from the older leaves to reuse the assimilated N for the support of the younger parts of the plant and especially the generative plant organs (Kant et al. 2010). As a result, photosynthesis and growth are reduced, and the plant tries to invest in younger plant parts with the aim of finishing its life cycle.

However, apart from the negative effects of N deficiency on growth and yield, the limitation of the N supply can have positive effects on the quality of crops. Chishaki and

Table 6.1 Overview of plant nutrients with name, element abbreviation, available forms, classification into macro- or micronutrient, phloem mobility and some key functions according to Bergmann 1992; Marschner 2012; Behboudian et al. 2016

Nutrient	Element symbol	Available forms	Classification	Phloem mobility	Key functional areas (examples)
Carbon	C	CO_2, amino acids, carbohydrates (both with minor relevance for C-nutrition)	Macronutrient	High	Basic element of carbohydrates (e.g. glucose), fats (e.g. phospholipids) and amino acids (e.g. adenine)
Hydrogen	H	H^+, H_2O	Macronutrient	High	Proton gradients (e.g. ATPase), ion uptake (cotransport), redox reactions, basic element of carbohydrates, fats and amino acids
Oxygen	O	O_2, H_2O	Macronutrient	Not applicable	Oxidative phosphorylation, basic element of carbohydrates, fats and amino acids, general oxidation agent, respiration
Nitrogen	N	NO_3^-, NH_4^+, organic compounds	Macronutrient	High	Component of amino acids, DNA, RNA, chlorophyll, enzymes, membrane proteins, secondary compounds
Phosphorus	P	PO_4^{2-}, phytic acid, orthophosphate (both poor availability)	Macronutrient	High	Energy transfer (e.g. ATP), membrane structure, regulatory functions
Potassium	K	K^+	Macronutrient	High	Osmoregulation, photosynthesis, enzyme activation and protein biosynthesis
Magnesium	Mg	Mg^{2+}	Macronutrient	High	Central element of chlorophyll, also required for enzymatic activation, carbohydrate partitioning, chlorophyll/protein synthesis

(continued)

Table 6.1 (continued)

Nutrient	Element symbol	Available forms	Classification	Phloem mobility	Key functional areas (examples)
Calcium	Ca	Ca^{2+}	Macronutrient	Low	Cell wall and membrane structure, osmoregulation, cell extension, signalling
Sulphur	S	SO_4^{2-}, SO_2	Macronutrient	High	Lipids, glucosinolates, cysteine, methionine, glutathione, coenzymes
Iron	Fe	Fe^{2+}, Fe^{3+}	Micronutrient	Intermediate to low	Redox systems, photosynthetic and mitochondrial electron transport chains
Zinc	Zn	Zn^{2+}, $ZnOH^{+}$	Micronutrient	Intermediate to low	Enzyme component/activator, membrane structure, protein synthesis
Copper	Cu	Cu^{2+}	Micronutrient	Intermediate	Enzyme component, lignification, flower/fruit formation, photosynthetic and mitochondrial electron transport chain
Boron	B	H_3BO_3, $B(OH)_4^-$	Micronutrient	Intermediate	Cell wall and membrane structure, flower production, pollen production
Molybdenum	Mo	MO_4^{2-}	Micronutrient	Intermediate	Enzyme component (e.g. nitrate reductase), seed dormancy, photosynthesis
Manganese	Mn	Mn^{2+}	Micronutrient	Low	Enzyme component/activator, photosynthesis
Chlorine	Cl	Cl^-	Micronutrient	High	Osmoregulation, photosynthesis (oxygen evolution)
Nickel	Ni	Ni^{2+}	Micronutrient	Depends on species	Enzyme component, urease activity, seed germination

Fig. 6.1 Nitrogen deficiency symptoms exhibited by a tobacco plant (*Nicotiana tabacum*)

