Volume 1, Issue 11 November 2005

Barr Report

Barr Report

with Tom Barr

Calcium's Role in Aquatic Macrophytes

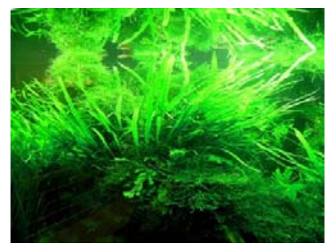
Special points of interest:

- Feature Article "Calcium's Role in Aquatic Macrophtes"
- Calcium Ratios
- Deficiency Symptoms

Inside this issue:

Introduction:

Calcium is an essential plant nutrient. As the divalent cation (Ca^{2+}), it is required for structural roles in the cell wall and membranes, as a counter-cation for inorganic and organic anions in the vacuole, and as an intracellular messenger in the cytosol (Marschner, 1995). Calcium plays a highly significant role in aquatic macrophyte metabolism (Tamura et al, 2001; Kauss 1987). Typical world wide surface water concentration are around 15 ppm, although some surface waters with Calcium bearing rocks and soil may be as high as 30 ppm, with high ranges up to 100ppm and lowest down to 0.2ppm (Florida Lake Watch, 2005). It is often overlooked and discussed in trivial terms in most aquatic plant books dealing with horticulture and often lumped into a section on "Water Hardness". Calcium activates enzymes, is a structural component of cell walls, influences water movement in cells and is necessary for cell growth and division. It is highly important in cell and plant signaling, acting as a type of "nervous system" for the macrophyte. Some macrophytes must have calcium to take up nitrogen and other minerals (Ca^{2+} and a NO_3^- are used at ion balance in the vacuoles). Calcium, once deposited in plant tissue, is immobile (non-translocatable) so there must be a constant supply for growth. Deficiency causes stunting of new growth in stems and also roots. Symptoms range from distorted new growth to black spots on leaves. Yellow leaf margins may also appear. Because Ca^{2+} is not retranslocated to new growth, deficiency symptoms usually appear first on young leaves, but not always, leaf margins may be affected as well as paleness and white tips (see below). Ca^{2+} deficiency also results in impaired root function and may predispose the rice to Fe toxicity. An important distinction here is that most of these deficiencies are take exclusively from terrestrial agricultural crops. Aquatic macrophytes have the option, unlike the terrestrial counter parts, to assimilate nutrients



Continued on page 2

Calcium's role in Aquatic Macrophytes

Calcium is required for structural roles in the cell wall and membranes ….

from the water column, as well as the sediment. There is scant evidence of submersed aquatic macrophyte Ca^{2+} deficiencies and what they appear like in aquatic plants other than in rice and other emergent wetland plants. Given the submersed plant is surrounded by Ca^{2+} dissolved in the water, transport is not very likely to be an issue. It is rare that Ca^{2+} is limiting, thus in most natural systems, DIC (CO2), Nitrogen and Phosphorus are the most common limiting nutrients. Examples of calcium containing minerals are calcite and aragonite which have the same chemical composition, CaCO3, but different crystal structure (called polymorphs) and hydroxyapatite, Ca5(PO4)3 (OH).

"There is scant evidence of submersed aquatic macrophyte Ca2+ deficiencies …It is rare that Ca2+ is limiting ..."

