

*Chapter 11*

## **NUTRIENT MANAGEMENT IN STRAWBERRY: EFFECTS ON YIELD, QUALITY AND PLANT HEALTH**

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### **ABSTRACT**

Strawberry is a widely grown hybrid species of the genus *Fragaria* (Rubiaceae family). It is cultivated worldwide for its fruit, which is an aggregate accessory fruit widely appreciated for its characteristic aroma, bright red color, juicy texture, and flavor. The world strawberry production reached 4,516,810 tons in 2012, being the USA, Mexico, Turkey, Spain, Egypt, Russia, South Korea, Japan, Poland and Germany the main producers. Strawberry is one of the most sensitive plants in horticultural production and nutrient management is a key factor to ensure high yields and fruit quality. Furthermore, an adequate management of nutrient elements is crucial to guarantee *health* food safety and food quality. As well, soil health plays a pivotal role in insect and disease management as well as in providing a foundation for building soil fertility. In this chapter we present the most important and recent advances on nutrient management of strawberry, in relation to macronutrients (nitrogen, phosphorus, potassium, sulfur, calcium and magnesium) and micronutrients (iron, boron, manganese, zinc, copper, molybdenum and nickel) that play a crucial role on production, quality, as well as pest and disease control. Moreover, we explore the potential use of some beneficial elements, as they may stimulate growth, can compensate toxic effects of other elements, or increase tolerance to biotic stress.

**Keywords:** *Fragaria* × *ananassa*, plant nutrition, macronutrients, micronutrients

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## INTRODUCTION

The common cultivated strawberry (*Fragaria* × *ananassa* Duch.) is a widely grown hybrid plant resulting from the breeding between two American species, *Fragaria chiloensis* of western North and South America and *Fragaria virginiana* of eastern North America. The hybridization of the two species occurred between the Centuries XVII y XIX in France and hundreds or even thousands of varieties have been selected and named since then [26]. Botanically, the strawberry is an aggregate accessory fruit (not a berry indeed), meaning that the fleshy part is derived not from the ovaries of the flower but from the receptacle, that holds the ovaries. Each apparent seed (properly named achene) on the outside of the fruit is actually one of the ovaries of the flower, with a seed inside it. This fruit is widely appreciated for its characteristic aroma, bright red color, juicy texture, and sweetness. It is consumed in large quantities, either fresh or in prepared foods such as preserves, fruit juice, pies, ice creams, milkshakes, and other desserts. According to FAO [34], in 2012 the main producers of strawberry were the United States, Mexico, Turkey, Spain, Egypt, South Korea, Japan, Russia, Germany and Poland (Table 1).

**Table 1. World strawberry production from year 2008 to 2012 (tons per year) [34]**

Position	Country	Production (tons a year)				
		2008	2009	2010	2011	2012
1	United States	1,148,350	1,270,640	1,294,180	1,312,960	1,366,850
2	Mexico	207,485	233,041	226,657	228,900	360,426
3	Turkey	261,078	291,996	299,940	302,416	353,173
4	Spain	281,240	266,772	275,355	262,730	289,900
5	Egypt	200,254	242,776	238,432	240,284	242,297
6	South Korea	192,296	203,772	231,803	171,519	192,140
7	Japan	190,700	191,400	190,700	184,700	185,000
8	Russia	180,000	185,000	165,000	184,000	174,000
9	Germany	150,854	158,563	156,911	154,418	155,828
10	Poland	200,723	198,907	153,410	166,159	150,151
Total world		4,130,279	4,596,586	4,352,869	4,328,129	4,516,810

The strawberry is a low-growing, herbaceous perennial plant with a fibrous root system and a crown from which arise basal leaves (Figure 1), features that are important in terms of agronomic management. Considering the time of flower bud initiation and therefore fruiting, there are two main types of strawberry plants. Short-day types initiate flower buds when days

are short (less than 14 h a day). Day-neutral types initiate flowers season-long within certain temperature ranges [84].

In the Mid-Atlantic Berry Guide for Commercial Growers 2013-2014, [84] the anatomy and morphology of strawberry plant is described in detail. Crown is a compressed modified stem where leaves, runners (stolons), branch crowns, and flower clusters (inflorescences) arise.

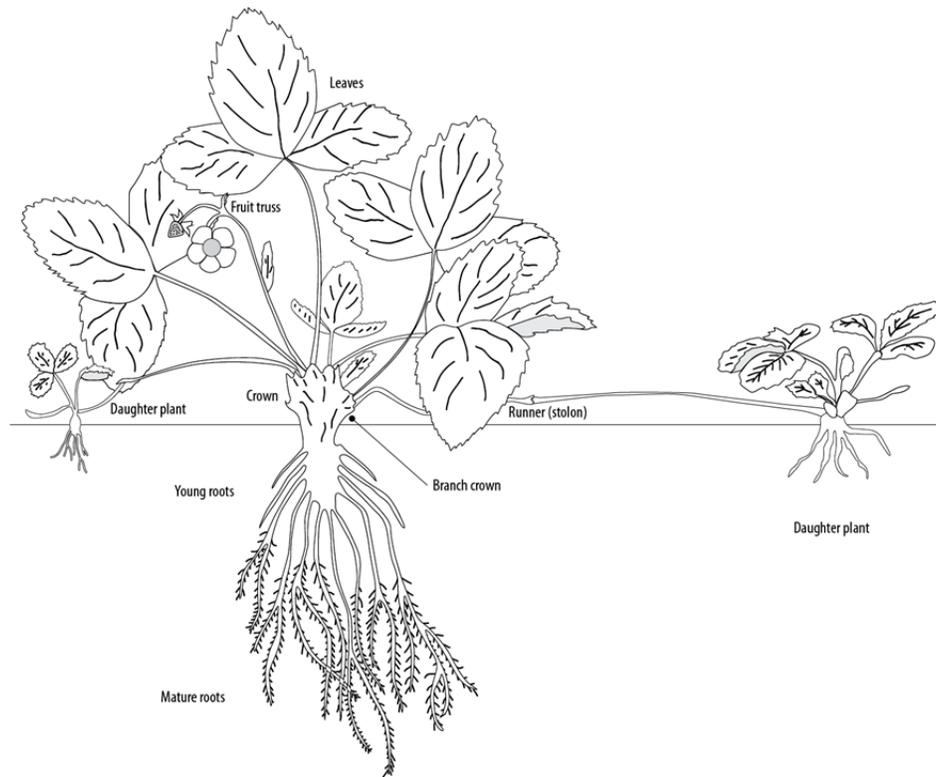


Figure 1. Morphology of a typical strawberry plant and its runners. Mature strawberry plant at flowering with stolons, showing the mother plant and the daughter emerging from the runner or stolon.

As roots are a crucial element in the plant nutrition process, we will focus on this system, considering runners or stolons as well. In strawberry plants, roots are most vastly produced during the spring and fall and are active until the soil freezes. Strawberry plants have two types of roots. Primary roots conduct water and nutrients to the crown and last more than one season. In successive years, primary roots are produced higher on the crown, so about 2.5 cm of soil should be thrown over the plants during renovation to encourage new primary root development. With good care, plants are able to produce new healthy primary roots above the old ones, thus allowing plants that have had a poor root system in the past to recover. Feeder roots branch off from the primary roots and live only for a few days or weeks. Their main physiological function is absorption of water and nutrients. Strawberry plants have shallow root systems, which result in sensitivity to deficient or excess water and high salt levels in the soil. Those characteristics should be taken into consideration when choosing and preparing a planting site. In light sandy soils, the roots penetrate the soil to approximately 30 cm deep

with half of the roots located in the lower 15 cm. In heavy soils, roots only grow about 15 cm deep. The runners or stolons are the means of vegetative propagation, as daughter plants arise from them. Runners form during long days with warm temperatures, beginning in late spring and continuing until fall. For short-day types, runners form when days are more than 10 h long and temperatures are at least 21°C. Formation stops when days are less than 10 h long and temperatures are freezing. In day-neutral types, the majority of runners are formed when days are long and temperatures are moderate. Runner formation is more sporadic for day-neutral types than short-day types. After the development of numerous lateral roots, the daughter plants become independent of the mother plant, usually after 2 to 3 weeks of attachment. Daughter plants that have had more time to develop have larger crowns and more flower buds, which result in higher yields. In later years, taking good care of renovated plantings during the summer encourages earlier production of runners, early establishment of daughter plants, and higher yields the following year [83, 84].

Each year, leaves and roots arise at higher points on the crown [83]. Thus, the plant tends to grow out of the ground and develop poor root-soil contact with age. The root system is shallow, with 80 to 90% in the top 15 cm of clay and 50% in the top of 15 cm of well-drained sandy loam soils (Figure 2). A primary root normally lives for one year. The plant then will initiate new roots at succeeding higher levels on the crown and, when exposed to cold or drought, may die while younger plants live. Fertility, water supply, and aeration at soil depths greater than 15 cm represent major constraints. Placing 2.5 cm of soil over the plant bed after harvest will enhance new root formation and make plant less vulnerable to cold and drought [83, 84].