Horiguchi (1997) carried out an experiment in which they showed a correlation between phenolic metabolism and N deficiency. The experiment revealed that rice (*Oryza sativa* L.) seedlings exposed to nitrogen deficiency showed higher values of phenolic compounds, especially p-coumaric acid and ferulic acid. Bongue-Bartelsman and Phillips (1995) showed that N deficiency can lead to the expression of genes responsible for enzymes that play a role in flavonoid biosynthesis. This might also explain the findings of Stewart et al. (2002) and Ibrahim et al. (2011). Ibrahim et al. (2011) determined that the content of total flavonoids and phenolics becomes higher with decreasing N fertilization in the Malaysian medicinal herb *Labisia pumila* Benth, whereas Stewart et al. (2002) found a flavonol accumulation in the leaves of mature tomato plants (*Lycopersicon esculentum* cv. Chaser). These results indicate that N deficiency can be used as a tool for the quality improvement for leafy vegetables, as also shown by Galieni et al. (2015) who have reported that lettuces (*Lactuca sativa* L.) grown in pots show the highest polyphenol concentrations with no N fertilization. Furthermore, an N deficiency can induce the accumulation of anthocyanins as a reaction to photoinhibitory stress. The degradation of both chlorophyll and proteins under N deficiency (◘ Fig. 6.1) leads to the reduction of photosynthetic capacity. In consequence, the application of light to the leaves can induce oxidative damage, since reactive oxygen species are formed (see ▶ Chap. 8). In order to shield the leaf from sun energy, plants accumulate anthocyanins to absorb harmful UV radiation under N deficiency (Steyn et al. 2002). Additional details about anthocyanins and their role in high light protection are given in ▶ Chap. 5 and in the next section of this present chapter. Moreover, a reduction in N fertilization can cause a decline in the concentration of the amino acid asparagine (ASPN) and of reducing sugars (RS) in potato tubers. Both ASPN and RS are precursors of acrylamide, which is formed during the processing (e.g. deep-frying) of potatoes and is suspected to be carcinogenic. The effects of reduced ASPN and RS are even more pronounced when reduced N fertilization is accompanied with increased K fertilization. In contrast, under conditions of a high N and low K supply, free amino acids such as ASPN are thought to accumulate, whereas a sufficient K supply reduces free amino acids because of the increased metabolic capability of the plant. The concentration of RS is positively correlated with the level of N fertilization but is reduced under an increased K supply. The reduced concentration of RS under high K levels has been ascribed to the regulation of osmotic homeostasis. With a higher K content in the tissue, less RS is needed to maintain the osmotic pressure in the cell (Gerendás et al. 2007). Although the potentially carcinogenic effects (e.g. breast and ovarian cancer) of acrylamide have not as yet been validated and are still the focus of current studies, the acrylamide concentration in some deep-fried products is limited in the European Union (Pedreschi et al. 2013, Commission Regulation (EU) 2017/2158). Various concentrations are however legal in the European Union for a range of products such as ready-to-eat French fries (500 µg per kg^{-1}), potato chips (750 µg per kg^{-1}), wheat-based bread (50 µg per kg^{-1}) and roast coffee (400 µg per kg^{-1}).

6.2 Phosphorus Deficiency

Phosphorus (P) is a major plant nutrient and is essential for energy metabolism. Energy (from glycolysis, photosynthesis, etc.) is used to form P-rich molecules such as ATP and GTP, which provide energy for cell metabolism. Thereby, ATP can regulate primary metabolism by driving ion pumps or phosphorylating enzymes. P also plays an important role as a structural element. As part of the so-called phospholipids, P serves an essential role in cell membranes. P is also a structural component of nucleic acids, namely, DNA and RNA. To cope with a P deficiency, plants have evolved various strategies to maintain growth and generative propagation. As a result, plants change their morphological, physiological and metabolic processes. This set of changes is called the phosphorus starvation response (PSR) (Plaxton and Tran 2011). A well-known morphological adaption to P deficiency is the alteration of the plant root system. Plants suffering from P deprivation enhance their root growth in order to gain access to distant pools of P (Shen et al. 2011). The increased root growth is facilitated by a relocation of carbohydrates (mainly sucrose) from the leaves to the root. As a result, plants decrease their leaf expansion to save assimilates causing a slowdown in their development leading to a higher root-to-shoot ratio (Shen et al. 2011). The reduced leaf expansion also causes the leaf to appear darker green or even bluish-

Fig. 6.2 Trichomes of a hemp plant (*C.sativa*, *L. sativa*) containing cannabinoids and aromatic compounds

green, because of an increase in the number of chloroplasts per leaf area. The consequence is a higher reflection of green light from the same leaf area because of a higher chlorophyll concentration (Valentinuzzi et al. 2015). Nevertheless, the yellowing of leaves and interveinal chlorosis followed by necrotic lesions are also known in a variety of cultivars. The P deficiency results in insufficient P for the relevant cotransporter (phosphate antiporter) for the export of triose phosphate in exchange. Therefore, the carbohydrates produced during photosynthesis within the chloroplast cannot be exported into the cytosol (Schleucher et al. 1998). This gives rise to oxygen-derived radicals (atoms or molecules with a free electron), because electrons that are excited from magnesium in photosystem II cannot be transferred to oxidized reduction equivalents or ferredoxin. Radicals can damage cellular structures and molecules. To avoid the formation of these radicals, the plant produces and accumulates anthocyanins under P deficiency (Liu et al. 2015). Anthocyanins absorb harmful UV radiation and act as scavengers of free radicals, such as reactive oxygen species (ROS). In this context, anthocyanins are assumed, on the one hand, to scavenge ROS and, on the other hand, to absorb UV light, thus protecting the photosystems from photoinhibitory damage. The accumulation of anthocyanins can cause the red to purple colouration of plant leaves, stems and petioles (▪ Fig. 6.2), which is a symptom often described during P deficiency (Hernández and Munné-Bosch 2015). The accumulation of anthocyanins has been reported in various plant species undergoing P deficiency. For example, P starvation induces anthocyanin accumulation in tomatoes (*Lycopersicon esculentum*) (Ulrychová and Sosnová 1970) and Chinese kale (*Brassica alboglabra* Bailey). (Chen et al. 2013). Stewart et al. (2002) detected an increase of flavonol in P-deficient tomato fruits at early ripening. A controlled P deficiency can also boost the content of alkaloids and phenolics in some plants. In an experimental cell culture of *Catharanthus roseus* (Knobloch and Berlin 1983), a rise in alkaloids such as tryptamine, indole alkaloids and phenolic was determined under P deficiency. This is especially interesting as *C. roseus* is known to contain anti-carcinogenic alkaloids (vincristine and vinblastine). An increase in phenolics has also been found in rice seedlings suffering from P deficiency (Chishaki and Horiguchi 1997). The enrichment of horticultural food products with secondary metabolites such as anthocyanins is desirable as these compounds considered to confer health benefits when part of the human diet (Khoo et al. 2017). For instance, anthocyanins are assumed to have anti-carcinogenic (e.g. cancer of liver and breast), neuroprotective or metabolism-improving (e.g. against diabetes mellitus) effects on the human body (Hoensch and Oertel 2015; Daotong et al. 2017). As a positive side effect, the attractive colouration of, for example, apples or strawberries attributable to increased anthocyanin synthesis is a quality-improving feature that appeals to the consumer (Jezek et al. 2018). Anthocyanins can also improve the storage properties of horticultural products. For example, the postharvest damage to tomatoes caused by *Botrytis cinerea* is significantly reduced if they contain higher anthocyanin concentrations. The fruits can remain in storage for longer, as the anthocyanins reduce the ROS in the fruits (Zhang et al. 2013).