The calcium content (need) of plants varies. In general monocots, grasses such as corn and other grains need less calcium than dicots. In a plant, a Ca: Mg ratio of 1-1.5:1 in rice shoots at initiation of growth is considered optimal. White leaf tips may occur when Ca: Mg is < 1. Note this is specifically for an aquatic macrophyte, not the terrestrial agricultural crops like *Lycopersium* (tomato). Most ratios tend to derived from terrestrial plants in aquatic horticultural advice. While rice is more similar than terrestrial plants, plant species needs can vary greatly. The rice plant's ratio shows how different Ca^{2+} ratios can be expressed. Whether this translates over to all submersed aquatic plants is not clear. Ca^{2+} is less mobile in rice plants than Mg^{2+} and K^+. In the soil, Ca^{2+} deficiency is likely when the Ca^{2+} saturation is <8% of the CEC (Cation Exchange Capacity). For optimum growth, Ca^{2+} saturation of the CEC should be >20%. Many aquatic substrates possess this upper range and contain calcium (Johnson, 2000). Those that have low CEC values, also have high calcium and magnesium content. The water column also typically possesses enough for aquatic Macrophytes as well (0.01-0.1mM). For optimum growth, the ratio of Ca: Mg should be > 3-4:1 for exchangeable soil forms and 1:1 in soil solution. Again, note the differences in the soil and the solution. Here again the solution in hydroponics is not the same as a submersed plants. Most of the suggestions have come from soil based terrestrial agricultural crop systems (3-4:1), not submersed macrophyte plant studies (?). How this influences uptake and demand is not clear. Calcium is a constituent of Ca^{2+} pectates, important cell wall constituents also involved in biomembrane maintenance. It helps in cell wall stabilization as an enzyme activator, in osmoregulation, and in the cation-anion balance. An adequate supply of Ca increases resistance to diseases such as bacterial leaf blight (caused by *Xanthomonas oryzae*) or brown spot (caused by *Helminthosporium oryzae*) in terrestrial systems and it has been speculated may provide some resistance to fungal pathogens in *Cryptocoryne* species. The rate of Ca uptake is proportional to the rate of biomass production (Dobermann and Fairhurst. 2000). This uptake proportion is useful information as it allows us to estimate roughly the amount of Ca^{2+} demand for aquatic Macrophytes relative to other nutrients.

Calcium activates enzymes … influences water movement in cells, and is necessary for cell growth and division.

Continued on page 3

Calcium's role in Aquatic Macrophytes

Some main critical functions are:

- Proper cell division and elongation
- Proper cell wall development
- Nitrate uptake and metabolism
- Enzyme activity
- Starch metabolism

Calcium ratios in *Aldrovandra vesiculosa*

Shoot segments	N	P	Ca	Mg	K	Na
Apices	1.31	0.48	0.17	0.16	1.86	0.35
1st – 6th whorls	0.98	0.30	0.32	0.21	2.11	0.59
7th – 10th whorls	0.66	0.23	0.38	0.16	2.36	0.84
11th – 14th whorls	0.76	0.21	0.50	0.16	2.56	1.03
15th – 18th whorls	0.77	0.16	0.49	0.16	1.93	0.86
Last living whorls	0.10	0.10	0.75	0.16	2.30	0.56
1st dead whorls	0.09	0.04	1.10	0.15	0.65	0.19
Turions	1.76	0.58	0.13	0.15	0.87	0.05

Adapted from (Amadec 1999): Table 1. Mineral content in shoot segments of successive ages of adult *Aldrovandra vesiculosa* and in turions. Last living whorls were still yellow-green, while the successive first dead ones were brownish. Data given in % of dry mass.

"No reliable research has indicated that there is any particular soil ratio of nutrients … Adequate plant nutrition is dependent on many factors other than a specific ratio of nutrients ..."

Of interest is the 1st dead whorl, it has the highest Ca^{2+} content, why? There is a definite trend as the plant becomes older, so does the concentration of Ca^{2+} in the tissues. In general, the rest of the nutrients decline as the plant parts age. It is not clear if this is the case for all aquatic macrophytes. Of interest is the Ca:Mg ratio is 1:1 initially (do new growing tips have high chlorophyll content development yet?), and the Mg^{2+} content remains stable throughout the life of plant whorls, but the Ca^{2+} increases steadily.

%Calcium in (*Stucknia* (formerly *Potamotogen*) *pectinatus*)

ELEMENT	UNIT OF MEASURE	RANGE
Calcium (Ca)	%	0.16 -22

Table 2, Sago pond weed calcium content (*Stucknia* (formerly *Potamotogen*) *pectinatus*) in % dry weight. Sago pondweed is well studied but the parts are often not separated in age groups like the *Aldrovandra vesiculosa* study. This change through time with respect to calcium is something to consider carefully before drawing a conclusion about a ratio or the needs of a macrophyte.

