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CHLORINE NUTRITION OF HIGHER PLANTS: PROGRESS AND PERSPECTIVES

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□ *Chlorine (Cl) occurs predominantly as Cl^- in soil and plant. It is an essential micronutrient of higher plants and participates in several physiological metabolism processes. Its functions in plant growth and development include osmotic and stomatal regulation, evolution of oxygen in photosynthesis, and disease resistance and tolerance. At adequate levels of supply, Cl improves the yields and quality of many crops such as onions and cotton if the soils are deficient in this nutrient. When excessive, Cl can be as a major component of salinity stress and toxic to plants. This paper provides a brief review of current progresses on Cl nutrition of higher plants.*

Keywords: chlorine, crop production, plant nutrition, soil and plant tests

INTRODUCTION

Natural inputs of Cl to soils come mainly from rainwater, sea spray, dust, and air pollution. In addition, human practices, such as irrigation and fertilization, contribute significantly to Cl deposition. The rates of Cl deposition to soils range from 1 to >1000 kg ha^{-1}, depending on location and cultural practices (White and Broadley, 2001). Chlorine occurs predominantly as Cl^- in soil and plants. Chlorine is an essential micronutrient for higher plants and participates in several physiological processes. It is also ascribed as a

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main resource of salinity stress. This paper provides a brief review on the major progresses of Cl nutrition of higher plants.

AVAILABILITY OF CHLORINE IN SOILS

The content of Cl^- varies greatly in soils. The plant available form of Cl is mainly Cl^- anion. Plants may be able to take up some metal-Cl complex such as $CdCl^+$ (Weggler et al., 2004), but with a minimal percentage. The Cl^- anion does not form complexes readily and since mineral soils mainly carry negative charge, Cl^- tends to be repelled from the surfaces of soil particles. Thus the concentration of Cl^- in the bulk solution is greater than in the diffuse layers surrounding soil particles. The movement of Cl^- within the soil is determined by water fluxes, and in particular, the relationship between precipitation and evapotranspiration.

During mineral weathering and soil development, Cl^- is readily leached out at early stages. Therefore, Cl^- concentration in most well-developed soil is low unless there is good input from rainfall, fertilizers, and irrigation. In the arid and semi-arid, Cl^- tends to be accumulated in the soil due to high evaporation/rainfall ratio, which drives salts from deeper soil layers to the surface. In these regions, salt stress and Cl toxicity may pose a challenge to crop production. In contrast, in the humid area, particularly tropical and subtropical regions, high rainfall often results in thorough leaching of Cl^- from soils and subsequent deficiency of Cl^- for plants. Fortunately, the internal requirement of Cl^- for most crop plants is small, and the inputs of Cl^- from rainfall, air pollution, fertilizers as secondary element, and irrigation may suffice their needs for normal growth. Therefore, Cl^- deficiency in crops does not occur frequently. However, with the cleaning of air, water, and increased purity of fertilizers, Cl^- deficiency may become an issue in the tropical and subtropical regions, particularly for those sensitive crops such as onion and kifi. For some crops such as wheat, barley, and corn, application of Cl^- fertilizers may increase their yield, and for cotton, Cl fertilizer can improve fibre quality if the soil is deficient in Cl.

CHLORINE DISTRIBUTIONS AND REQUIREMENTS IN HIGHER PLANTS

Chlorine, existing in plants mainly as Cl^- anion, is distributed in the vegetative organs such as the shoots and leaves. The amount of Cl^- in the nutritional organs is more than 80% of the total amount, and it accumulates more in the lower layer leaves or the elder leaves than the upper or the younger ones (Li et al., 2002). There is limited Cl, varying from 1.0% to 2.9%, accumulated in plant seeds. Using ^{36}Cl as a trace indicator, Tang et al. (1996) found that the distribution sequence of Cl in cotton was: leaf > stem >

root > seed > fiber; for rice the sequence was: shoot > crust > brown rice > root; and for lettuce it was: leaf > shoot > root. The distributions of Cl in soybean, tobacco, tea tree, straw, and amaranth are also similar to the above crops.