6.3 Potassium Deficiency and Other Nutrient Deficiencies

Although only a few examples of quality improvements in horticultural crops have as yet been established because nutrient deficiencies are usually accompanied by yield losses, some hints regarding effective nutrient deficiencies have been reported. Potassium (K) is a crucial element for the growth, development and reproduction of plants. K is relevant for the generation of turgor, for the activation of many enzymes (e.g. for the carbon metabolism), for the source-to-sink transport of metabolites or for the adjustment of guard cell aperture (Cakmak 2005; Hafsi et al. 2014; Behboudian et al. 2016; Zörb et al. 2019). Troufflard et al. (2010) have observed the induction of the biosynthesis of oxylipins (OL) and glucosinolates (GS) in the model plant *Arabidopsis thaliana*. Both OL and GS are assumed to accumulate as a reversible storage for nitrogen (N) and sulphur (S), which cannot be assimilated during K deficiency (Abdin et al. 2003; Barrelet et al. 2006; Armengaud et al. 2009). Both metabolites, namely, OL and GS, are thought to promote human health (Traka and Mithen 2009; Zivkovic et al. 2011). Gorelick and Bernstein (2017) report that K deficiency is correlated with increased tetrahydrocannabinol content in wild hemp *(Cannabis sativa* L. *sativa*) (◘ Fig. 6.2), whereas Gremigni et al. (2001) have shown significant increases in alkaloid content in several varieties of lupins (*Lupinus angustifolius*). Another hint of alkaloid increase has been presented by Khan and Harborne (1991) who have witnessed alkaloid accumulation in *Atropa acuminata* during K deficiency in a hydroponic experiment.

Calcium (Ca) plays a crucial role as a structural element in cell walls and membranes and acts a counter ion for anions in the vacuole. Ca also acts an intracellular messenger and is thereby responsible for various responses to environmental factors (White and Broadley 2003). Chishaki and Horiguchi detected a rise in p-coumaric acid in the Ca-deficient seed coats of broad beans (*Vivia faba* L.). In addition, Tavares et al. (2013) have established that an enrichment of anthocyanins occurs in S-deficient grapevine (*Vitis vinifera* L.) plantlets. S has various functions in plants from pathogen defence to structural functions in enzymes and further to building aromatic compounds.

6.4 Practical Note

The challenge for the horticulturist is to implement nutrient deficiencies without yield losses. This can be achieved in two ways. The indirect method employs soils poor in nutrients from the beginning of cultivation. This requires accurate cost calculations and a suitable choice of crops in advance. Nevertheless, many uncontrollable factors are involved with regard to soil cultures. Therefore, the use of nutrient deficiency techniques in hydroponic cultures is highly recommended as these enable the gardener to control the nutrient solution directly. To avoid yield and quality losses, nutrient deficiencies should be performed only for short time periods and at intervals. The plants should be exposed to the nutrient deficiency only for 12 h every third to fourth day in the last 2 weeks prior to harvest. This can be achieved by omitting a nutrient when the nutrient solution is prepared. Another way of provoking nutrient deficiency is by decreasing a nutrient's availability via the changing of the pH of the solution to an unfavourable point. For example, the plant-available forms of P in a hydroponic solution reach a maximum at a pH of around 5, whereas the availability significantly starts to decrease with a pH of 6 and higher, thereby causing a P-deficient environment for the plant (Trejo-Téllez and Gómez-Merino 2012). The choice concerning which nutrient to pick for deficiency techniques strongly depends on the crop being cultured and those secondary metabolites that are desired to be accumulated.

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