Continued on page 4

Calcium's role in Aquatic Macrophytes

Factors Affecting Ca^{2+} Availability:

Calcium is found in many of the primary or secondary minerals in the soil. In this state it is relatively insoluble. Calcium is not considered a leachable nutrient. However, over hundreds of years, it will move deeper into the soil. Because of this, and the fact that many soils are derived from limestone bedrock, many soils have higher levels of Ca, and a higher pH in the subsoil.

Soil pH
Acid soils tend to have less Ca^{2+}, and high pH soils normally have more. As the soil pH increases above ~ pH 7.2, due to additional soil Ca^{2+}, the additional "free" Ca^{2+} is not adsorbed onto the soil. Much of the free Ca^{2+} forms nearly insoluble compounds with other elements such as phosphorus (P), thus making P less available. Note the slightly high pH. This will govern the precipitation whereas at lower pH's, this will not occur as much.
Soil CEC
Lower CEC soils hold less Ca^{2+}, and high CEC soils hold more.
Cation competition
Abnormally high levels, or application rates of other cations, in the presence of low to moderate soil Ca^{2+} levels tends to reduce the uptake of Ca^{2+}.
Alkaline soil (high sodium content)
Excess sodium (Na) in the soil competes with Ca^{2+}, and other cations to reduce their availability to plants.
Sub-soil or parent material
Soils derived from limestone, marl, or other high Ca^{2+} minerals will tend to have high Ca^{2+} levels, while those derived from shale or sandstone will tend to have lower levels.

Table 3

Interaction

Other cations
Being a major cation, calcium availability is related to the soil CEC, and it is in competition with other major cations such as sodium (Na^{+}), potassium (K^{+}), magnesium (Mg^{++}), Ammonium ($NH4^{+}$), iron (Fe^{++}), and aluminum (Al^{+++}) for uptake by the plant. High K+ applications have been known to reduce the Ca^{2+} uptake in apples, which are extremely susceptible to poor Ca^{2+} uptake and translocation within the tree. Does this also apply to aquatic plants? It does not appear so, although some have suggested it. The question is, how much and will the interaction express itself at stunted new growth that is an assumption when many plants respond quite differently to Calcium levels and deficiencies.
Sodium(Na^{+})
High levels of soil Na will displace Ca^{2+} and lead to Ca^{2+} leaching. This can result in poor soil structure and possible Na toxicity to the crop. Conversely, applications of soluble Ca, typically as gypsum, are commonly used to desalinate sodic (alkaline high Na+) soils through the displacement principle in reverse. This how water softeners work.
Phosphorus(P)
As the soil pH is increased above pH 7.0, free or un-combined Ca^{2+} begins to accumulate in the soil. This Ca^{2+} is available to interact with other nutrients. Soluble P is an anion, meaning it has a negative charge. Any free Ca^{2+} reacts with P to form insoluble (or very slowly soluble) Ca-P compounds that are not readily available to plants. Since there is typically much more available Ca^{2+} in the soil than P, this interaction nearly always results in less P availability.
Iron(Fe^{++}) and Aluminum(Al^{+++})
As the pH of a soil decreases, more of these elements become soluble and combine with Ca^{2+} to form essentially insoluble compounds.
Boron(B^{-})
High soil or plant Calcium levels can inhibit B uptake and utilization. Calcium sprays and soil applications have been effectively used to help detoxify B over-applications.

Table 4. The Ca^{2+} interactions are wide spread and could be many things, not just merely a K+ <=> Ca^{2+} dynamics. It is interwoven into many aspects of plant metabolism and response.

Continued on page 5

Calcium's role in Aquatic Macrophytes

Balances and Ratios:

For many years, there have been a few people who claim that there is an "Ideal" ratio of the three principal soil cation nutrients (K, Ca, and Mg). This concept probably originated from New Jersey work by Bear in 1945 that projected an ideal soil as one that had the following saturations of exchangeable cations 65% Ca, 10% Mg, 5% K, and 20% H. The cation ratios resulting from these idealizes concentrations are a Ca:Mg of 6.5:1, Ca:K of 13:1, and Mg:K of 2:1. It is generally accepted that there are some preferred general relationships and balances between soil nutrients. There is also a significant amount of work indicating that excesses and shortages of some nutrients will affect the uptake of other nutrients. However, no reliable research has indicated that there is any particular soil ratio of nutrients. There is even less research done with respect to rice and certainly few studies done on growth of many of the species kept in the aquarium plant hobby. Over the years, a significant amount of conversation revolved around the concept of the ideal Ca:Mg ratio. Most of the claims for the ideal ratio range between 3-4:1 in aquariums and 5-8:1 in agriculture. Research indicates that plant yield or quality is not appreciably affected over a wide range of Ca:Mg ratios in the soil (Barber, 1995). This appears to be the case for aquatic plants as well. Wisconsin research found that yields of corn and alfalfa were not significantly affected by Ca:Mg ratios ranging from 2.3:1 to 8.4:1 in all cases, when neither nutrient was deficient, the crops internal Ca:Mg ratio was maintained within a relatively narrow range consistent with the needs of the plant. These findings are supported by most other authorities. A soil with the previously listed ratios would most likely be fertile. However, this does not mean that a fertile soil requires these *specific* values (or any other). Adequate plant nutrition is dependent on many factors other than a specific ratio of nutrients. It is rare that any gain in growth is achieved by adjusting this ratio, rather, the base line concentration in terms of limitation is the real determinant. This concept is much less specific than claiming that there is a value to a specific numerical ratio.

"… Calcium influences many biochemical and developmental processes in plants .... It may act as an enzyme component or as an enzyme regulator ..."

Deficiency Symptoms:

Calcium deficiency symptoms can be rather vague since the situation often is accompanied by a low soil pH or very soft water systems. Calcium, for all practical purposes, is not considered to have a directly toxic effect on plants. Most of the problems caused by excess soil Ca^{2+} are the result of secondary effects of high soil pH of high alkalinity in aquatic systems as Ca^{2+} alone does not influence pH. Another problem from excess Ca^{2+} may be the reduced uptake of other cation nutrients. Before toxic levels are approached in the plant, crops will often suffer deficiencies of other nutrients, such as phosphorus, potassium, magnesium, boron, copper, iron, or zinc. Whether this occurs in wetland Macrophytes is not clear, but experience has show the range to be wide with respect to cal-

Continued on page 6

Calcium's role in Aquatic Macrophytes

cium. Calcium deficiency affects growth of water hyacinth more than nitrogen or phosphorous (Desougi, 1984). In the absence of Ca^{2+} the water hyacinth will neither grow nor will it reproduce vegetatively (Desougi, 1984) and even death may occur (Talatala, 1974). Singh et al (1984) reported that the optimum Ca^{2+} concentration for the growth of water hyacinth was 30 mg l-1 and that at higher concentrations it promoted biomass increase and multiplication. Oki et al (1978) reported that the threshold concentration of Ca for growth of water hyacinth as 5 mg/L. Calcium requirement in plants is influenced by the concentration of other cations in the external medium (Wyn Jones and Lunt, 1967). pH also influences the uptake of Ca^{2+}. Okali (1977) reported that low pH makes Ca^{2+} less available in lake water. At low pH the Ca^{2+} concentration has to be several times higher in order to counteract the adverse effects of high H+ concentration on root elongation (Marschner, 1986).

A general typical symptom of Ca^{2+} deficiency is the disintegration of cell walls and the collapse of the affected tissues, such as petioles and upper parts of stems (Marschner, 1986). Sutcliffe and Baker (1974) related damage of meristematic tissues to Ca^{2+} deficiency. However, Ca^{2+} may also cause adverse effects in plants. It precipitates inorganic phosphate in the cells and thus inhibits phosphate based energy metabolism (Fink, 1991). Therefore cytoplasmic concentration of Ca^{2+} has to be kept very low (<1 µM), the excess Ca^{2+} has to be removed. This is done by actively pumping Ca^{2+} out of the cytoplasm into the vacuole and in some cases precipitating it as Ca-oxalate. Because Ca^{2+} is not mobile in the phloem they are therefore not transported out of the leaves and accumulate with age increasing the need for continuous removal out of the cytoplasm (Fink, 1991). The oxalate ion which binds Ca^{2+} is widely distributed in the plant world. Calcium oxalate crystals are distributed among all taxonomic levels of photosynthetic organisms from small algae to angiosperms (Franceschi and Nakata, 2005). It is synthesized inter cellular for charge compensation in nitrate reduction in some plants, while others synthesis malate for the same reason (Marschner, 1986).