The concentrations of Cl in higher plants have been reported by several researchers. Early on, Johnson et al. (1957) suggested a critical Cl concentration in plant tissue of approximately 0.1 g kg^{-1}, which derived from the solution culturing experiments. Approximately 1.5 g kg^{-1} was the critical Cl concentration of above ground plant at head emergence. The average contents of chlorine in plants are in the range of 2–20 g kg^{-1} dry matter (DM) which is typical of the content of macronutrients. In most plant species the chlorine requirement for optimal plant growth, however, is in the range of 0.2–0.4 g kg^{-1} dry matter, i.e. about 10 to 100 time lower (Marschner, 1995). The reported exceptions are kiwifruit, which requires 2.13 g kg^{-1} dry matter in their leaves to maintain healthy growth (Smith et al., 1987); sugar beet (*Beta vulgaris* L.) with concentrations of 0.71 g kg^{-1} dry matter (Terry, 1977); members of the palmae such as coconut (*Cocos nucifera* L.) and oil palm (*Elaes guineensis* Jacq.) with concentrations of 2.49 g kg^{-1} dry matter (Ollagnier et al., 1983; von Uekull, 1984). Soil Cl levels >43.5 kg ha^{-1} (60 cm) or 75kg ha^{-1} (120 cm) were adequate for near-maximum wheat yield.

FUNCTION OF CHLORINE IN HIGHER PLANTS

Stomatal Regulation

Chlorine plays an essential role in stomatal regulation. The opening and closure of stomata is mediated by the fluxes of potassium and accompanying anions such malate and chloride (Marschner, 1995). In plant species such as *Allium cepa,* chloride is essential for stomatal functioning, and stomatal opening is inhibited in the absence of chloride (Marschner, 1995). In coconut a close correlation occurs between potassium and chloride fluxes during stomatal opening from the subsidiary cells into the guard cells and vice versa, during stomatal closure; in chlorine-deficient plants stomatal opening is delayed by about 3h (Marschner, 1995). Impairment of stomatal regulation in palm trees is considered to be a major factor responsible for growth depression and wilting symptoms in chlorine deficient plants (von Uekull, 1985).

Photosynthetic O_2 Evolution Cl^- Anion

A large number of studies have showed that Cl is necessary for the water-splitting reaction, or Hill reaction, in photosystem II. It was shown in spinach chloroplast panicles with depleted chlorine, the photosynthetic O_2 evolution increased with the increase of external Cl^{-1} supply. Besides manganese, chloride plays a fundamental role in the water-splitting system of PS II (Ball et al., 1984). Chlorine may either act as a bridging ligand for stabilization of the oxidized state of manganese (Critchley, 1985), or as a structural component of the associated (extrinsic) polypeptides (Coleman et al., 1987).

Chlorine in plants mainly accumulates in chloroplast, and is essential to photosynthetic function. The chlorine-deficient plant showed leaf symptoms of wilt, chlorosis, necrosis, and an unusual bronze discoloration (Li et al., 2002).

Osmoregulation

The critical level of Cl deficiency is approximately 2 mg kg^{-1} dry weight. However, Cl concentrations in plants generally exceed this critical deficiency level by two orders of magnitude and become important in osmotic adjustment and plant water relations (Flowers, 1988; Marschner, 1995). In this concentration range Cl^- becomes the dominant inorganic anion in the vacuole. In the phloem sap Cl^- concentrations may be in the order of 120 mM and seem to play a role in phloem loading and unloading of sugars (Fromm and Eschrich, 1988). Chloride, together with potassium (K^+), has a particular function in osmoregulation in the grass stigma (Heslop-Harrison and Reger, 1986). The stigma of grasses such as *Pennisetum americium* L. often extend within minutes at anthesis by cell elongation and this is mainly mediated by the rapid transfer of K^+ and Cl^- from the surrounding tissue into the stigma primordium.