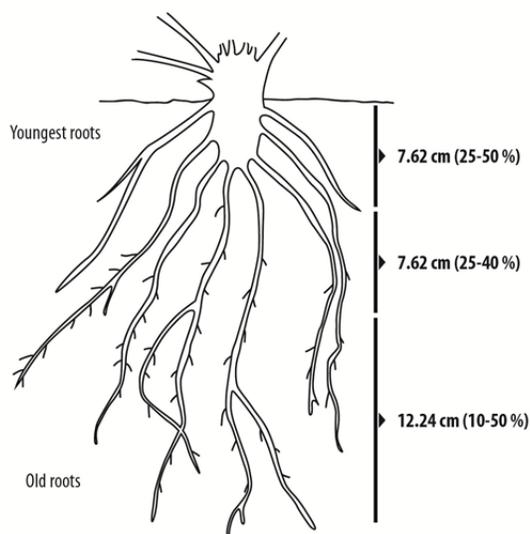


Figure 2. Details of the root system distribution in a typical strawberry mature plant. The root system is shallow, with approximately 80 to 90% in the top 15 cm of clay and 50% in the top of 15 cm of well-drained sandy loam soils.

Strawberry plants can be grown on crop fields or in hydroponics under greenhouse conditions. Indeed, now a day, hydroponics production of strawberry in greenhouse is common in many countries. In any case, soil or substrate analyses will reveal the percentage

of organic matter, pH, cation exchange capacity and nutrient contents, among other physical and chemical properties. After the crop is established, plant tissue analysis is recommended to guide adjustments to the corresponding nutrient program. On crop fields, strawberries are grown on a wide range of soil types worldwide. Fertilizer programs and soil preparation depend largely on the soil's natural nutrient content, soil organic matter content and previous cropping history of the site. Consequently, in this chapter we review the importance of macro, micronutrient and beneficial elements on the physiology and productivity of strawberry, and analyze how each element influence yield, quality and plant health [83, 84].

## MACRONUTRIENTS

### Nitrogen (N)

Nitrogen (N) is most important for plant growth, runner production, and fruit bud formation. During periods of rapid growth, leaves of nitrogen-deficient plants remain small and may turn from green to light green or yellow. In older leaves, the leaf stalk reddens and the leaf blades become brilliant red. Fruit size is reduced, and the calyx around the fruit becomes reddish [86].

Nitrogen nutrition affects fruit firmness, quality and shelf life of strawberry [62]. Indeed, the fertigation of 225 kg ha<sup>-1</sup> N for the crop life is more effective in maintaining fruit quality of strawberry up to 21 days' storage, compared to all other nitrogen treatments (300, 450, and 600 kg ha<sup>-1</sup> N).

Neuweiler [67] found that the response of vegetative plant development to increasing N fertilization is controlled largely by readily availability of N in the rooting zone. The response of vegetative plant development to an increased availability of N was usually positive when the N requirements of the strawberry plants were high. This occurs between the beginning of flowering and the end of the harvest. Banded applications of mineral N fertilizers after planting (i.e., when N requirements are low), may have detrimental effects on the initial development of strawberry plantations. Therefore, N fertilization has to be carefully adjusted to the low demand of young plants during this period. Furthermore, demand-driven N fertilization corrected for soil N secures fruit yield and quality.

Yoshida et al. [95] studied the effects of nutrient deficiency (N, P and K) on color development and anthocyanin accumulation in strawberry fruit. They determined that in fruits of N deficient 'Nyoho' strawberries red color began to develop faster, while L\* value and hue angle were lower at 24 days after anthesis (DAA) compared to those of control or P and K deficient plants, but there was no significant difference at 27 to 36 DAA. The concentration of total anthocyanins was significantly higher in N deficient fruits than that in control at 24 DAA, but was significantly lower in N deficient fruits compared to that in controls at 33 or 36 DAA. In three other cultivars: 'Tochiotome', 'Sachinoka' and 'Hokowase', L\* value, hue and chroma were significantly higher, and the concentration of total anthocyanins was also lower in N deficient fruits compared to the other treatments. It was concluded that the anthocyanin synthesis in strawberry fruits may be reduced by N deficiency.

Nitrogen may also affect disease resistance in strawberry. For instance, in the cv. 'Nyoho', elevated nitrogen and potassium concentrations in the fertilizer solution increased

anthracnose severity in contrast to phosphorus and calcium. The dry weight of the strawberry plants increased significantly with elevated concentrations of nitrogen and phosphorus, but was not influenced by the elevated amounts of potassium and calcium concentrations. Treatment with either  $\text{NH}_4^+$  or  $\text{NO}_3^-$  nitrogen was not significantly different [63]. Accordingly, Cárdenas-Navarro et al. [16] reported that growth of the mother plants was not affected by the variations on  $\text{NH}_4^+$  and  $\text{NO}_3^-$  ratios ( $\text{NH}_4^+:\text{NO}_3^-$  ratios were: T0 = 0:4, T1 = 1:3, T2 = 2:2, T3 = 3:1, and T4 = 4:0, at a constant nitrogen (N) concentration of  $4 \text{ mol m}^{-3}$ ). However, the number of fruits increased with the proportion of  $\text{NH}_4^+$  in the nutrient solution. The number of daughter plants produced was affected only at high  $\text{NH}_4^+$  proportions, and their size (dry matter per daughter plant) and fertility (number of second-generation plants per first-generation plants) were reduced. The N or C content of the plants was not significantly affected by the treatments, but the C/N ratio in the crowns of mother plants was higher in treatments with 25% and 50%  $\text{NH}_4^+$  in the nutrient solution. Interestingly, when studying the effect of the variation of  $\text{NH}_4^+:\text{NO}_3^-$  ratios ( $\text{meq L}^{-1}$ : 0:100, 40:60, 50:50, 65:35 and 100:0) in the nutrient solution on strawberry var. 'Seolhyang' in hydroponics,  $\text{NO}_3^-$  as the sole source of nitrogen in the nutrient solution resulted in the highest vegetative growth among the treatments tested. On the contrary, the exclusive use of  $\text{NH}_4^+$  in the nutrient solution suppressed plant growth severely. The introduction of the two nitrogen forms as the treatment ratio 60:40 ( $\text{NH}_4^+:\text{NO}_3^-$ ) resulted in the optimal growth performance and nutrient uptake of this variety [21]. Therefore, different responses to nitrate and ammonium relations can be observed according to varieties and agronomic management.

Increasing N level in the nutrient solution (40, 80, 120, and  $160 \text{ mg L}^{-1} \text{ N}$ ) significantly increased the number of runners. Neither early nor total marketable yields were significantly affected by N level or media. Increasing N level in the nutrient solution significantly decreased fruit-soluble solids on two of the three sampling dates. Higher values of soluble solids occurred during the cooler months of the season. The soluble solids content in the fruit was reduced as the temperature increased. Thus, N levels as low as  $40$  to  $80 \text{ mg L}^{-1} \text{ N}$  in a constant fertigation system can be used to produce strawberries in either coconut coir or pine bark media in a greenhouse environment [15].

The carbohydrate and the amino acid content increase when applying  $3 \text{ mM Ca}(\text{NO}_3)_2$  in drip system and  $9 \text{ mM Ca}(\text{NO}_3)_2$  in the furrow system, compared with the unfertilized treatment, but do not increase further at  $20 \text{ mM}$  nitrogen. The organic acids content decreases as the nitrogen fertilization increases. Therefore, an excessive use of fertilizer and irrigation water does not enhance the content of the compounds related with the sensorial quality of the strawberry [69].

The effect of increased doses of nitrogen was evaluated in drip and gravity irrigation systems (0, 23, 77, 231, 693 y  $1\ 537 \text{ kg ha}^{-1} \text{ N}$ ). A significant decrease in plant dry matter was observed when irrigation changed from drip to gravity. When plants are supplied with 231, 693 and  $1,537 \text{ kg ha}^{-1} \text{ N}$ , dry matter production increased. Nevertheless, the change from 231 to 693 and from 231 to  $1\ 537 \text{ kg ha}^{-1} \text{ N}$ , involve an increase of 3 and 6.6 times respectively in the quantity of fertilizer and represents proportional economic increases. The water consumption in drip irrigation was 21% minor, but his efficiency in the production of fruit was 29% higher. The efficiency of nitrogen in fruit production in drip irrigation was 19% greater than the obtained on gravity system [91].

By measuring the interaction of short-day (SD) and timing of nitrogen fertilization on growth and flowering of 'Korona' strawberry, a general enhancement of growth at all times

of N fertilization was observed [81]. This was paralleled by an increase in leaf chlorophyll concentration, indicating that the control plants were in a mild state of N deficiency. The amount of flowering was generally increased by N fertilization although the effect varied greatly with the time of N application. The greatest flowering enhancement occurred when N fertilization started 1 week after the first SD when the number of flowering crowns and the number of inflorescences per plant were more than doubled compared with the SD control, while fertilization 2 weeks before SD had no significant effect on these parameters. Importantly, the total number of crowns per plant was not affected by N fertilization at any time, indicating that enhancement of flowering was not due to an increase in potential inflorescence sites. No flowering took place in the control plants in long-day (LD) [81].