The Role of Calcium Oxalate Crystals In Plants:

Calcium oxalate crystals are bound generally intracellularly, often in cells called idioblasts, a specialized cell entirely different from its neighbors. The crystals may occur as single and massive (styloids); as large single prisms or pyramids (prismatic); as needles shaped in packets of as many as 2,000 crystals per cell (raphides), multiple star-shaped (druse), or in fine crystals (crystal sand).The crystals are produced and contained within a vacuole, a membrane bound structure that is found within the cell's cytoplasm, a watery fluid in which the organelles of the cell float. Crystals are formed in crystal chambers formed by membranes. The crystal vacuole is surrounded by a membrane called the tonoplast (Esau, 1977**)**. The mechanism that brings the calcium and oxylate together is unknown. It has been suggested that a calcium pump may be present and that it transports calcium from the cytoplasm to the chamber which is already loaded with oxalate.

Other species of plants have calcium oxalate crystals; the reason for crystal formation varies with the species and with the environmental conditions. In some plants, such as the Jack-in-the-Pulpit, the crystals may be formed to discourage predation from insects, snails, and other animals. One bite of the stalk will prove it to you by the burning sensation caused by its raphides. Water lilies and water hyacinth possess high calcium oxalate content and various crystal structures. Not much has been written on its possible structural or skeletal significance. It is interesting to note that in the case of Nymphaea, the crystals are associated with the cell wall of a structural cell of the leaves. The particular conditions of life have impressed themselves strongly upon the forms and functions of the waterlilies, as previously discussed. Once spread out upon the water surface, the leaves are subjected to the stress of currents in air and water. Perhaps the presence of the crystals provides

Continued on page 7

Calcium's role in Aquatic Macrophytes

some strength. In contrast to other ions, Ca^{2+} to an appreciable extent diffuses into plants passively with water in the transpiratory stream is taken up primarily in the youngest root zone where the endodermis is not yet established, to enter the apoplast . An increase in the concentration of Ca^{2+} in the external solution leads to increase in Ca^{2+} levels in the leaves but not in organs with low respiratory rates such as fleshy fruits and flowers (Marschner, 1986). Ca^{2+} is generally immobile in the phloem and as such it is not transported out of plant leaves, resulting in accumulation with age. Recall the pattern seen in Table 1 with *Aldrovadra*. In the cell, outside the cytoplasm is found in the vacuoles or in cell walls. In the cell walls it may be present as either anionic constituents (pectins) or as CaCO3. Many marine plants deposit CaCO3 as well as marl forming freshwater macrophytes such as *Chara* and *Potamogeton*. Calcium influences many biochemical and developmental process in plants (Zindler-Frank, 1995). It functions mainly outside the cytoplasm in the apoplast. It is a building block for the cell walls, where it holds together the basic lattice work of pectin in the middle lamella and is a stabilizer in cytoplasmic membranes (Taiz and Zeigler, 1998). It may act as an enzyme component or as an enzyme effector, a regulator for active substances such as calmodulin, behave as an osmotic component of cell sap. The number of Ca-oxalate crystals formed depends on calcium supply (Zindler-Frank et al, 1988) Another role played by oxalic acid is that by precipitating Ca^{2+} it makes Ca^{2+} osmotically neutral (Marschner, 1986). Ca-oxalate crystals have specific shapes and locations and are, therefore, of taxonomic importance (Fink, 1991). Determining only a fraction of a mineral nutrient of plant tissue contents - for example, the fraction that is soluble in water (water soluble Ca^{2+}) or in dilute acids (Ca-oxalate) - sometimes gives a better indication of the physiological status of a plant (Marschner, 1986). On the other hand, total Ca^{2+} determination portrays the general nutrient status of a plant (Kinzel, 1989 .There is little literature on the behavior of Ca^{2+} in the water hyacinth, yet, Ca^{2+} plays a very central role in the growth and reproduction of this plant (Desougi, 1984).