In conclusion, Cl^- has important functions in osmoregulation at different levels. At high concentrations in plant (50–150 mM Cl^-)it is a main osmoticum in the vacuoles of the bulk tissue, together with potassium. At low concentrations (1mM Cl^- or below), these osmoregulatory functions of Cl are presumably confined to specialized tissues or cells, such as the extension zones of roots and shoots, pulvini and stigma, and guard cells, where the chloride concentrations may be much higher than the average of the bulk tissue (Marschner, 1995).

Interactions with Other Nutrient Ions in Higher Plants

It was reported that Cl somewhat affects the uptakes and utilities of nitrogen (N), phosphorus (P), K, calcium (Ca), manganese (Mn), silicon (Si), sulfur (S), zinc (Zn), magnesium (Mg), iron (Fe), and copper (Cu) in higher plants (Zhong and Ma, 1993). The studies on rice, soybean, cabbage, strawberry, peanut and spring wheat showed that Cl has the effect of acceleration or antagonism to other ions, for example, the contents of nitrate (NO_3^-), phosphoric acid ($H_2PO_4^-$), and K^+ in plants were found being affected by Cl^- concentration, and Cl has an extremely competitive effect on NO_3^- absorption (Li et al., 2002; Huber and Watson, 1974). The effects on phosphorus remained disputable, according to the report of Ma et al. (1993), the application of Cl-containing fertilizers did not decrease P in potato grown in the P rich soil, and the P concentrations in older leaves and stems were even increased. However, the reverse was true in the study with soybean, which revealed that the relatively higher Cl concentrations in plants influenced P transport to the seeds. Wang et al. (1990) suggested Cl can affect P intake only when the Cl concentration is above 400 mg kg^{-1}. The effects of Cl on K also depend on the level of external Cl supply. Even under low levels of external Cl supply, the plants absorb more K^+ to balance the negatively charged Cl^- in it, however, when Cl^- level is high enough to be toxic, K^+ absorption decrease because of the disordered cell metabolism. The studies on kiwifruit showed that increasing concentrations of Cl^- in the nutrient solution had no consistent effect on the potassium concentrations in the leaves. By contrast, the concentration of chloride in the leaves was influenced in part by the potassium status of the plant. Increasing concentrations of potassium resulted in lower chloride concentrations in the leaves at any given yield. It was also suggested this effect was more likely to be the consequence of chloride simply accumulating in the tissues of the severely potassium-deficient plants than any specific physiological effect (Smith et al., 1987). As Schnabl and Raschke (1980) reported there seemed being a closer association between K and Cl, such as that found in the guard cells of some plants, then the Cl status of the plants would have been expected to have increased with that of K. Yang et al. (1996) also reported that, compared to the treatment of urea (with the same amount of N), the Ca, Mg, K, Mn, Zn, and Cu concentrations increased in the ammonium chloride (NH_4Cl) treated radish and Chinese cabbage. These studies suggested that plant species differ in chlorine's interaction with other ions.

CHLORINE AND DISEASE RESISTANCE AND TOLERANCE IN HIGHER PLANTS

The vast literature on Cl^- is about its role as a major component of salinity stress, which may reduce plant tolerance to pathogens, if not its resistance directly. However, there is also literature reporting Cl enhancing plant resistance to disease, in which fairly large amounts of Cl^- were required. These amounts are far greater than those required to fulfill its role as a micronutrient, but far less than those required to induce effects of salinity. Many diseases in different crops were reported to be suppressed by Cl at the levels of macronutrients. These include: corn (*Zea mays* L.) stalk rot, *Gibberella zeae* (Warren et al., 1975) or *G. fujikuroi* (Younts and Musgrave, 1958); stripe rust on wheat, *Puccinia striiformis* West (Russell, 1978; Christensen et al., 1981, 1982, 1987; Taylor et al., 1983) and downy mildew (*Sclerophthora macrospora*) of millet (*Pennisetum typhoides* L.) (Hedge and Karande, 1978). Chloride may also suppress septoria in wheat, either directly or indirectly through its effects on take-all (Christensen et al., 1982). A number of these studies have distinguished the effects of Cl^- from the other accompanying cations. However, the mechanism of Cl^- effect on resistance is largely unknown (Marschner, 1995).

