Calcium Offers Most Crop Per Drop

Of key importance in promoting water-use efficiency

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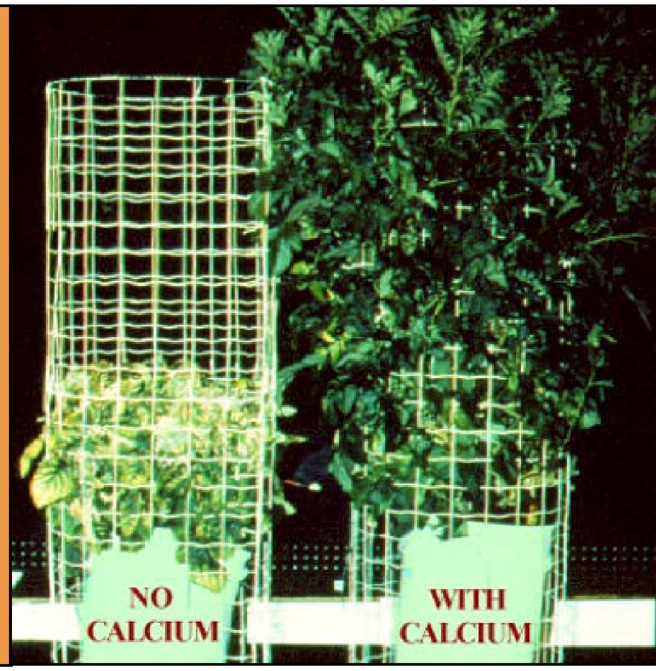
Summary: *Amongst the tools we have available for effective crop production is calcium fertilization. Its beneficial effects in terms of crop yield, fruit quality, and plant health are well known. Most importantly, it increases water use efficiency (WUE) and can be incorporated into a drought stress management plan.*



In previous Fluid Journal editions, we were informed about current water scarcity problems and the challenges created for production agriculture. This topic is very timely since it is elementary that plants and fertilizer will neither survive nor function without water. In these articles, the authors suggested increasing the efficiency of our water use via:

1. Optimum irrigation systems
2. Limiting water loss during delivery to the systems.

But, can we optimize plant water usage as well? Can specific nutrients applied during fertilization maximize available water uptake/usage by plants?

Recent research during the past few decades indicates that nutrients can play a vital role in plant (WUE). Specifically, calcium fertilization will be the focus of our attention here.

Calcium's role

We learned long ago that calcium is essential for cell wall development/ thickness, plasma membrane structure/ water regulation as well as nutrient uptake, and cell division or mitosis. We now know that calcium and calmodulin (calcium modulated protein—CaM) act as a messenger molecule to initiate plant protection mechanisms, aid in hormone responses and control plant water relationships. How then, does calcium/ CaM help increase a plant's (WUE)?

Growth under drought

In the chloroplasts of plant cells, oxygenated radical compounds are formed during photosynthesis. Under normal growing conditions, these compounds are eliminated by the plant. But during drought stress, they can accumulate and attack and damage the plasma membranes of cells, causing water and nutrient leakage at the cellular level.

To control these radical compounds, the plant releases mobile Ca stored in vacuoles to stabilize and maintain plasma membrane integrity, as well as control oxygenated radical concentrations.

Therefore, we can observe the effect of calcium mitigating oxygen radical (H_2O_2- hydrogen peroxide) concentrations in plants under drought stress (Figure 1).

Maximizing cellular water content with minimal damage to the plasma membrane is the result (Figure 2). Without water soluble calcium availability to the plant, damage to the plasma membrane can:

- greatly reduce the water content of plants during drought stress
- reduce plant growth
- limit yield.

Water uptake

To maximize water uptake efficiency, plants growing under drought conditions will require a large healthy rooting system for maximal root surface area to extract available water from the soil. So a large root mass with a large number of root hairs is beneficial. The root hair zone is the most water permeable in the rooting system and increases the root diameter, promoting increased water uptake.

Calcium plays a vital role in root (Figure 3) and root hair production (Figure 4), since it is a major nutritional component of roots and aids in cell division during root and root hair development.

With the increased production of larger roots and root hair with calcium application, rooting systems have greater surface area and become significantly more effective in increasing available water uptake by 55 percent in a sandy soil on a theoretical basis (Figure 5).