Uptake and pathways:

The relative contributions of the apoplastic (between cell walls) and symplastic (through the internal cell) pathways to the delivery of Ca^{2+} to the xylem are unknown (White, 2001). However, the movement of Ca through these pathways must be finely balanced to allow root cells to signal using cytosolic Ca^{2+} concentration to control the rate of Ca delivery to the xylem, and prevent the accumulation of toxic cations in the shoot. Calcium enters plant cells through Ca^{2+}-permeable ion channels in their plasma membranes (White, 2000). Since a high Ca^{2+} cytosol is cytotoxic, a submicromolar cytsol Ca^{2+} is maintained in unstimulated cells by Ca^{2+}-ATPases and H^{+}/Ca^{2+}-antiporters (Sze *et al*., 2000; Hirschi, 2001). These enzymes remove cytosolic Ca^{2+} to either the apoplast or the lumen of intracellular organelles, such as the vacuole (with the anion balance, the NO3-) or endoplasmic reticulum (ER). The rapid influx of Ca^{2+} through cation channels in the plasma membrane, tonoplast and/or ER generates $[Ca^{2+}]_{cyt}$ perturbations that initiate cellular responses to a diverse range of developmental cues and environmental challenges (White, 2000; Sanders *et al*., 2002). What does this mean to aquatic plant hobbyists? It means that Ca^{2+} acts to control many proteins and signals inside the cell and has a diverse set of enzymes that control this process. Basically calcium acts like the plant's "nervous system" to some degree. The toxicity can cause cell damage and the crystals that are formed may be a way to address the excess Ca^{2+} build up in some species. This does not imply high levels in the substrate or water column are bad, it is just a way that plants deal with Ca^{2+} internally inside the cell. By understanding this process, we can better predict the responses from other nutrients in relation to Ca^{2+}as well as what the plant's response to low Ca^{2+} might be like if it becomes limiting.

Continued on page 8

Calcium's role in Aquatic Macrophytes

This is a partial listing of some pathways and responses that are controlled by Ca^{2+}
Cell division (Bush, 1995)
Red light (Shacklock et al. 1992; Malhó et al., 1998)
Blue light (Malhó et al., 1998; Baum et al., 1999)
Circadian rhythms
CO_2 Ca is elevated in guard cells (Webb et al., 1996)
Increasing apoplastic Ca^{2+} (McAinsh et al., 1995; Allen et al., 1999, 2000)
Xylem K^+ loading (De Boer, 1999)
Root cell elongation (Cramer and Jones, 1996; Demidchik et al., 2002a)
Root hair elongation (Wymer et al., 1997; White, 1998; Bibikova et al., 1999)
Senescence
UV-B
Oxidative stress (paraquat, superoxide, H_2O_2, ozone) (Price et al., 1994; Levine et al., 1996; McAinsh et al., 1996; Knight et al., 1998; Malhó et al., 1998; Clayton et al., 1999; Allen et al., 2000; Kawano and Muto, 2000; Knight, 2000; Klüsener et al., 2002; Lecourieux et al., 2002)
Anoxia
Salinity (NaCl)
Hypo-osmotic stress
Mechanical stimulation (motion, touch, wind)