Andriolo et al. [6] tested five nutrient solutions at nitrogen concentrations of 6.5, 8.0, 9.5, 11.0 and 12.5 mmol L<sup>-1</sup>. Number of leaves, shoot and root dry mass and crown diameter decreased by effect of increasing N concentrations in the nutrient solution. The N concentration used for the strawberry crop in soilless growing systems can be reduced to 8.9 mmol L<sup>-1</sup> without any reduction in fruit yield.

Janisch et al. [44] reported that increasing N concentration in the nutrient solution from 5.12 to 15.12 mmol L<sup>-1</sup> reduces growth of crown, roots and leaf area index of strawberry stock plants but did not affect emission and growth of runner tips. For the commercial production of plug plants, they recommended an optimal nitrogen concentration in the nutrient solution of 5.12 mmol L<sup>-1</sup>.

Nitrogen is an essential element, affecting not only growth but also fruit quality such as color, flavor and shelf life, among others. Using two strawberry varieties and different doses of nitrogen (120, 170, 220, 270, 320 kg ha<sup>-1</sup>), D'Anna et al. [24] showed a rather wide variability of results, depending on levels available for plants and doses distributed between the cultures. The lowest doses (120 and 170 kg ha<sup>-1</sup>) provided the firmest fruits, 735 g, with an high content in total soluble solids content, 7.3 °Brix, and highest vitamin C, 53 mg 100 g<sup>-1</sup> of fresh weight, and a very bright orange-red color. They conclude that in greenhouses cultivation, the application of low doses of nitrogen achieves the same production, as higher doses, and high fruit quality, reducing environmental and production costs.

Rodas et al. [73] tested four nitrogen doses (100, 200, 300 and 400 kg ha<sup>-1</sup>) using urea source in strawberry plants cv. 'Aromas'. Fruit chemical properties and fruit external color rates were influenced by the treatments. In the case of total soluble solids (TSS), 7 °Brix or higher (a good indicator of fruit quality concerning TSS) were achieved with the application of 200 and 400 kg ha<sup>-1</sup> N.

Using different strawberry cultivars, namely 'Camarosa', 'Camino Real', 'Candongá', and 'Ventana', Agüero and Kirschbauma [2] fertilized plants at different nutrient rates. Productivity from the applied-nutrients was inversely proportional to the applied-nutrient rate, and it was higher in high-yielding cultivars ('Camarosa' and 'Ventana'). Optimal N dose (in kg ha<sup>-1</sup>) was 183, 196, 165, and 150, for 'Camarosa', 'Ventana', 'Camino Real', and 'Candongá', respectively. Apparently, nutrient use efficiency is cultivar related, and might become a useful tool for adjusting fertilization programs and characterizing new cultivars in breeding programs.

Concluding, N has not only a pivotal role on plant growth and development, but also on fruit quality parameters such as fruit firmness, size, health and correction of fruit disorders, chemical components, and shipping qualities.

## Phosphorus (P)

Phosphorus (P) is one of the 17 essential nutrients for plants and is found in every living plant cell. It is involved in several vital plant functions, including energy transfer, photosynthesis, transformation of sugars and starches, nutrient movement within the plant and is part of the genetic material of all cells (DNA and RNA).

Phosphorus can be limiting in strawberry production. Keeping the pH near 6.5 will aid in maintaining the optimal uptake of P. After planting, a permanent monitoring of plant nutrient needs with a combination of tissue analyses, soil tests, and observations of leaf conditions is highly recommended [83].

In P-deficient strawberry plants, small, yellowish green leaves becoming uniformly yellow are commonly observed. Furthermore, with the age, older leaves become reddish. Fruit size reduction is also observed as deficiency becomes greater [25].

Molina et al. [59] applied different doses of  $P_2O_5$  (from 0 to 1,250 kg ha<sup>-1</sup>) to strawberry plants cv. 'Chandler' either at planting (first experiment) or fractionated in three applications: at planting, 30 and 60 days later (second experiment). In the first experiment, there was a low response to P applications and only the yield of grade B fruits was higher when 800 kg ha<sup>-1</sup> were applied. In the second experiment, the split application increased the yield. It was observed that the high retention capacity showed by the Andosol where the plants grow is the main reason for the plant responses and therefore, a split application is highly recommended.

May and Pritts [56] observed that soil-applied P, B and Zn had significant effects on several yield components of 'Earliglow' strawberries, but responses depended on the levels of other nutrients or the soil pH. At a soil pH of 5.5, yield responded linearly to B and quadratically to P. At pH 6.5, P interacted with B and Zn. Fruit count per inflorescence was the yield component most strongly associated with yield followed by individual fruit weight. However, these two yield components responded differently to soil-applied nutrients. Foliar nutrient levels generally did not increase with the amount of applied nutrient, but often an applied nutrient had a strong effect on the level of another nutrient. Leaf nutrient levels were often correlated with fruit levels, but foliar and fruit levels at harvest were not related to reproductive performance. Therefore, plant responses to single nutrients depend on soil chemistry and the presence of other nutrients.

Gunes et al. [36] studied the effectiveness of the phosphorus-solubilizing microorganisms *Bacillus* FS-3 and *Aspergillus* FS9 in enhancing strawberry yield and mineral content of leaves and fruits on a P-deficient calcareous Aridisol, alone or in combination with five increasing rates of P addition (0, 50, 100, 150, and 200 kg ha<sup>-1</sup>). Strawberry yield increased with P addition (quadratic function) reaching a maximum at 200 kg ha<sup>-1</sup> P in the absence of P-solubilizing microorganisms. At this yield level, *Bacillus* FS-3 and *Aspergillus* FS9 inoculation resulted in P-fertilizer savings of 149 kg ha<sup>-1</sup> and 102 kg ha<sup>-1</sup> P, respectively. Both microorganisms increased yields beyond the maximum achievable with sole P-fertilizer addition. Microorganism inoculation increased fruit and leaf nutrient concentrations of N, P, K, Ca, and Fe, with the largest increases upon addition of *Bacillus* FS-3. Therefore, *Bacillus* FS-3 and *Aspergillus* FS9 show great promise as yield-enhancing soil amendments in P-deficient calcareous soils. However, moderate additions of P fertilizer (50-100 kg ha<sup>-1</sup>) are required for highest yield.

Optimizing plant nitrogen (N) and phosphorus (P) nutrition is required in healthy propagation of strawberry nursery plants for fruit production. Strawberry plants cv.

'Darselect', 'Mesabi', 'V151', 'Seneca', 'Serenity', 'K93-20' and 'Jewel' were supplied with NPK at the rates of 105, 145 and 165 kg ha<sup>-1</sup>, based on soil testing and regional recommendation [50]. Results showed that strawberry nursery plant propagation and productivity expressed using runner and daughter-plant variables were significantly different among the seven cultivars. The cultivars 'Seneca' and 'Jewel' showed a significantly higher ability of N and P acquisition. However, only higher N and P acquisition in 'Seneca' was corresponding to significantly higher runner numbers (23 runners per mother-plant) and daughter plants (42 daughters per mother-plant). Significantly lower productivity was associated with lower N and P uptake in the cultivars 'Darselect', 'Mesabi' and 'V151'. Whole plant P accumulation increased with increasing of N accumulation. It was suggested that strawberry nursery plant propagation could be enhanced with nutrition accumulation ranges of 2.47-3.26 g N per plant and 0.25-0.34 g P per plant. Runner thinning would be an option for regulating strawberry plant N and P nutrition and nursery plant productivity [50].

Phosphates (Pi, salts of phosphoric acid, H<sub>3</sub>PO<sub>4</sub>) are traditionally used for plant fertilization, and phosphites (Phi, salts of phosphorous acid, H<sub>3</sub>PO<sub>3</sub>) are being used as fungicides. Moreover, phosphite (Phi) may have beneficial effects in plants when it is supplied in sufficient quantity of P as phosphate. In strawberry plants cv. 'Polka', Moor et al. [60] showed that Phi fertilization does not affect plant growth and had no advantages in terms of yield increase, compared to traditional Pi fertilization. However, fruit acidity increased and total soluble solids decreased due to foliar fertilization with Phi. Soaking plants in Phi fertilizer solution prior planting was effective in activating plant defense mechanisms, since fruit ascorbic acid and anthocyanin content increased. Accordingly, Estrada-Ortiz et al. [31], concluded that the addition of 30% of total P to the nutrient solution as phosphite stimulates the accumulation of biomolecules such as sugars, chlorophylls, total free amino acids and soluble proteins fruits of in strawberry plants cv. 'Festival' during the fructification stage. In addition, Estrada-Ortiz et al. [32], evaluated the effect of Phi at different doses (0, 20, 30, 40 and 50%) in the nutrient solution of strawberry plants cv. 'Festival' and observed that treatments did not affect dry matter of shoots. The addition of 20% of P as Phi increased the sugar concentration and °Brix of fruits and their firmness. As a conclusion, under sufficient level of P, there were no effects of Phi addition on dry matter weight of shoots but rather on parameters that determine fruit quality of strawberry, and the addition of 20% de P as Phi in the nutrient solution improves some characteristics related to fruit quality. Just recently, Estrada-Ortiz et al. [33] reported that the highest pH, EC and anthocyanin concentration were identified in the fruit of plants treated with 30% Phi. These results suggest that supplying Phi at 30% or less in the nutrient solution does not significantly affect yield but does affect fruit quality and activates plant defense mechanisms by producing a higher concentration of anthocyanins.

