



The Role of Plant Nutrients in Disease Development with Emphasis on Citrus and Huanglongbing

TIMOTHY M. SPANN* AND ARNOLD W. SCHUMANN

¹University of Florida, IFAS, CREC, Lake Alfred, FL 33850

ADDITIONAL INDEX WORDS. disease resistance, nutrient deficiency, boron, calcium, magnesium, potassium

Mineral nutrients are important for the growth and development of plants and microorganisms, and are important factors in plant–disease interactions. How each nutrient affects a plant’s response to disease is unique to each plant–disease complex, and in general, nutrient–pathogen interactions are not well understood. Plant nutrients may affect disease susceptibility through plant metabolic changes, thereby creating a more favorable environment for disease development. For example, calcium deficiency can lead to membrane leakage of sugars, amino acids, and other low-molecular weight compounds that then become available for pathogen use. Many nutrient metals at elevated concentrations have broad antibacterial properties so pathogens that directly or indirectly reduce these plant nutrients may have an advantage. Relatively little is known about the changes in plant nutrition associated with huanglongbing (HLB) despite its leaf symptoms often being characterized as “nutrient deficiency-like.” Recent analyses comparing symptomatic (blotchy mottle) and asymptomatic leaves from HLB-infected trees and leaves from healthy trees have shown that HLB increased K while Mg, Ca, and B decreased. The micronutrients Zn and Mn, whose deficiency symptoms are commonly seen on HLB-infected trees, were not actually deficient in HLB-infected samples when the dry mass of the samples was corrected for the large amounts of starch accumulation caused by HLB. It remains to be seen whether remedial foliar applications of these or other nutrients can reduce the effects of HLB. Here we provide a brief review on plant nutrition and disease susceptibility, with an emphasis on K, Ca, Mg, and B, and discuss the changes in these nutrients associated with HLB infection in citrus.

Infection of a plant by a pathogen alters the host plant physiology, particularly nutrient uptake, assimilation, translocation, and utilization (Marschner, 1995). Pathogens may immobilize nutrients in the soil rhizosphere, or in infected tissues, or they may interfere with vascular translocation (Dordas, 2008), as in the case of huanglongbing (HLB) or utilization and cause nutrient deficiency or toxicity (Huber and Graham, 1999). Pathogens may themselves utilize nutrients, reducing availability to the plant, and thereby increasing its susceptibility to secondary infections due to nutrient deficiency (Timonin, 1965).

Effects of soilborne pathogens are particularly serious when nutrient levels are below optimum, especially for immobile nutrients. Such infections can cause root starvation and plant death, even though the pathogen itself may not be toxic. In general, healthy, well-nourished plants are less susceptible to pathogens and disease than nutrient-deficient plants. The purpose of this review is to discuss plant nutrition and disease susceptibility with an emphasis on changes in K, Ca, Mg, and B associated with HLB infection in citrus.

POTASSIUM. Added potassium (K) generally reduces the susceptibility of plants to pathogens up to the level required for optimum growth. However, beyond sufficient levels of K, there is no additional benefit from supplying additional K (Huber and Graham, 1999). K-deficiency is linked to plant pathogen susceptibility because of the role K plays in plant metabolism.

Under K-deficiency, the synthesis of proteins, starch, and cellulose is impaired. K is also important in the development of cell walls, which may directly correlate to a pathogen’s ability to enter plant tissues.

CALCIUM. Calcium (Ca) has been identified as an important nutrient in plant disease resistance because of two critical roles that Ca plays in plant growth and development. First, Ca is important in the development and structural integrity of plant membranes. Under Ca-deficiency, compounds such as sugars and amino acids may leak into areas between cells (the apoplast) where these compounds become available for pathogen use (Marschner, 1995). Second, similar to K, Ca is important in cell wall development; plants deficient in Ca are more susceptible to pathogen attack, particularly by fungi.

MAGNESIUM. Magnesium (Mg) is an important component of the chlorophyll molecule, and is associated with rapid growth, cell division, and carbohydrate metabolism (Jones and Huber, 2007). Unlike other macronutrients, the role of Mg in plant disease responses has not been extensively studied. There are few reports of direct relationships between Mg and disease but Mg has been shown to decrease disease severity in one species and increase disease severity in another, even for the same pathogen (Jones and Huber, 2007).

BORON. Boron (B) is the least understood essential plant nutrient (Brown et al., 2002). B plays a direct role in cell wall structure, and, thus likely directly effects pathogen susceptibility. In addition, B plays an essential role in carbohydrate transport through the phloem (Stangoulis and Graham, 2007). Low B can cause phloem to collapse and leaf veins to become “corky” (Marshner, 1995). In addition to its role in cell wall structure and plant metabolism, B is known to be toxic to pathogenic fungi (Pratt, 2000).