During drought stress, plants release abscisic acid (ABA), a hormone that increases water conductivity (movement of water from roots to shoots) in the plant. With or without ABA, Ca also increases water conductivity. With ABA and Ca, water conductivity is significantly increased (Figure 6).

So, water uptake efficiency, maximal root and root hair mass, and optimal water conductivity are necessary for strong healthy productive plants during drought. Calcium plays a vital role in both plant mechanisms.

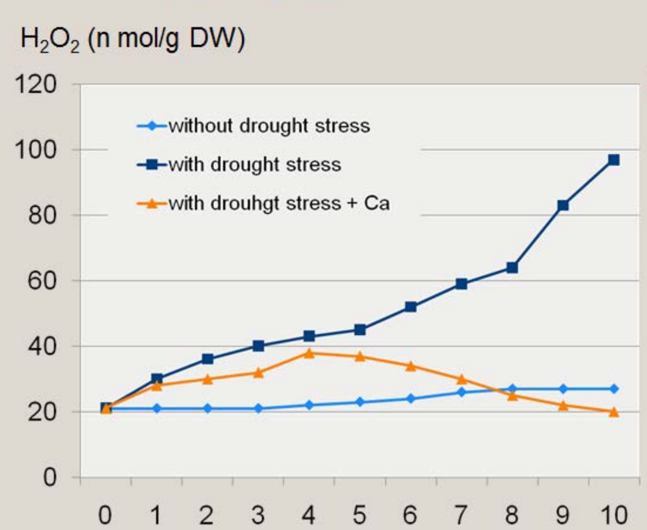
Transpiration

Stomata. Available soil water is taken up by plant roots and translocated to the xylem, which moves the water in a continuous flow into leaves. Water is converted to water vapor near the stomata and when open, escapes into the atmosphere as the plant acquires CO_2 and releses O_2. Stomatal transpiration, as described, accounts for 90 to 95 percent of the water transpired through the leaves.

The ability of the plant to regulate its stomatal opening and closing is imperative in order to obtain a carbon source for photosynthesis and to limit water loss from tissue and prevent desiccation. Tissue damage or plant death can occur when plant tugor is low and the stomata are open.

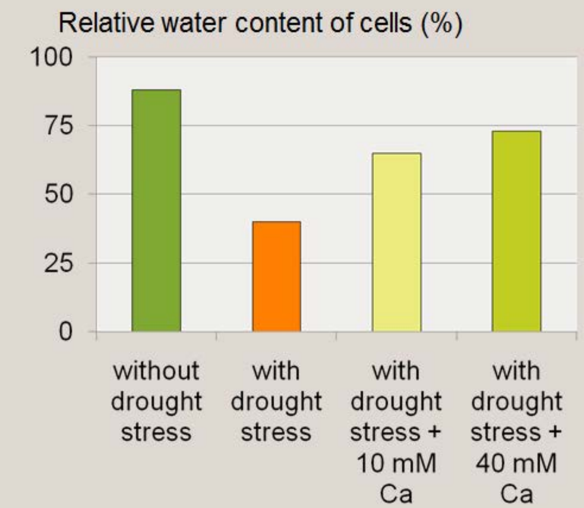
It is well known that potassium is key

Figure 1. Ca lowers the concentration of oxygen radicals (e.g. H_2O_2) in the cell at drought stress



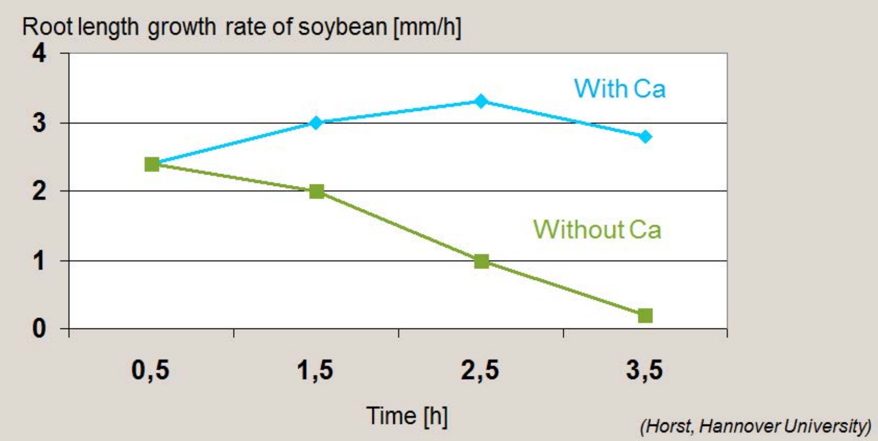
Method: In a cell tissue culture of a traditional Chinese medical crop (Liquorice), water stress was induced by addition of 10 % polyethylene glycol (PEG) with and without 40 mM/l Ca.