Odongo et al. [68] evaluated the effect of farmyard manure (FYM) and triple super phosphate (TSP) on quality and profitability of strawberries. They found that dosages of 54 t ha<sup>-1</sup> FYM plus 34 kg ha<sup>-1</sup> P and 36 t ha<sup>-1</sup> FYM plus 17 kg ha<sup>-1</sup> P are recommended for large-sized and sweetest, long-storing berries, respectively. The relationship between treatments and profitability was sigmoid, and dependent on site and season. Thus, profitable strawberry mineral nutrition packages have to be developed for each site and season.

In the cultivars 'Keumhyang' and 'Seonhong', young leaves of plants grown with nutrient solution P levels higher than 4 mM and 2 mM, respectively, developed interveinal chlorosis [22]. Tissue concentrations of metallic micronutrients Fe, Cu, Mn, and Zn, in both

cultivars did not decrease, but the total amount absorbed by the aboveground plant tissue decreased in the treatments in which nutrient deficiencies were observed. These results indicate that total amount of micronutrients is a better indicator of P-induced micronutrient deficiency.

In terms of P metabolism in plants, the enzyme pyrophosphate: fructose 6-phosphate 1-phosphotransferase (PFP) catalyzes the first committed step in glycolysis by reversibly phosphorylating fructose-6-phosphate to fructose-1,6-bisphosphate. The position of PFP in glycolytic and gluconeogenic metabolism, as well as activity patterns in ripening strawberry, suggest that the enzyme may influence carbohydrate allocation to sugars and organic acids. Using a transgenic approach, Basson et al. [9] confirmed that fructose content increased at the expense of sucrose during the first season. In the second season, total sugar content and composition remained unchanged while the citrate content increased slightly. This enzyme enables the cell to rapidly address changes in carbon availability, as may occur when the plant is experiencing unfavorable conditions that impact on the availability of carbon in sink tissues. Considering that metabolic conditions are largely determined by the external environment, PFP may not be an advisable target for biotechnological manipulation of fruit carbohydrate content via P mobilization.

Therefore, experimental data show that P has a more evident effect on fruit quality parameters and on the activation of defense mechanisms than on yield and productivity. Interestingly, under P-sufficient conditions, Phi may improve fruit quality and defense responses.

## **Potassium (K)**

Potassium (K) plays an important role in the plant development, as it promotes the elongation of the cells, takes part in the water management of plant and in the synthesis of carbohydrates. When strawberry plants are well supplied with K, they can synthesize more sugar, so that the fruits will be sweeter [88].

Lester et al. [49] established that among the many plant mineral nutrients, K stands out as a cation having the strongest influence on quality attributes that determine fruit marketability, consumer preference, and the concentration of critically important human health-associated phytonutrients. However, many plant, soil, and environmental factors often limit uptake of K from the soil in sufficient amounts to satisfy fruit K requirements during development to optimize the aforementioned quality attributes. For instance, Lamarre and Lareau [48] showed that N and K had no significant effect on yield and fruit size, when plants were grown on a light sandy humo-ferric Podzol and fertilizers were applied in an irrigation system. However, Ebrahimi et al. [28] showed that 300 ppm of K in nutrient solution increased vitamin C content, total soluble solids, fruit number, fruit weight, yield of plant, root weight, root dry weight and length of root. They also observed different responses to K among cultivars tested ('Camarosa', 'Silva' and 'Parus'), being 'Parus' the cultivar showing better performance. Consequently, Lester et al. [49] noted that some experimental results stand out because they report little or no change (i.e., improvement) in fruit quality due to K fertilization. Interestingly, these studies have a common denominator in that K is applied directly to the soil and in many cases little information is given regarding timing of application or soil chemical and physical properties. These factors can influence soil nutrient

availability and plant uptake, and soil fertilizer K additions under some conditions may have little or no effect on uptake, yield, and fruit quality.

Rodas et al. [73] evaluated the effect of potassium (150, 300, 450 and 600 kg ha<sup>-1</sup> K<sub>2</sub>O) fertigation in strawberry crop under field conditions on chemical properties and fruit external color rates. Results showed that strawberry fruit chemical properties and fruit external color rates were influenced by potassium fertigation, varying according to the studied property. For instance, the highest total soluble solids content and titrable acidity were found in fruits of plants receiving 344.50 kg ha<sup>-1</sup>.

Potassium has also an important role on plant stress tolerance. For example, strawberry plants exposed to 40 mM salinity stress showed alleviation when 10 mM foliar KNO<sub>3</sub> were applied, resulting in increase in plant root dry weight (50%), shoot dry weight (50%), leaf relative water content (8.2%) and membrane permeability decrease (27.4%), in comparison to control plants not receiving KNO<sub>3</sub> [94].

Though contrasting responses of strawberry may be observed among cultivars and agronomic management conditions, in general, K has an important effect on fruit quality and stress responses.

## Sulfur (S)

In general, agricultural soils are normally sufficient in sulfur (S). However, soil testing to assess the availability of this element may be beneficial. Sulfur is found in the amino acids cystine, cysteine and methionine. It activates certain enzymatic systems and is a component of vitamins. Sulfur has been found to produce nematicidal compounds and to prime stress resistance. As well, sulfur may impart certain characteristic odors and flavors [84].

When plants face S-deficiency, middle to upper leaves develop a light green coloration [92]. Over time the leaves become more uniformly yellow in coloration. With severe S deficiencies the pale yellow leaves can develop necrotic spotting due to sunburning. The fruit can also be smaller in size, but have normal color. Nitrogen deficiency can be confused with sulfur deficiency. However, N deficiencies begin on the oldest leaves and work their way up the plant. As a result of the burning of coal, atmospheric sulfur provides sufficient levels of the element to prevent deficiencies from occurring, and hence, S deficiencies are rare. Tissue testing will help identify any nutritional disorders. Symptoms begin in the middle part of the plant and move upward. The sufficiency range for sulfur in strawberries vary by source. The widest recommended range is 0.25% to 0.8%. Values lower than 0.25 to 0.35% are considered deficient, while levels above 0.8% are considered excessive [92].

The aroma of fresh strawberries is comprised of a complex mixture of volatile components, with methyl and ethyl esters predominating. Other compounds that contribute to aroma include furanones, aldehydes, terpenes and sulfur compounds [7]. Many factors influence the volatile composition, including cultivar, fruit maturity and postharvest environment [35]. Although important progress has been made just recently, a limited understanding of the mechanisms controlling the synthesis of aroma volatiles still remains. Genes, enzymes, metabolites and the whole pathways involved in the production of aroma volatiles may led to genetic and environmental manipulation to improve strawberry flavor following shipping and marketing.

Concerning parameters of quality, Schulbach et al. [75] monitored methane thiol, hydrogen sulfide, sulfur dioxide, dimethyl sulfide, carbon disulfide, methyl thioacetate, dimethyl sulfide, methyl thiobutyrate, and dimethyl trisulfide after heating strawberry puree at 95 °C for different time points (from 0 to 10 min). After heating 10 min, dimethyl trisulfide increased from 0.11 to 0.41 ng mL<sup>-1</sup>, and dimethyl disulfide decreased from 1.3 to 0.3 ng mL<sup>-1</sup>. Concentrations of methyl thiobutyrate and methyl thioacetate were approximately 6 and 60 ng mL<sup>-1</sup>, respectively, and essentially unaffected by heating. Dimethyl sulfide (cabbage aroma) was not detected in fresh puree but increased exponentially during heating, reaching a value of 500 ng mL<sup>-1</sup> (100 × its odor threshold) at 10 min. Dimethyl sulfide was the major sulfur aroma impact compound in heated strawberry puree and a major contributor to the flavor change associated with heated strawberry puree.

The influence of sodium bisulfite (NaHSO<sub>3</sub>) and benzyladenine (BA) on gas exchange and millisecond delayed light emission (ms-DLE) was investigated using 2-month-old strawberry plants [37]. Results showed the net photosynthetic rate (*A*) in leaves was promoted by both NaHSO<sub>3</sub> and BA. Intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) was significantly decreased by NaHSO<sub>3</sub>. The enhancement of *A* by NaHSO<sub>3</sub> and BA was only a short-term effect, lasting approximately 5 days for NaHSO<sub>3</sub> and 30 h for BA. The enhancement of *A* by the application of low concentrations of NaHSO<sub>3</sub> appears to be associated with increased cyclic electron flow.

Erdal et al. [29] applied elemental S and S containing waste from a S factory, corresponding to 500 and 1000 kg ha<sup>-1</sup> of S, and 20 kg ha<sup>-1</sup> of Fe, from Fe-SO<sub>4</sub> and Sequestrene Fe-138 (Fe-chelate) to the soil where strawberry plants were growing. While soil pH was 8.3 without S application, applied S corresponding to 500 and 1,000 kg ha<sup>-1</sup> from both sources, decreased pH to 7.9 and 7.7 for elemental S and 7.9 and 7.8 for waste application, respectively. Leaf Fe concentration, chlorophyll content, green color intensity and fruit yield increased with single and combined applications of S and Fe. The results showed that S containing waste could be used as an alternative to elemental S for improvement of Fe nutrition in calcareous soils under similar conditions.