Acknowledgments. We thank the FCPRAC for research funding, and Southern Gardens Citrus, McKinnon Corporation, Gardiner Florida Citrus, and Carlton and Carlton Citrus for allowing us grove access for sample collection.

*Corresponding author; email: spann@ufl.edu; phone:(863) 956-1151

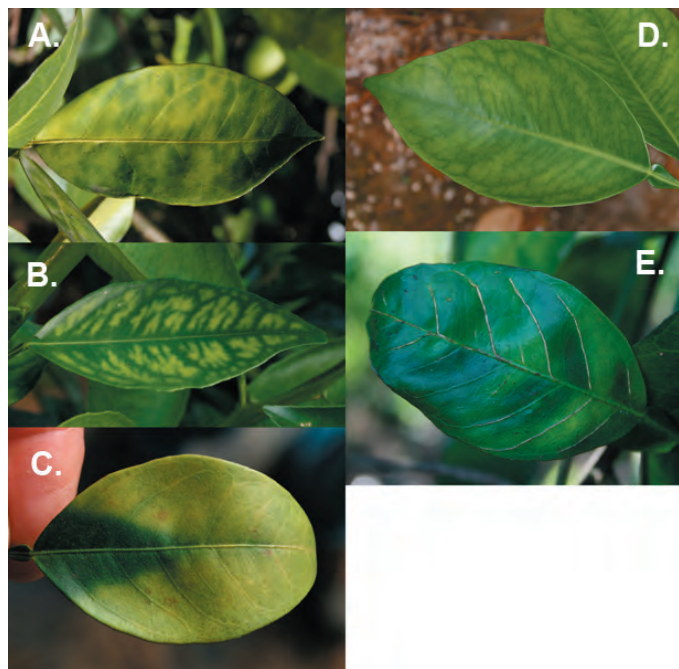


Fig. 1. Leaves showing the blotchy mottle symptom of (A) HLB, (B) Zn deficiency, (C) Mg deficiency, (D) Mn deficiency, and vein corking associated with HLB, but also indicative of (E) B deficiency. Note the lack of symmetry about the mid-vein in the blotchy mottle leaf compared to the nutrient deficient leaves.

Huanglongbing and Nutrition

HLB is a destructive disease of citrus associated with the phloem-limited bacterium *Candidatus Liberibacter* spp. and spread by citrus psyllid insects (Bové, 2006). The characteristic leaf symptom of HLB is commonly referred to as “blotchy mottle” or asymmetrical chlorosis (Fig. 1). These terms describe the irregular yellowing of leaves, in which multiple shades of yellow and green exist on the leaf with no clear boundary between

colors. The yellowing along one side of a leaf mid-vein is not symmetrical to the yellowing along the other side. This lack of symmetry distinguishes HLB from nutrient deficiencies (Fig. 1). Another symptom commonly found on leaves of HLB-infected trees is enlarged, swollen, and corky veins (Fig. 1), also a symptom of B deficiency. In addition, leaves on HLB-infected trees accumulate large amounts of starch (Schneider, 1968), presumably because the bacterium causes phloem plugging, imparting a thick, leathery texture to the leaf. High leaf starch can disrupt chloroplasts resulting in loss of chlorophyll and leaf yellowing (Bondada and Syvertsen, 2005).

The similarity of HLB symptoms and nutrient deficiencies did not go unnoticed by early HLB researchers. Koen and Langenegger (1970) analyzed the macronutrient content of leaves from HLB-infected and HLB-free groves and found that K increased, and Ca and Mg decreased with HLB infection when leaf nutrients were expressed as a standard percentage of leaf dry weight. Leaf Zn content also decreased with HLB infection (Aubert, 1970; as cited in da Graça, 1991). More recently, Pustika et al. (2008) surveyed ‘Siem’ mandarin trees on different soil types in Indonesia and found a decrease in Mg and an increase in K with HLB infection. However, K only increased in trees growing on clay-loam soil and K decreased in trees growing on sandy soil. No hypothesis was offered for this variation due to soil type.

During 2008, a survey was made of ‘Valencia’ and ‘Hamlin’ sweet orange trees [*Citrus sinensis* (L.) Osbeck.], from four commercial citrus groves throughout the citrus growing regions of Florida to assess foliar nutrient content of HLB infected trees compared with healthy trees. We analyzed symptomatic (blotchy mottle) leaves sampled from HLB infected trees (PCR+ = HLB++), asymptomatic (healthy green leaves) leaves sampled from HLB infected trees (PCR+ = HLB+-), and healthy green leaves sampled from healthy trees (PCR- = healthy) non-infected trees (Table 1). Similar to previous reports, significant decreases in Ca, Mg, and Zn, and a significant increase in K was found with HLB. However, with the exception of Ca, the changes were not consistent across all four groves sampled, generally changing only in three of the four groves. In addition to these four nutrients, S decreased in

Table 1. Leaf nutrient concentrations expressed as a percentage of dry weight in leaves collected from HLB infected and healthy ‘Valencia’ and ‘Hamlin’ trees in four commercial citrus groves in FL.