Table 4

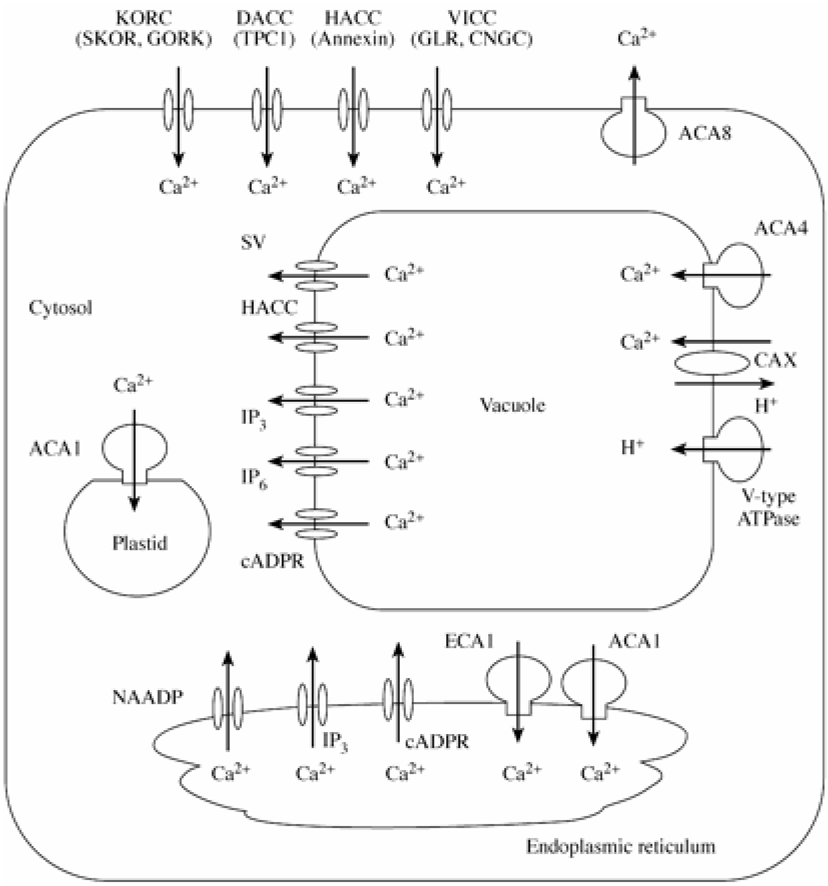
Calcium uptake and movement to the shoot

Each pathway of Ca^{2+} movement across the root confers distinct advantages and disadvantages. The apoplastic (between the cell walls) pathway allows Ca^{2+} to be delivered to the xylem without impacting on the use of Ca^{2+} (cytosolic) for intracellular signaling (White, 1998). Intracellular signaling requires Ca^{2+} (cytosolic) to be maintained at submicromolar levels in the resting cell and to increase rapidly in response to developmental cues or environmental challenges. Since the Ca^{2+} fluxes required for Ca^{2+} (cytosolic) signaling are minute com-

Continued on page 9

Calcium's role in Aquatic Macrophytes

pared with those required for adequate nutrition, both these requirements for signaling might be compromised by high nutritional Ca^{2+} fluxes through root cells (White, 2001). Furthermore, the apoplastic pathway is relatively non-selective between divalent cations (White, 2001; White *et al*., 2002*b*), and its presence could result in the accumulation of toxic solutes in the shoot. By contrast, the symplastic pathway allows the plant to control the rate and selectivity of Ca transport to the shoot (Clarkson, 1993; White, 2001) By regulating the expression and activity of these transporters, Ca^{2+} could be delivered selectively to the xylem at a rate consistent with the requirements of the shoot.



.
Figure 1. Some Ca^{2+} transporter locations and functions in a plant cell. There are various enzymes (ECA 1 and 2, KORC etc) that have specific functions that have been identified genetically. This is not a simple process in plants, nor is it in an animal's nervous system! This figure gives a simplified view of some of the Ca^{2+} processes and locations of uptake and regulation. Realize the uptake for growth demand and regulation inside the cell are different processes.

Calcium as a Ubiquitous Signal in Plants:

All living cells use a network of signal transduction pathways to conduct developmental programs, obtain nutrients, control their metabolism, and cope with their environment. A major challenge for cell biologists is to understand the "language" of these signaling systems. For simplicity, signaling pathways usually have been studied in isolation, with experimenters attempting to define a single pathway through which a given stimulus evokes a response. However, cells are not simple, and for any given stimulus (input), the final response

Continued on page 10

Calcium's role in Aquatic Macrophytes

(output) is likely to be the result of complex interaction, or cross-talk, between multiple pathways (Trewavas and Malhó, 1997; Jenkins 1998). Presumably, this cross-talk evolved as a mechanism to enable a relatively small number of messengers to help cells process a much larger array of potential stimuli in an appropriate fashion. In plant cells, the list of messengers used by signaling pathways includes Ca^{2+}, lipids, pH, and various enzymes. However, no single messenger has been demonstrated to respond to more stimuli than has cytosolic free Ca^{2+}.