Hydrogen sulfide (H<sub>2</sub>S) has been recently found to act as a potent priming agent. Christou et al. [23] applied H<sub>2</sub>S pretreatment of roots resulting in increased leaf chlorophyll fluorescence, stomatal conductance and leaf relative water content as well as lower lipid peroxidation levels in comparison with plants directly subjected to salt (100 mM NaCl) and non-ionic osmotic stress (PEG 10%), thus suggesting a systemic mitigating effect of H<sub>2</sub>S pretreatment to cellular damage derived from abiotic stress factors. In addition, root pretreatment with NaHS minimalized oxidative and nitrosative stress in strawberry plants, manifested via lower levels of synthesis of NO and H<sub>2</sub>O<sub>2</sub> in leaves and the maintenance of high ascorbate and glutathione redox states, following subsequent salt and non-ionic osmotic stresses. Furthermore, gene expression analysis suggests that H<sub>2</sub>S plays a pivotal role in the coordinated regulation of multiple transcriptional pathways including antioxidant, transcription factors and salt responsive genes. Overall, H<sub>2</sub>S-pretreated plants managed to overcome the deleterious effects of salt and non-ionic osmotic stress by controlling oxidative and nitrosative cellular damage through increased performance of antioxidant mechanisms and the coordinated regulation of the SOS pathway, thus proposing a novel role for H<sub>2</sub>S in plant priming, and in particular in a fruit crop such as strawberry.

Santos [74] studied the response of strawberry plants to different rates of preplant S fertilization. The preplant S rates were 0, 25, 50, 125, 200, and 275 lb acre<sup>-1</sup> and elemental S

was used as the nutrient source. Preplant S application did not affect plant canopy diameters or shoot dry biomass. However, leaf greenness increased with preplant S. The foliar concentrations of S and Mg also increased when the S rate reached 50 lb acre<sup>-1</sup>, whereas the application of S rates of 125 lb acre<sup>-1</sup> or higher increased the concentration of Mn in the leaves. Total marketable fruit weight increased by 10% with 50 lb acre<sup>-1</sup> of S in comparison with the non-treated control. There were no further yield increases with S rates higher than 50 lb acre<sup>-1</sup>. Preplant S rates higher than 50 lb acre<sup>-1</sup> did not improve strawberry marketable fruit weight. A similar response was found for strawberry root dry biomass at the end of the season.

Summarizing, sulfur affects strawberry fruit quality and may act as an important priming factor in response to environmental cues such as osmotic stress impaired by salinity and artificial dehydration and pathogen attack.

## Calcium (Ca)

Calcium increases cell wall strength and thickness, and therefore, this is a pivotal nutrient for fruit firmness [27, 84]. Calcium has also been shown to trigger signaling pathways related to growth, development and responses to both abiotic and biotic stresses including pathogen attack. It also improve the N use efficiency [27].

In Ca deficient soils where strawberry plants grow, leaf blades are crinkled, tips fail to expand fully, and becoming black (“tip-burn”); leaf and flower stalks become freckled, frequently exude globules of syrup, and collapse near their mid-points. Fruits develop a dense cover of achenes either in patches or over the entire fruit; fruits are hard in texture, and acid to the taste [25].

In strawberry cv. ‘Nyoho’ the spray of 200 ppm Ca<sup>2+</sup> chelated with carboxylic acids resulted in a remarkable increase of fruit firmness. Skin puncture force of Ca-applied berries was higher. Ca treatment increased ascorbic acid and Ca contents, and maintained fruit soundness by delaying decay caused by gray mold. Ca treatment significantly decreased water soluble pectin (WSP) and increased hydrochloric acid soluble pectin (HSP). After storage at 20 °C for 2 days, WSP increased whereas HSP decreased greatly especially in control berries from the north side of the plastic house in comparison to those grown in the south side [64].

In strawberry plants cv. ‘Cardinal’ and ‘Fern’ grown in a clayey silt loam soil, Markus and Morris [53] tested the supplemental addition of Ca on the nutrimental status of the plants. Mineral nutrient concentrations in dry matter basis in decreasing order were: K, P, Ca, Mg, Al, Na, Fe, Mn, Zn, B and Cu for the spray treatment. Interestingly, concentrations of all other nutrients except Ca were unaffected by supplemental Ca.

Strawberry plants cv. ‘Oso Grande’ and ‘Canarosa’ were grown in sand culture out-of-doors to investigate the effectiveness of supplementary Ca applied to the nutrient solution on plant growth at high salt concentration (35 mM NaCl) [45]. Dry matter, fruit yield and chlorophyll content of stressed plants were less than control plants. Supplementary Ca ameliorated the negative effects of salinity on plant growth and fruit yield, as well as water use efficiency and membrane permeability.

Wójcik and Lewandowski [93] examined the effects of foliar applications of calcium (Ca) and boron (B) on yield and fruit quality of ‘Elsanta’ strawberries grown on a sandy loam

soil with low status of available B. Results showed that fruit and leaves from Ca-treated plants had increased Ca concentrations. Sprays with B increased status of this microelement in fruit and leaf tissues. Fruits sprayed with Ca or B plus Ca were firmer and more resistant to *Botrytis* rot at harvest and after 3 days of holding at 18 °C compared to those of control plots. Moreover, sprays of Ca or B plus Ca increased soluble solids concentration and titratable acidity of fruit after 3 days of holding at room temperature. These results indicate that sprays of CaCl<sub>2</sub> with addition of Tween 20 should be recommended to improve quality and shelf-life of strawberry fruit, particularly in proecological production where application of fungicides is restricted.

Van Buggenhout et al. [89] optimized vacuum infusion (VI), freezing, frozen storage and thawing conditions in order to minimize the texture loss of frozen strawberries. Slow freezing caused severe loss in textural quality of the strawberries. A remarkable texture improvement was noticed when infusion of pectinmethylesterase (PME) and calcium was combined with rapid or cryogenic freezing. The highly beneficial effect of PME/Ca-infusion followed by high-pressure shift freezing (HPSF) on the hardness retention of frozen strawberries was ascribed to the combined effect of the infused PME (53% reduction in degree of esterification (DE) of the strawberry pectin) and the high degree of supercoiling during HPSF. During frozen storage, textural quality of PME/Ca-infused high-pressure frozen strawberries was maintained at temperatures below -8 °C, whereas the texture of PME/Ca-infused strawberries frozen under cryogenic freezing conditions was only preserved at temperatures below -18 °C. Thawing at room temperature seemed to be an appropriate method to thaw strawberries.

According to Singh et al. [78], strawberry fruits harvested from plants, which were sprayed either with Ca or Ca + B had significantly lesser incidence of albinism (6.7 and 6.5%), and grey mould (1.3 and 1.2%) than those harvested from plants sprayed either with B alone or in control. Although B alone could not influence the incidence of albinism and grey mould, it reduced indeed fruit malformation (3.4 and 3.1%) significantly. The lowest marketable fruit yield (149.3 g per plant) was recorded in plants under control, and the highest (179.2 g per plant) in plants sprayed with Ca + B. Similarly, such fruits were firmer, had lower total soluble solids, higher acidity and ascorbic acid content at harvest than those in control. In addition, after 5 days storage, such fruits were firmer and brighter, and have significantly lower TSS (7.9 and 7.8%); higher ascorbic acid content (43.7 and 45.0 mg/100 g pulp) and acidity (1.08 and 1.07%) than those in control or those receiving B alone. Incidence of grey mould was significantly lesser in fruit, which received Ca (2.2%) or Ca + B (1.9%) than those, which received either B (8.1%) alone or those in control (8.4%). These results indicated that pre-harvest foliar application of Ca + B is quite useful for reducing the incidence of disorders and getting higher marketable yield in 'Chandler' strawberry.

Hernández-Muñoz et al. [42] treated strawberries either with 1% calcium gluconate dips, 1.5% chitosan coatings or with a coating formulation containing 1.5% chitosan + 1% calcium gluconate and stored at 20 °C for up to 4 days. Calcium dips decreased surface damage and delayed both fungal decay and loss of firmness compared to untreated fruits. No sign of fungal decay was observed in fruit coated with 1.5% chitosan which also reduced fruit weight loss. Chitosan coatings markedly slowed the ripening of strawberries as shown by their retention of firmness and delayed changes in their external color. To a lesser extent titratable acidity and pH were also affected by coatings. Whilst addition of calcium gluconate to the chitosan coating formulation did not further extend the shelf-life of the fruit, the amount of calcium retained by strawberries was greater than that obtained with calcium dips alone, thus

resulting in increased nutritional value of the strawberries. Subsequently, Hernández-Muñoz et al. [41] showed that the addition of calcium gluconate to the chitosan coating formulation increased the nutritional value by incrementing the calcium content of the fruit.