Location (sample date)	Disease status ^z	N	P	K	Ca	Mg	S	B	Fe	Zn	Cu	Mn
		%							ppm			
<i>Valencia</i>												
Dover, FL (Feb. 2008)	HLB ++	2.04 ^{by}	0.11 ^b	1.55 ^a	3.14 ^c	0.27 ^a	0.24 ^c	89.6 ^b	130.8 ^a	42.9 ^b	35.6 ^a	35.2 ^c
	HLB +-	2.46 ^a	0.14 ^a	1.22 ^a	3.60 ^b	0.27 ^a	0.27 ^b	94.4 ^{ab}	146.1 ^a	49.9 ^{ab}	34.8 ^a	42.2 ^b
	Healthy	2.43 ^a	0.13 ^a	1.18 ^b	4.00 ^a	0.27 ^a	0.30 ^a	95.7 ^a	141.6 ^a	60.1 ^a	38.2 ^a	51.9 ^a
Ft. Meade, FL (May 2008)	HLB ++	2.07 ^b	0.10 ^c	1.27 ^a	3.71 ^c	0.29 ^b	0.27 ^b	62.2 ^a	77.6 ^b	16.4 ^b	5.8 ^b	14.1 ^b
	HLB +-	2.47 ^a	0.11 ^b	1.04 ^b	4.25 ^b	0.33 ^a	0.29 ^{ab}	62.0 ^a	99.4 ^a	19.1 ^{ab}	6.8 ^a	15.0 ^b
	Healthy	2.54 ^a	0.13 ^a	0.88 ^b	4.69 ^a	0.32 ^a	0.30 ^a	67.4 ^a	99.4 ^a	21.6 ^a	7.9 ^a	19.7 ^a
<i>Hamlin</i>												
Lake Placid, FL (May 2008)	HLB ++	1.93	0.10	1.64	1.15	0.21	0.17	13	56	8	1	13
	HLB +-	2.68	0.12	1.70	2.82	0.37	0.25	17	75	12	2	18
	Healthy	2.76	0.17	2.06	2.96	0.6	0.43	25	52	29	18	14
Felda, FL (Dec. 2008)	HLB ++	2.48 ^b	0.15 ^a	1.08 ^a	2.84 ^b	0.29 ^c	0.26 ^b	48.4 ^b	51.2 ^a	44.8 ^a	8.9 ^a	107.1 ^a
	HLB +-	2.84 ^a	0.15 ^a	0.81 ^b	4.09 ^a	0.34 ^b	0.31 ^a	53.7 ^b	52.8 ^a	36.3 ^a	8.7 ^a	85.9 ^a
	Healthy	2.70 ^a	0.14 ^b	0.94 ^c	4.32 ^a	0.41 ^a	0.30 ^a	76.0 ^a	55.6 ^a	38.0 ^a	8.9 ^a	83.1 ^a

^zHLB ++ = symptomatic leaves (blotchy mottle) sampled from HLB-infected (PCR+) trees; HLB +- = asymptomatic (healthy green leaves) sampled from HLB-infected (PCR+) trees; and Healthy = healthy green leaves sampled from healthy (PCR-) trees.

^yMeans within a column and sampling location followed by different letters were significantly different, $P < 0.05$.

Table 2. Leaf nutrient content expressed on a leaf area basis for 'Hamlin' trees in the Felda, FL sample shown in Table 1.

Disease status ^z	N	P	K	Ca	Mg	S	B	Fe	Zn	Cu	Mn
----- (mg·m ⁻²) -----											
HLB ++	2670 b ^y	164.3 a	1161 a	3047 b	310 b	284 a	5.20 b	5.53 a	4.87 a	0.968 a	11.63 a
HLB +-	2871 a	151.7 b	813 b	4138 a	348 b	309 a	5.46 b	5.33 a	3.70 a	0.883 a	8.75 b
Healthy	2759 ab	140.8 c	950 c	4407 a	423 a	307 a	7.74 a	5.66 a	3.87 a	0.903 a	8.46 b
P =	0.053	<0.001	<0.001	<0.001	<0.001	0.084	<0.001	0.752	0.186	0.737	0.045

^zHLB ++ = symptomatic leaves (blotchy mottle) sampled from HLB-infected (PCR+) trees; HLB +- = asymptomatic (healthy green leaves) sampled from HLB-infected (PCR+) trees; and Healthy = healthy green leaves sampled from healthy (PCR-) trees.