Figure 2. Ca maintains the water content of cells under drought stress



Method: In a cell tissue culture of a traditional Chinese medical crop (Liquorice), water stress was induced by addition of 10 % polyethylene glycol (PEG). Different Ca concentrations were applied to the growth medium (10 and 40 mM/l Ca)

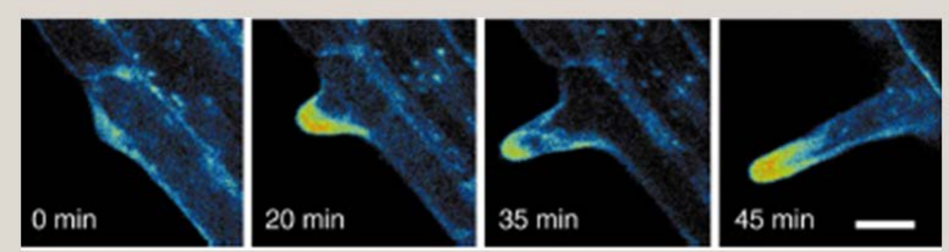
Figure 3. Root growth is strongly depending on sufficient Ca supply by the soil



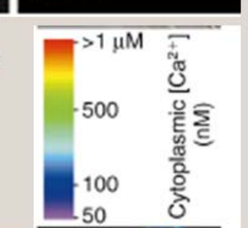
(Horst, Hannover University)

Figure 4. Ca is essential for root hair growth

A tip-focused Ca gradient in root hairs is a pre-requisite for root hair growth; Here Ca leads the direction of tip growth and is a crucial component of the tip-growth machinery.



- **Gradients in cytoplasmic Ca associated with tip growth of Arabidopsis roots hairs.**



in stomatal regulation. Potassium ions are actively transported (requiring biochemically derived energy) into guard cells around the stomata. With the change in osmotic potential, an influx of water hydrates and expands the guard cell, resulting in a "swelling" and closing of the stomata. But we also know that increasing calcium concentration in the apoplast near the guard cells leads to stomata closure and a decreasing calcium concentration leads to opening of the stomata (Figure 7).

So, calcium also plays a role in plant water efficiency, like potassium, but we do not know unequivocally the mechanism involved. Some hypotheses include calcium signaling the initiating of ATP formation and energy production for active transport of potassium into the guard cells. Regardless of mechanism, it is certain that calcium controls stomatal openings. Plants with a low available calcium status cannot fully close their stomata, which results in tissue desiccation pictured in the potato photo shown at the lead of this article.

Cuticle. The cuticle is a waxy resinous material covering the epidermis of leaves and other plant parts. As water vapor moves through the leaf, approximately 5 to 10 percent of the water transpired by the leaf is lost through breaks in the cuticle and is termed cuticular transpiration. Some plant species, growing in a desert environment, have thick cuticles while others do not. Generally, the thickness of the cuticle decreases the amount of water vapor lost. However, when stomata are closed, higher rates of cuticular transpiration can occur.

Plant-available calcium helps reduce cuticular transpiration. Stronger thicker cell walls create a barrier to reduce water loss. Wrapper leaves of lettuce, for example, exhibit a significant water loss reduction through the cuticle with increasing calcium concentration (Figure 8).

Summing up

Considering all of the beneficial effects of calcium nutrition in terms of yield, fruit quality, and plant health, it is also appropriate to consider that sufficient calcium supply to plants is necessary to increase plant WUE and be incorporated into a drought stress management plan. We have observed that:

- Calcium protects cell membranes against drought-induced oxidative stress
- With calcium, water content of stressed cells is maintained
- Calcium improves water uptake and transport to the shoot
- Calcium reduces transpiration losses.

Given the challenge of water scarcity, we must use all of our tools to address the challenge. A crop with good drought stress management will produce greater harvest per given amount of water, resulting in higher WUE or, in European terminology, "most crop per drop." Calcium fertilization is one of our important available tools.