Chen et al. [18] studied the effects of  $\text{CaCl}_2$  (0, 1 and 4%) treatment on quality attributes and cell wall pectins of strawberry fruits stored at 4 °C for 15 days. Fruits treated with 1%  $\text{CaCl}_2$  displayed better quality attributes, including decay rate, weight loss and soluble solids content. During storage, the chain widths and lengths of water-soluble pectin (WSP), chelate-soluble pectin (CSP) and sodium carbonate-soluble pectin (SSP) decreased. Strawberry softening seemed to be due to modifications of CSP and SSP, especially the side chains.  $\text{CaCl}_2$  treatment significantly slowed the breakdown of CSP and SSP chains by strengthening the ionic crosslinkages among these pectin molecules. These results illustrate the fundamental  $\text{CaCl}_2$  effects and will help improve the application of  $\text{CaCl}_2$  to postharvest fruits.

Using strawberry plants cv. 'Luna' and 'Zanta', Bieniasz et al. [12] showed that foliar fertilization with calcium preparation did not significantly increase the yield and fruit mass of strawberries, however, significantly improved the firmness of the fruit. The application of calcium foliar sprays increased the storage time of fruit and increases the possibility of transport, especially for cultivars with a very delicate fruit.

Calcium carbonate and calcium citrate are the main calcium salts added to foods in order to enhance the nutritional value [13]. Other forms of calcium used in the food industry are calcium lactate, calcium chloride, calcium phosphate, calcium propionate and calcium gluconate, which are used more when the objective is preserving or enhancing firmness. For processed strawberries, calcium chloride has been widely used as firming agent [55].

Dipping treatments favors the dispersion of the solution on the surface of the vegetable. This method has an extra benefit since the enzymes and substrates released from the injured cells during the minimal procedure are rinsed, avoiding oxidation reactions that could lead to browning and off-flavors [80]. Different factors (pH, immersion time, temperature, and concentration) can affect product integrity. With whole strawberries, Suutarinen et al. [82] reported dipping treatments of Ca lasted 15 min.

Coating is also a technique that can be used to enrich minimally processed fruits and vegetables with calcium. Han et al. [39] working with strawberries used a chitosan-based coating formulated with calcium lactate and calcium gluconate. Adding calcium proved to extend the shelf life by decreasing the incidence of decay and weight loss, changes in color, titratable acidity and pH. However, Moayednia et al. [58] showed that coating with calcium alginate had no significant effects on weight loss or physicochemical parameters when compared to control fruit, but it did result in the postponement of visible decay during refrigerated storage. Therefore, a need of more studies on the effects of Ca in coating approaches is needed.

Fruit calcium content and lipoxygenase (LOX) activity in relation to albinism disorder in strawberry was investigated by Sharma et al. [77]. Among strawberry cultivars, 'Etna' had highest incidence of albinism (48.6%) and 'Sweet Charlie' the lowest (16.2%). Dry matter content was lower in albino fruit (5.23%) than normal fruit (7.36%). The concentration of N, P and Mg did not differ significantly, but that of K (1.87 mg g<sup>-1</sup> fresh weight) was notably higher and of Ca (0.105 mg g<sup>-1</sup> fresh weight) was lower in albino fruits than normal fruits. Consequently, the nutrient ratios, N/Ca (9.78) and K/Ca (16.96) were higher in albino fruit than normal fruit. Cultivars differed widely in respect to dry matter, mineral content and nutrient ratios. LOX activity determined on dry weight or fresh weight basis was significantly

higher in albino fruit than normal fruits, with significant differences among cultivars. It appears that calcium and LOX activity may not be the basic cause of albinism in strawberry, but these may be involved in senescence or fruit ripening process, as LOX activity was lower in albino than in normal fruits.

Calcium is involved in plant cell wall integrity and has an important role in improving storage life of several fruits. Addition of calcium to fruit can either enhance resistance of fruit to postharvest pathogens or reduce susceptibility to postharvest diseases and disorders. As an alternative to fungicides, manipulation of calcium nutrition has been suggested as a means of disease management [65].

Motamedi et al. [61] confirmed that Ca increased the post-harvest life of strawberry fruits and had positive effects on plant growth. The combination of 240 mg L<sup>-1</sup> N and 300 mg L<sup>-1</sup> Ca caused the better performance of strawberry plants. Furthermore, Kazemi [46] recently demonstrated that salicylic acid (0.25 mM) and calcium chloride (2.5 mM) spray either alone or in combination (0.25 mM SA+2.5 mM Ca) affect vegetative and reproductive growth. Yield and quality of strawberry plants were improved in low salicylic acid and calcium chloride concentration. Hence, salicylic acid and calcium chloride application can be helpful for yield improvement and prevent of decreasing yield.

Yildirim et al. [94] found that the application of 10 mM foliar Ca(NO<sub>3</sub>)<sub>2</sub> increases plant root dry weight (50%), shoot dry weight (50%), leaf relative water content (8.2%) and membrane permeability decrease (27.4%) at 40 mM NaCl. Phosphorus, Fe and Zn contents in shoots and roots of plants also increased with Ca treatments, but they were still much lower than those of non-salt stress treatment. Sulphur, Fe, Mn, Zn, and Cu contents of roots reached the values of non-salt stress treatment when Ca(NO<sub>3</sub>)<sub>2</sub> was applied.

## Magnesium (Mg)

Magnesium (Mg) ions are found in the center of chlorophyll molecules. As chlorophyll is a key component in the reaction of photosynthesis, which produces energy for growth, Mg ions are therefore essential for plant biology. Magnesium also plays a substantial part in phosphorus transport in the plant; it assists in phosphate metabolism, plant respiration, protein synthesis, and activation of several enzyme systems [54]. Though its pivotal role as nutrient element, just a few studies have been carried out on strawberry crop and postharvest.

Magnesium deficiencies are characterized by marginal yellowing, browning and scorching of older leaf blades; interveinal areas become chlorotic, then necrotic. Young leaves remain normal. Fruit appear nearly normal, except for a lighter red color and a tendency to albinism [25].

Magnesium deficiencies in strawberry plants grown on soils are rather common, but can be easily remediated. The most common source of magnesium is dolomitic. Magnesium sulfate (MgSO<sub>4</sub>) also known as epsom salts, is another way to alleviate Mg deficiencies on soils, and may also be applied to plants as a foliar spray. Other cations such as K can compete with Mg for root uptake, and should therefore be kept in an appropriate balance (4/1, K/Mg) to prevent one of these nutrients from overriding the other, thereby creating a deficiency [86].

In the cultivar 'Tribune' Lammarre and Lareau [48] applied three rates of Mg (0, 25 and 50 kg ha<sup>-1</sup>) and observed a lightly increased fruit yield in the early stages of the experiment, but not on the overall yield after three years of measurements. Additionally, different

concentrations of this element (0, 0.4, 0.7, 1.4 and 2.8 meq L<sup>-1</sup>) were tested on the varieties ‘Seonhong’, ‘Maehyang’, ‘Kaumhyang’ and ‘Seolhyang’ grown in an inert medium. The different concentrations of Mg tested did not affect chlorophyll content. Instead, a clear effect of the genotypes was observed, being ‘Maehyang’ and ‘Kaumhyang’ the varieties that showed higher chlorophyll content [20].

Yildirim et al. [94] showed that the application of 10 mM foliar Mg(NO<sub>3</sub>)<sub>2</sub> displayed the highest alleviation effect in strawberry plants under salt stress (40 mM NaCl), and chlorophyll content showed its highest level. It is important to remind that Mg ions are found in the center of chlorophyll molecules.

Concluding, Ca plays a crucial role in fruit firmness and cell wall structure. Furthermore, Ca affects plant and fruit growth, and mediates responses to salinity. As a second messenger, Ca is an essential element that modulate plant biology overall.

## MICRONUTRIENTS

### Iron (Fe)

As micronutrient, iron (Fe) is required by plants in small amounts, though it forms part of many important compounds and is involved in physiological processes in plants. For instance, iron is involved in the manufacturing process of chlorophyll, and it is required for certain enzyme functions. Fe’s involvement in chlorophyll synthesis is the reason for the chlorosis (yellowing) associated with Fe deficiency. Iron is found in the iron-containing (heme) proteins in plants, examples of which are the cytochromes. Cytochromes are found in the electron transfer systems in chloroplasts and mitochondria. Iron is also associated with certain non-heme proteins such as ferredoxins [43]. Ferredoxins are iron-sulfur proteins that mediate electron transfer in a range of metabolic reactions in plants.

The chlorosis induced by Fe deficiencies is mainly observed in young leaf blades, progressing to bleaching and browning. It may also be observed a slight reduction of fruit size and number of fruit produced per plant [25]. Iron deficiency may not indicate insufficient iron supply from the soil solely. It may be related to various conditions that may affect iron availability, including carbonate levels in the soil, salinity, soil moisture, low temperature, concentration of other elements (phosphorus, calcium), among others. Indeed, Pestana et al. [70] established that iron chlorosis does not result from a small level of iron in soils but rather from impaired acquisition and use of this metal by plants. Calcium carbonate, present in great amounts in calcareous soils, and the resulting large levels of bicarbonate ions, are the main causes of iron deficiency. Iron chlorosis affects several metabolic processes and leads to nutrient imbalances in sensitive plants. Decreased yield and poor quality of fruit resulting from the iron deficiency justify the development of methods to diagnose and correct this disorder. No single approach has been found to solve iron chlorosis satisfactorily, making it one of the most complex nutritional deficiencies known.