Concluding remarks:

Given the nature of the apoplastic and smyplastic pathways and trades offs of each for uptake, having Ca^{2+} in both the water column and the substrate seems to be the best option. Ca^{2+} has many expressions as far a deficiency, many roles within the plant and is poorly understood as far aquatic macrophytes are concerned. Upper ranges are likely very high before they become toxic to plants, the lower limiting levels are likely of more interest to aquarist that wish to maintain soft water. Ratios matter little in terms of K+, Mg^{2+} and Ca^{2+}. Nitrate and calcium play a significant role balancing the cation/anion ratio inside the plant cell. A great deal is yet known about Calcium's role in aquatic plants, but in the future, many of the roles will uncovered and addressed. As aquarist, we can see how the plants respond to the various levels of calcium as long as we also ensure the other parameters are non limiting and stable. That is key to uncovering the ranges for particular plants and can cause great confusion when not addressed.
Conversions for Ca^{2+} and Mg^{2+} from CaCO3 equivalent numbers: (4.1 x Mg^{2+} ppm) + (2.5 x Ca^{2+} ppm)/17.86 = GH (in degrees)

References:

Barber, S. 1995 Soil Nutrient Bioavailability: A Mechanistic Approach 2nd ed. Wiley, John & Sons, Inc.
Edited by L. A. Desougi. H.J. Dumont Edited by A. I. Moghraby 1984. Limnology and Marine Biology in the Sudan. Dr W Junk Pub Co

Dobermann A, Fairhurst T. 2000. Rice. Nutrient disorders & nutrient management. Handbook series. Potash & Phosphate Institute (PPI), Potash & Phosphate Institute of Canada (PPIC) and International Rice Research Institute. 191 p.

Esau, K 1977, Plant Anatomy. 576 pages 2nd Edition edition John Wiley & Sons Canada, Ltd
FINK, S. 1991. Comparative microscopical studies on the patterns of calcium oxalate distribution in the needles of various conifer species. *Bot. Acta* **104:** 306-315.

Franceschi V. R. and Nakata, P. A. 2005**.** 2005 CALCIUM OXALATE IN PLANTS: Formation and Function Annual Review of Plant Biology Vol. 56: 41-71 June.

Johnson, J. Substrates for the planted aquarium. 2000. http://home.infinet.net/teban/jamie.htm

Kauss H., Some Aspects of Calcium-Dependent Regulation in Plant Metabolism

Annual Review of Plant Physiology, June 1987, Vol. 38, Pages 47-71

Marschner, H. 1995, 1986. Mineral Nutrition of Higher Plants. Academic Press, London.
OKALI, D.U.U. and ATTIONU, R.H. 1974. The quantities of some nutrient elements in *Pistia stratiotes L.* from the Volta Lake. *Ghana Jnl Agric. Sci.* **7:** 203-208.

Continued on page 11

Calcium's role in Aquatic Macrophytes

Oki. Ito, M. and Ueki, K. 1978. Studies on the growth and reproduction of water hyacinth, *Eichhornia crassipes* (Mart.) Solms. 1. Effect of nutrients on the growth and reproduction. *Weed res., Tokyo* **23:** 115-120.

SINGH, H.D., NAG, B.,SARMA, A.K., and BARUAH, J.N. 1984. Nutrient control of water hyacinth growth and productivity. In G. Thyagarajan (Ed) Proc. Int. Conf. Water Hyacinth. UNEP, Nairobi p243-263.

SUTCLIFFE, J.E. and BAKER, D.A., 1974. *Plants and Mineral salts.* Edward and Arnold, London.

Talatala, R.L. 1974. Some aspects of the growth and reproduction of water hyacinth *Eichhornia crassipes* (Mart.) Solms. Southeast Asian Workshop on aquatic Weeds, Malang, June 1974. mss. 27pp

Tamura S., Kuramochi H. and Ishizawa K. Involvement of Calcium Ion in the Stimulated Shoot Elongation of Arrowhead Tubers under Anaerobic Conditions Plant and Cell Physiology, 2001, Vol. 42, No. 7 717-722

WYN JONES, R.G. and LUNT, O.R. 1967. The function of calcium in plants. *Bot. Rev.* 33**:** 407-426.

Zipkin, Isadore, 1973. *Biological Mineralization*, John Wiley & Sons, NY.