^yMeans within a column followed by different letters were significantly different, $P < 0.05$.

all four groves, and B and Zn decreased in 3 of 4 groves. These grove-to-grove variations led us to suspect that high leaf starch content associated with HLB infection may be confounding leaf nutrient analyses when presented on a dry weight basis.

Leaf nutrient analyses that report nutrient levels on a percentage dry weight basis may not provide accurate data when analyzing leaves from HLB infected trees because leaf dry weight per unit of leaf area is naturally higher than in healthy leaves due to starch accumulation (Spann and Schumann, 2009). This is important because starch merely increases the dry mass of a leaf without adding any additional nutrients. Thus, when nutrient levels are expressed on a dry weight basis, the high starch content artificially dilutes the percentage of nutrient levels. This apparent anomaly can be corrected for by expressing nutrient levels on a leaf area basis. The leaf thickness and weight per unit area may increase due to HLB-induced starch accumulation, but the total area does not change after a leaf is fully expanded. Table 2 shows how the nutrient analyses for the Felda sample shown in Table 1 change when nutrient content is expressed based on leaf area. The apparent HLB-induced decreases in S and Zn were not significant when the additional leaf mass from starch accumulation is accounted for. Thus, decreases in Zn and S appear to be dry weight dilutions caused by the high starch content of HLB infection. However, the increase in K and decreases in Ca, Mg, and B remain highly significant, indicating that these changes were real with respect to HLB infection.

The HLB-induced increase in leaf K may be the result of the reduced tree growth and an apparent concentration of K caused by HLB. However, this apparent concentration was only seen in symptomatic leaves. Asymptomatic leaves from HLB-infected trees actually showed a significant decrease in K. Since K deficiency is linked to plant pathogen susceptibility, the decrease in K in asymptomatic tissue may actually increase the susceptibility of those tissues. It is likely that the decreases in Ca, Mg, and B are from restrictions of nutrient uptake, transport, or metabolism induced by HLB infection. It remains to be determined whether remedial applications of these nutrients can reduce the effects of HLB, and prolong tree health and productivity.

Literature Cited

- Aubert, B. 1979. Progrés accompli dans la lutte contre le greening des citrus à la Réunion. *Revue Agricole et Sucrière* 58:53–56.
- Bondada, B.R and J.P. Syvertsen. 2005. Concurrent changes in net CO₂ assimilation and chloroplast ultrastructure in nitrogen deficient citrus leaves. *Environ. Expt. Bot.* 54:41–48.
- Bové, J.M. 2006. Huanglongbing: A destructive, newly-emerging, century-old disease of citrus. *J. Plant Pathol.* 88:7–37.
- Brown, P.H., N. Bellaloui, M.A. Wimmer, E.S. Bassil, J. Ruiz, H. Hu, H. Pfeffer, F. Dannel, and V. Romheld. 2002. Boron in plant biology. *Plant Biol.* 4:205–223.
- da Graça, J.V. 1991. Citrus greening disease. *Annu. Rev. Phytopathol.* 29:109–136.
- Dordas, C. 2008. Role of nutrients in controlling plant diseases in sustainable agriculture: A review. *Agron. Sustain. Dev.* 28:33–46.
- Huber, D.M. and R.D. Graham. 1999. The role of nutrition in crop resistance and tolerance to disease, p. 205–226. In: Z. Rengel (ed.). *Mineral nutrition of crops fundamental mechanisms and implications.* Food Product Press, New York.
- Jones, J.B. and D.M. Huber. 2007. Magnesium and plant disease. In: L.E. Datnoff, W.H. Elmer, and D.M. Huber (eds.). *Mineral nutrition and plant disease.* APS Press, St. Paul, MN.
- Koen, T.J. and W. Langenegger. 1970. Effect of greening virus on the macro-nutrient content of citrus leaves. *Farming South Africa* 45:65.
- Marschner, H. 1995. *Mineral nutrition of higher plants.* 2nd ed. Academic Press, San Diego, CA.
- Pratt, J.E. 2000. Effect of inoculum density and borate concentration in a stump treatment trial against *Heterobasidion annosum*. *For. Pathol.* 230:277–283.
- Schneider, H. 1968. Anatomy of greening diseased sweet orange shoots. *Phytopathol.* 58:1155–1160.
- Spann, T.M. and A.W. Schumann. 2009. Citrus greening-associated nutrient deficiency. *Citrus Industry* 90:14–17.
- Stangoulis, J.C.R. and R.D. Graham. 2007. Boron and plant disease. In: L.E. Datnoff, W.H. Elmer, and D.M. Huber (eds.). *Mineral nutrition and plant disease.* APS Press, St. Paul, MN.
- Timonin, M.E. 1965. Interaction of higher plants and soil microorganisms, p. 135–138. In: C.M. Gilmore and O.N. Allen (eds.). *Microbiology and soil fertility.* Oregon State University Press, Corvallis.