Chaturvedi et al. [17] demonstrated that the application of zinc sulphate at 0.4% and ferrous sulphate at 0.2% in strawberry increased the number of leaves (29.93 and 23.24), flowers (2.22 and 3.33), fruit set (2.6 and 2.8), fruits (16.10 and 16.88) and fruit yield (133.82 and 140.47 g per plant); plant height (18.85 and 18.28 cm) and ascorbic acid content (66.1

and 65.94 mg), respectively. Increase in fruit weight (8.12 and 7.98 g) and acidity (0.97 and 0.96%), TSS content (9.42 and 9.330 °Brix) of fruits were also found with 0.2% of ferrous sulphate and 0.4% of zinc sulphate. The number of runners also increased with the 0.4% zinc sulphate. Higher concentration of zinc sulphate resulted in enhanced shelf life of fruits (2.95 days) at ambient temperature. On the other hand, higher concentration of ferrous sulphate had toxic effect on the plant and negatively affected growth, yield and quality attributes.

Kazemi [47] reported that sprays of zinc sulfate at 150 mg L<sup>-1</sup>, iron at 1,000 mg L<sup>-1</sup> and calcium at 10 mM improved number of flowers, weight of primary and secondary fruit. The highest percentage of total soluble solids, titratable acidity and ascorbic acid was attained in fruits treated with zinc sulfate at 150 mg L<sup>-1</sup> and the lowest was achieved in control. In general, spraying zinc sulfate at 150 mg L<sup>-1</sup>, iron at 1,000 mg L<sup>-1</sup> and calcium at 10 mM concentration is recommended for increasing the strawberry yield.

## **Boron (B)**

Boron (B) is essential for good root growth and pollination of the flowers. It is easily leached from the soil and is often deficient. Although boron is often recommended as a nutrient supplement for strawberries, excessive levels can be toxic to the plants, so care must be taken to make sure that the plant has enough, but never too much B [40]. In events of B deficiencies, marginal yellowing and crinkling of young leaf blades, progressing to tip-burn are observed; interveinal areas of leaf blades become chlorotic. Reduced flower size and decreased pollen production, resulting in small, “bumpy” fruit of poor quality [25] are also common in B-deficient strawberry plants.

A positive interaction between B and P was reported by May and Pritts [56], as branch crowns per plant and yield increased with increasing B at a high P level. Other growth parameters such as aboveground plant weight and individual fruit weight were also positively affected by B.

As cited above, there is a positive interaction between Ca and B application on strawberry growth and yield. In the cv. ‘Elsanta’, Wójcik and Lewandowski [93] showed that plants treated with Ca + B were firmer and more resistant to *Botrytis* rot at harvest. In addition, sprays of B plus Ca increased soluble solids concentration and titratable acidity of fruit after 3 days of holding at room temperature. Accordingly, Ca plus B foliar application on strawberry plants cv. ‘Chandler’ caused lesser incidence of albinism and grey mould, as well as higher firmness, acidity and ascorbic acid content [78].

Proper nutrient at the right time increases fruit quality, and yield of strawberry plants. Abdollahi et al. [1] reported that boron (150 and 300 mg L<sup>-1</sup>) increased number of leaves and leaf area, although some quality variables such as vitamin C and total soluble solids were reduced.

## **Manganese (Mn)**

Manganese (Mn) is an essential micronutrient for many plant functions. It participates in the assimilation of carbon dioxide in photosynthesis. It aids in the synthesis of chlorophyll and in nitrate assimilation. Manganese activates fat forming enzymes and functions in the

formation of riboflavin, ascorbic acid, and carotene, as well as in electron transport during photosynthesis. Its deficiency may cause yellowing of young developing leaves; light green develops into very fine, netted veining or clear dotting. Manganese-deficient plants may also show main veining remains dark green, with interveinal areas becoming light-green to yellow, followed by scorching and upward turning of leaf blade margins, as well as decrease in fruit size [25].

Plants of short-day strawberry cv. 'Elsanta' were grown in a greenhouse in order to evaluate the application of different amounts of Mn in the nutrient solution [51]. Manganese-deficient plants displayed a Mn leaf value lower than 20 ppm and leaf deficiency symptoms. On the other hand, at the highest application rate, leaf values of 1,600 ppm Mn were found without any visible toxicity symptoms. In both cases the yield was reduced with 10%. Therefore, a Mn concentration of 10  $\mu\text{mol L}^{-1}$  nutrient solution is considered sufficient for the variety 'Elsanta' grown on peat in normal conditions.

In barberry (*Berberis vulgaris* L.) plants Mehdi et al. [57] reported that the addition of 20 mg  $\text{L}^{-1}$  of Mn as spray to the leaves significantly increased the weight of fruits (20.6 g) and number of fruits (240 fruits) in comparison to control plants receiving only water as spray (18.8 g and 180 fruits, respectively).

In a hydroponic approach, Shahrokhi et al. [76] found that the application of 1.5 g  $\text{L}^{-1}$  Mn decreased number of leaves and increased dry weight of shoot at 3 g  $\text{L}^{-1}$ . Lower number of flower was obtained at higher concentration of manganese sulfate (i.e., 3 g  $\text{L}^{-1}$ ). Number of fruits was greater in plants treated with 1.5 g  $\text{L}^{-1}$  manganese, whereas vitamin C content and total soluble solids in fruits were increased.

## Zinc (Zn)

Zinc (Zn) is a plant micronutrient involved in many physiological functions. Its inadequate supply will reduce crop yields [38]. Zinc plays very important roles in plant metabolism by influencing the activities of hydrogenase and carbonic anhydrase, stabilization of ribosomal fractions and synthesis of cytochrome [5]. Plant enzymes activated by Zn are involved in carbohydrate metabolism, maintenance of the integrity of cellular membranes, protein synthesis, regulation of auxin synthesis and pollen formation [54]. Furthermore, the regulation and maintenance of some genes required for the tolerance of environmental stresses in plants are Zn dependent [14].

Zinc deficiency is the most wide spread micronutrient deficiency problem in crop plants. Almost all crops and calcareous, sandy soils, peat soils, and soils with high phosphorus and silicon are expected to be Zn-deficient. Zinc deficiencies can affect plant by stunting its growth, decreasing number of tillers, chlorosis and smaller leaves, increasing crop maturity period, spikelet sterility and inferior quality of harvested products [38].

Zinc deficiency is easily distinguished by the green 'halo' that develops along the serrated margins of young, immature leaf blades. As the leaves continue to grow the blades become narrow at the base and eventually become elongated with severe deficiency. Yellowing and green-veining are also common in Zn-deficient strawberry plants [86].

With 'Earliglow' strawberry, May and Pritts [56] showed that yield increased with increasing Zn at a high P level, but decreased at a low P level, reflecting an interaction of P

with Zn. Leaf Zn was positively influenced by the level of applied P but not by the level of applied Zn.

Zinc sulphate (0.4%) has been proved to increase the number of leaves, flowers, fruit set, fruits and fruit yield per plant, plant height and ascorbic acid content. Increases in fruit weight and acidity, total soluble solids content of fruits were also found with 0.4% of zinc sulphate. The number of runners also increased with the 0.4% zinc sulphate. Higher concentration of zinc sulphate resulted in enhanced shelf life of fruits at ambient temperature [17].

Abdollahi et al. [1] demonstrated that foliar application of zinc sulfate (100 and 200 mg L<sup>-1</sup>) had positive effects on leaf number, leaf area, length and diameter of petiole, fresh and dry shoot root ratio, yield, total soluble solid, acidity and vitamin C. Zinc prior to flowering was recommend to increase fruit quality and yield of strawberry.

In the cultivar 'Camarosa', the foliar application of paclobutrazol (30 mg L<sup>-1</sup> PBZ) and zinc sulfate (150 mg L<sup>-1</sup> ZnSO<sub>4</sub>) prior to flowering stage increased total soluble solid (8.30%). Leaf area maximized (42.20 cm) by the application of 90 mg L<sup>-1</sup> PBZ and 100 mg L<sup>-1</sup> ZnSO<sub>4</sub>. When applying 100 mg L<sup>-1</sup> ZnSO<sub>4</sub> the longest length of petiole (8.80 cm) were recorded. The treatment of 90 mg L<sup>-1</sup> PBZ along with 150 mg L<sup>-1</sup> ZnSO<sub>4</sub> had the greatest effect on the fruit set (87.10%). Maximum and minimum fruit weight (9.50 and 8.20 g) was observed in treatments of 90 mg L<sup>-1</sup> PBZ along with 150 mg L<sup>-1</sup> ZnSO<sub>4</sub> and control, respectively. In general, all yield and fruit quality traits in plants treated with different concentrations of PBZ and ZnSO<sub>4</sub> had higher value than those of the control plants [52].