CHLORINE AND CROP YIELD

Several studies have demonstrated the importance of fertilizing crops with Cl to maintain grain yields. Studies by Fixen et al. (1986a) showed that at least some of the observed yield increases were due to the Cl^- in the fertilizer and that they were quite economical, provided responsive soils could be identified. Several studies showed Cl^- fertilizer, basically applied in the form of KCl, improved the productivity of wheat and other crops in the Great Plains and the Pacific Northwest regions of the USA. Diaz-Zorita et al. (2004) reported in wheat (*Triticum aestivum* L.), with the application of 253 kg ha^{-1}, 7% grain yield increment over the control without Cl^- application was observed. And it was also found chloride fertilizer could promote better vegetative growing conditions, yielding a greater grain number per unit surface. The studies on onion showed onion seems a high Cl-requiring plant, and the onions which received Cl application through irrigation water have healthier, darker green foliage (Randle, 2004). Several studies also have been performed in the staple crops and vegetables in China. These results revealed, for the rice, wheat, rape, Chinese cabbage, and asparagus, increased yield can be obtained through applying more chlorine-containing fertilizer (Li et al., 1989, 1991; Hu et al., 1991; Zhang et al., 1995). After having conducted field trials at 14 sites over a 3-yr period, Fixen et al. (1986a) suggested that the Cl concentration of wheat plants was highly correlated with Cl^- content in the top 60 cm of the soil profile, and the soil Cl levels > 43.35 kg ha^{-1} were adequate for near-maximum wheat yield. The lack of detectable disease was also observed, which indicated that Cl was having a beneficial effect that was more general than disease reduction. In Fixen et al. (1986b), cereal species appeared to differ in their reponsiveness to KCl fertilization. Spring wheat responded significantly at four out of six sites with an average increase of 0.2 Mg ha^{-1}. Barley responded significantly at three out of six sites, whereas oats did not respond to KCl at any of the five locations tested. This study indicated that wheat and barley were more responsive to KCl fertilization than oats.

Yield response to Chloride follows the concept of response of crops to mobile nutrients. This means the yield can be related directly to the amount of Cl, given that this nutrient is the most limiting one in the soil. It is also important to note that Cl is mobile and subject to leaching, so crops grown in soils where the soil Cl is low, such as sandy and sandy loam soils, would benefit more from Cl fertilizer (Freeman and Girma, 2006). Research conducted in

Canada between 1996 and 1998 on clay loam and fine sandy loam textured soils revealed that soil Cl levels were low in all years at the fine sandy loam site and the clay loam site (Roberts, 1999). Freeman and Girma (2006) reported Cl fertilizer significantly increased wheat grain yields in 50% of the sites with 0, 15 and 30 kg Cl ha^{-1} rates, and the increases were more notable on the sandy loam soil. It was found in wheat the yield responded positively to Cl rates less than 50 kg ha^{-1}. Research conducted in the Great Plains of the United States showed that yield response occurs about half the time when plant Cl is between 0.12 and 0.4%, but it occurs 80% of the time when plant Cl concentrations are 0.12% or less (Lamond, 2003).

CHLORINE DEFICIENCY AND TOXICITY

Wilting of leaves, especially at leaf margins, is a typical symptom of Cl deficiency, even in water culture, when plants are exposed to full sunlight (Broyer et al., 1954). With severe deficiency, curling of the youngest leaves followed by shriveling and necrosis may occur (Whitehead, 1985). In palm trees which have a particularly high Cl^{-1} requirement (6 mg g^{-1} dry weight) (Ollagnier and Wahyuni, 1983), besides wilting and premature senescence of leaves, frond fracture and stem cracking are typical symptoms of Cl deficiency.