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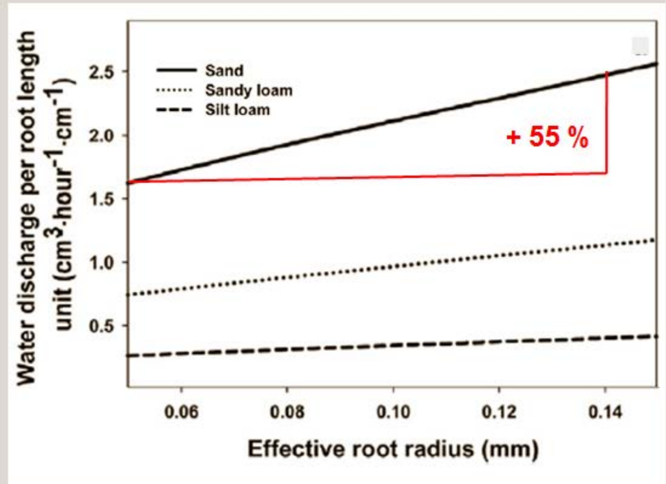
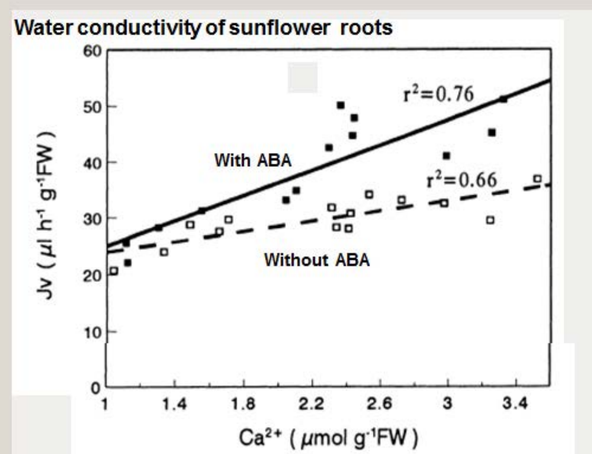
Figure 5. Root hair enhances effective root radius, which improves water uptake



Simulation of water uptake per unit root length at different root diameters.

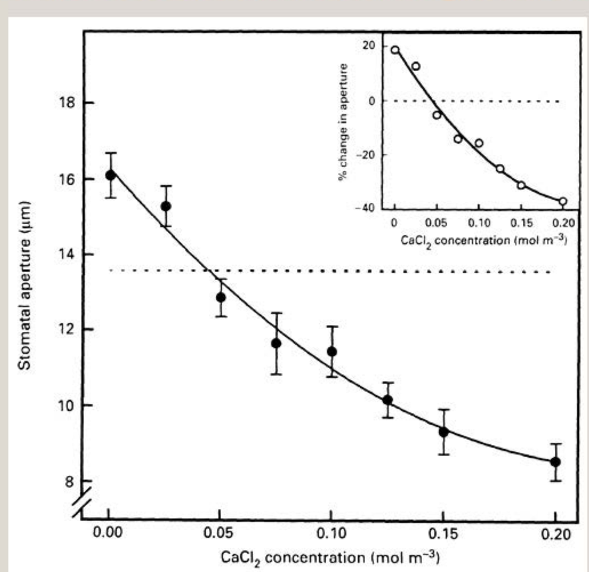
e.g. a single root 1 mm in diameter with root hairs 1 mm in average length, growing in sand, will improve the water uptake rate per unit root length by 55%.

Figure 6. An adequate Ca status improves water conductivity of roots and its sensitivity to ABA (abscisic acid, a stress hormone)



- Increasing the water conductivity of roots appears to be a plant adaptation to drought stress. Water conductivity increases with abscisic acid (ABA), a stress hormone produced and released by the plant during drought stress.
- Increasing Ca supply enhanced
  - water conductivity of sunflower roots.
  - their sensitivity to ABA.

Figure 7. Stomata opening is controlled by Ca concentration outside the guard cells (apoplast)



Response of open stomata in epidermis cells of C. communis to Ca in the incubation medium after 3 hours; main figure = absolute stomatal aperture; inserted figure = relative change compared to initial value

Figure 8. A good Ca status reduces the water losses through the cuticle

- **Ca helps the plant to reduce transpiration losses during the night, when the stomata are closed.**

Transpiration in relation to leaf area [g H_2O/m^2xh]