## Copper (Cu)

In comparison with other micronutrients, copper (Cu) is of minor importance to strawberries. It plays a role in fixation of N, the uptake of Ca and is an important constituent of chloroplasts [11]. Copper deficiency symptoms are characterized by a uniform light-green color of young, immature leaves; interveinal areas become very light-green with primary veins remaining initially green; gradually, interveinal areas and veins, except for a broad, green border, become bleached [25]. Leaf blades with less than 3 ppm of Cu on dry basis are copper deficient; no specific symptoms of deficiency were observed on fruit of strawberry [87]. For 'Elsanta' grown on perlite, increased Cu concentrations had no significant effect on pollen germination, fruit set, fruit size and subsequent yield, and a nutrient solution containing 0.5 μmol Cu per liter was sufficient to obtain satisfactory growth and fruit quality. At the beginning of harvest, 36% of the Cu in the plants was located in the roots, 32% in the crowns, 17% in crowns and leaves and 1.5% in fruits [51].

## Molybdenum (Mo)

Molybdenum (Mo) is an essential component of two major enzymes in plants, nitrogenase and nitrate reductase. Nitrate reductase is the most well-studied molybdenum-containing enzyme. It catalyzes the reduction of NO<sub>3</sub><sup>-</sup> to NO<sub>2</sub><sup>-</sup> [4].

Since the most important function of Mo in plant metabolism is in the reduction of N sources, molybdenum deficiency may basically resemble nitrogen deficiency [4]. However, some particularities might be identified. For instance, a leaf blade value of molybdenum (Mo)

of less than 0.4 ppm on a dry weight basis, will indicate deficiency. Young mature leaves initially develop a pale green coloration. Necrotic spotting between the veins usually follows. With severe deficiencies marginal necrosis develops. Nevertheless, neither fruit size nor quality are affected appreciably by a mild deficiency of Mo [87, 71]. However, it is shown that vitamin C and sugar content increase linearly with Mo application rates up to 8 kg ha<sup>-1</sup> for 'Redcoat' strawberry grown on light soil, deficient in Mo [16, 66].

### **Nickel (Ni)**

Nickel (Ni) is a recognized essential mineral nutrient element for higher plants, though its agricultural and biological significance is poorly understood. Whereas many proteins contain Ni, Ni nutrition of higher plants and its physiological significance, have received little attention [8].

Nickel, in low concentrations, fulfills a variety of essential roles in plants, bacteria, and fungi. Therefore, Ni deficiency produces an array of effects on growth and metabolism of plants, including reduced growth, and induction of senescence, leaf and meristem chlorosis, alterations in N metabolism, and reduced Fe uptake. In addition, Ni is a constituent of several metallo-enzymes such as urease, superoxide dismutase, NiFe hydrogenases, methyl coenzyme M reductase, carbon monoxide dehydrogenase, acetyl coenzyme-A synthase, hydrogenases, and RNase-A.

Therefore, Ni deficiencies in plants reduce urease activity, disturb N assimilation, and reduce scavenging of superoxide free radical. High Ni concentrations in growth media severely retards seed germinability of many crops. This effect of Ni is a direct one on the activities of amylases, proteases, and ribonucleases, thereby affecting the digestion and mobilization of food reserves in germinating seeds. Ultimately, all of these altered processes produce reduced yields of agricultural crops when such crops encounter excessive Ni exposures [3].

### **Chloride (Cl)**

Chloride (Cl) is considered an essential element, as some plants, but not all, can take up as much Cl as they do some macronutrients. Chloride has a critical role in plant metabolism, essentially along with K in opening and closing of the stomata. It also diminishes plant pathogens infections. Chloride uptake by the plant roots may be affected by nitrates, which have been linked to disease severity. Chloride ions are highly soluble and susceptible to leaching. If potassium chloride is applied during fertilization, Cl deficiencies may be scarce [90].

Chloride and sodium are the main ions contributing to soil salinity in many regions but chloride is an essential element necessary for plant growth, development, as well as biotic and abiotic stress responses. In the cv. 'Selva' and 'Camarosa' grown in hydroponic, Esna-Ashari and Gholami [30] showed that plant growth, total fruit yield, fruit firmness and leaf chlorophyll content were higher in plants grown in the solution containing potassium chloride. When using 1.5 mmol L<sup>-1</sup> magnesium chloride in a nutrient solution, an increase in the height of plants as well as total fruit production was observed. Therefore, adding the

chloride ion to the nutrient solution had no negative effects on fruit quality and leaf chlorophyll content.

According to Bellof and Schubert [10], Cl fulfills several important functions in plant growth and photosynthesis. Former studies indicate an influence of Cl on Mn availability in soils. Due to its high mobility in the vascular system of plants, high Cl concentrations might also be associated with improved Mn transport. Nevertheless, strawberry is characterized as a Cl sensitive plant species. They demonstrated that a moderate Cl nutrition has no negative effect on fruit yield and fruit quality, regarding sugar and acid concentrations of strawberry fruits. Furthermore, Cl does not improve Mn uptake and translocation within the plant. However, the results of the soil experiments suggest a role of Cl in Mn availability, indicating that a moderate Cl nutrition could compensate insufficient Mn supply.

## **BENEFICIAL ELEMENTS**

Selenium (Se) and sodium (Na) are also considered as beneficial nutrients. Sodium can substitute for potassium in regulating the stomata. Vanadium (Va) may be required by some plants, but in very small amounts. Moreover, other elements such as aluminum (Al), cerium (Ce), cobalt (Co), lanthanum (La), silicon (Si), titanium (Ti) and iodine (I) can have beneficial effects on plant growth, development, production and yield quality [72, 85].

While it has been known for some years that these elements have beneficial effects on plant nutrition, a physiological function for strawberry has so far not been established. Therefore, there is a dire need for studying the influence of such elements on strawberry growth, development, production and responses to environmental cues, both of biotic and abiotic nature.

## **CLOSING REMARKS AND RECOMMENDATIONS**

Strawberry is a hybrid species cultivated worldwide for its fruit, which is highly appreciated for its characteristic aroma, bright red color, juicy texture, and flavor. Profitable strawberry production requires careful attention to many cultural practices, including nutrient management.

In order to achieve the best performance of strawberry plants, issues related to plant genotypes, soil types, and environmental factors must also be taken into consideration. An adequate management of nutrient elements is crucial to guarantee not only plant growth and development, but also fruit production and responses to environmental cues. We reviewed how the current experimental data is allowing an integrate management of nitrogen, phosphorus, potassium, sulfur, calcium and magnesium, as macronutrients, as well as the micronutrients iron, boron, manganese, zinc, copper, molybdenum and nickel, and give some cues on beneficial elements.

The analysis of the current literature demonstrates that both macro- and micronutrients display positive but also negative effects on strawberry crop production. Depending on plant cultivars, predominant environmental conditions and soil characteristics, nutrient application may have a definite undesirable effect on fruit quality characters. Quantification of nutrient

availability in soils and nutrient demands by plants are highly desirable. Leaf analysis can help assess the nutrient status (deficiency, sufficiency and toxicity) of strawberry plants and more accurately determine fertilizer requirements, develop or modify fertilizer programs. Results can be interpreted using leaf analysis standards displayed on Table 2.

**Table 2. Leaf analysis standard for strawberry plants [79, 86]**

Nutrient	Deficient	Adequate	Toxic
N (%)		2.5 - 3.5	
P (%)	< 0.1	0.3 - 0.5	
K (%)	< 1.0	1.5 - 2.5	
S (%)		0.1 - 0.2	
Ca (%)	< 0.3	1.0 - 2.0	
Mg (%)	< 0.2	0.4 - 0.6	
Na (mg kg <sup>-1</sup> )		< 0.3	> 0.3
Cl (mg kg <sup>-1</sup> )		0.1 – 0.5	> 0.5
I (mg kg <sup>-1</sup> )		60-200	
Cu (mg kg <sup>-1</sup> )	< 3.0	5.0 – 10.0	
Zn (mg kg <sup>-1</sup> )	< 20.0	30-50	
Mn (mg kg <sup>-1</sup> )	< 30.0	50-350	
Fe (mg kg <sup>-1</sup> )	< 50.0	70-200	
B (mg kg <sup>-1</sup> )	< 25.0	30-50	
Mo (mg kg <sup>-1</sup> )	< 0.5	> 0.5	

Nitrogen has one of the most important effects on strawberry quality. Potassium may influence the uptake of Ca and Mg. A right balance in the ratios of potassium and calcium plus magnesium ( $K/[Ca + Mg]$ ) of the nutrient solution or soil, is important for a balanced uptake of these elements in plants. Boron, zinc and calcium have a direct effect on fruit quality.

When plants are deficient in B and Zn, a reduction of fruit set is evident. Moreover, the deficiency of all three elements reduces fruit size. Calcium is a determinant nutrient for fruit firmness, whereas B and Mo may influence content of vitamin C and sugars in fruits. Interestingly, most of the studies show that P, Mg, Cu, Fe and Mn have no major direct effect on plant growth and fruit quality. Finally, a lack of studies on the effect of beneficial elements (Al, Ce, Co, I, La, Na, Se, Si, Ti and Va) on strawberry crop production is also evident.

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