In leaves and roots, besides cell division, cell extension is particularly impaired in Cl-deficient plants, and in roots this is associated with subapical swelling (Smith et al. 1987) and enhanced formation of short laterals, giving the roots a stubby appearance (Johnson et al., 1957).

In plant species such as red clover with relatively low Cl^{-1} requirements ($<$1 mg Cl g^{-1} leaf dry weight), the demand can be met by a concentration of 100 μM Cl^- in the nutrient solution; at 10 μM Cl^- supply, the shoot dry weight drops to 50% (Chisholm and Blair, 1981), indicating that the selectivity of Cl uptake is not very high as compared, for example, with phosphorus, of which the high requirement can be met by supply of even less than 10 μM P.

The question is often raised as to the occurrence of Cl deficiency under field conditions. Assuming a critical deficiency content of 1 g Cl kg^{-1} shoot dry weight, the crop requirement would be in the range 4–8 kg Cl ha^{-1}, which is about the input from rain in areas far distant from oceans, and about 10 times lower than the input from rain at sits near oceans (Marschner, 1995). However, in highly leached soils with a low Cl input from rain and other sources, Cl deficiency may occur even in plant species with low Cl requirements (Ozanne, 1958). The probability of Cl deficiency and, thus response to chloride fertilizers, increases in plant species with a high Cl requirement such as kiwifruit (Smith et al., 1987; Buwalda and Smith, 1991) and palm trees in particular (von Uekull, 1985; Braconnier and d'Anzac, 1990).

High levels of Cl concentration in soil influence plant growth. Mao (1996) suggested that crop yield or quality was not influenced, but even was promoted for some plant species and sometimes by applying Cl below 100–200 mg kg^{-1} to soil; the negative effects could be observed in some crops when applied amount increased to 200–400 mg kg^{-1}; for most crops the negative effects could be obvious when the applied amount increased to 400–600 mg kg^{-1}; and the yields of most crops decreased rapidly when the applied Cl exceeded 800 mg kg^{-1}. Based on the different endurance abilities of plants to the external Cl (Mao, 1996), Wang et al. (1990) divided the plants into three categories: I) the crops with high Cl endurance, such as corn, sugar beet, grain sorghum, cotton and spinach, can endure the Cl of >600 mg kg^{-1} with no visible negative effects; II) the crops with mid-Cl endurance, such as wheat, rice, cucumber, tomato, cabbage, peanut and grape seedling, can endure the Cl of 300–600 mg kg^{-1}; and III) the crops with low Cl endurance, such as soybean, lettuce, sweet potato, strawberry and apple seedling, can't endure the environmental Cl when it exceeds 300 mg kg^{-1}. The yield of tobacco was reported not to be influenced by the high external Cl, but the quality decreased greatly, so it could not be ascribed as a high Cl endurance plant.

CONCLUSIONS

As a yield- and growth-limiting nutrient, the physiological functions of Cl in higher plants include osmotic regulation, stomatal regulation, evolution of oxygen in photosynthesis, disease resistance and tolerance. Except for some plant species, the average concentrations of chlorine in plants are in the range of 2–20 g kg^{-1} dry matter (DM), which is easy to be met by irrigation, rain, fertilizers, and air pollution. On a worldwide basis there is much more concern about Cl toxicity than deficiency in plants. However, the practices of avoiding fertilizers containing metallic salts of Cl may enhance the possible deficiency of Cl in some areas, especially in high-yielding deep sandy soils with low organic matter. Numerous researches have reported improved crop yield by applying Cl-containing fertilizers for several crops, indicating the necessity of further studies of various cropping systems and soil conditions regarding the need of Cl for improving crop yield and quality. Furthermore, plants differ in their responses to Cl fertilizer and limited information is available on the internal and external requirement of major crops for Cl and previous studies were mainly limited to few cultivars. Future studies on crop yield and quality-Cl availability relationships should be expanded to a wide range of soils and cultivars of crop plants.

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