

Nitrogen Metabolism During Stress of the Hass Avocado

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Avocado trees are subjected to varying degrees and different forms of stress. Stress can be caused by abiotic factors in the tree's environment: salinity, mineral nutrient deficiencies and toxicities, high or low temperatures, and water-deficit. The avocado tree has a number of "built-in" mechanisms for coping with stress. These mechanisms are elicited in response to stress to compensate for the physiological changes it caused and to maintain the normal biochemical balance of the tree. These homeostatic mechanisms preserve tree health. The results of our current research suggest that we have identified a key homeostatic mechanism that compensates for a physiological change in plant tissues caused by a number of different abiotic stresses. We have been investigating the hypothesis that any stress that suppresses the growth of a plant or causes carbohydrate depletion will result in the accumulation of ammonia (measured as the combined pool of $\text{NH}_3\text{-NH}_4^+$) in young and old leaves as an early response of the plant to stress. The reduction in growth can be as dramatic as inhibition of shoot growth, or as subtle as failure of individual leaves to fully expand. As part of our hypothesis, we are testing the corollary that stress-tolerant plants maintain homeostasis by detoxifying their cells of ammonia through increased biosynthesis of arginine. When this homeostatic mechanism fails, ammonia accumulates to toxic levels and results in characteristic leaf symptoms, e.g., tip burn, margin necrosis, and increased leaf abscission (Rabe and Lovatt, 1986; Nevin and Lovatt, 1987).

Are there reasons of practical importance for studying the accumulation of ammonia during abiotic stress? Water costs are now as high as 50% of the gross revenue in some avocado-growing areas of California. To cut costs, growers have reduced the number of irrigations applied later in the season. This leads to the accumulation of levels of ammonia toxic to the leaves, resulting in leaf damage, reduced photosynthesis, and leaf abscission (Nevin and Lovatt, 1987). The concentration of ammonia in the youngest, fully expanded leaves of Hass avocado trees (*Persea americana* Mill) on clonal Duke 7 rootstock increased during water-deficit stress: compare $1508 \pm 102 \mu\text{g NH}_3\text{-NH}_4^+$ per g dry weight leaf tissue from well-watered control trees to $2061 \pm 248 \mu\text{g}$ per g dry weight leaves from water-deficit stressed trees (Nevin and Lovatt, 1987). Secondly, the availability of irrigation water of good quality is becoming increasingly limited. High boron and saline soils are becoming impediments to avocado production in California.

Salinity alters nitrogen metabolism and causes $\text{NH}_3\text{-NH}_4^+$ to accumulate to toxic levels

in leaves of herbaceous annuals (Lovatt, 1986). The amount of ammonia that accumulated increased in parallel with the increased amount of salt added, and with the length of time that the plants were grown in a saline environment. This work needs to be extended to woody perennials, especially to avocado, which is very sensitive to salinity.

Supplying nitrogen for crop production by application of commercial nitrogenous fertilizers represents a significant expense to the grower. The accumulation of $\text{NH}_3\text{-NH}_4^+$ in leaves of avocado trees grown under reduced irrigation, or under saline conditions, suggests that nitrogen fertilization probably needs to be managed differently if growers are going to reduce irrigation or if salinity problems exist in a grove. Certainly, it is essential to determine if the ammonia that accumulates during stress comes from the reduction of nitrate fertilizer to ammonia, from diminished protein synthesis and subsequent degradation of unused amino acids, or from some other sources in order to develop the best cultural practice to prevent the accumulation of ammonia to a toxic level during stress.

Damaging side effects of stress. The side effects of stress are damaging to the tree. Ammonia is toxic. At high concentrations, it causes cell death in leaves and shoots. This results in premature leaf abscission and shoot dieback. The loss in tree canopy diminishes the photosynthetic capacity of the tree. The reduced photosynthetic area provides less carbohydrate and energy to the tree for growth, maintenance, repair, and reproduction. Knowledge of the homeostatic mechanisms operating during stress, especially an understanding of why specific coping mechanisms like arginine biosynthesis fail to remove ammonia during some stresses, but not others, or in some plants, but not others, may provide a key for improving avocado tree health and longevity.

Stress can maximize productivity. It is important to understand the physiological changes brought about by abiotic environmental stresses and the homeostatic mechanisms that are elicited by each stress, because some stresses when not excessive in duration or severity do improve tree crop productivity. For tropical and subtropical tree crops such as citrus, avocado, coffee, lychee, and mango, flowering is recurrent under tropical and subtropical conditions due to the tropical phylogenetic background of these species, unless synchronized into a well-defined period of concentrated bloom by external conditions. Flower formation in tropical and subtropical species is promoted by drought or low temperature followed by restoration of climatic conditions favorable for growth (Monselise & Halevy, 1964; Monselise & Goren, 1969; Monselise, 1978, 1985; Southwick & Davenport, 1986).

Results of research in my lab employing either low temperature or water-deficit stress to induce flowering in healthy trees of 'Washington' navel orange (*Citrus sinensis* L. Osbeck) and 'Frost Lisbon' lemon (*Citrus limon* L. Burm), respectively, demonstrated that floral intensity (flower number) increased with increased duration or severity of the stress ($p < 0.01$). Of all the parameters measured, only the leaf concentration of $\text{NH}_3\text{-NH}_4^+$ changed in a manner that paralleled both the degree of stress and flower number ($p < 0.01$). Furthermore, under minimal, non-inductive stress conditions (either low-temperature or water-deficit), which result in a low flower number that is not significantly different from the unstressed control trees, floral intensity was increased 2.5-fold by artificially raising the leaf content of $\text{NH}_3\text{-NH}_4^+$ through the foliar application of low biuret

urea. The number of flowers produced by urea treated trees was significantly greater ($p < 0.001$) than that of minimally stressed trees not treated with urea and equal to the number of flowers produced by trees receiving maximum stress. While leaf carbohydrate content did not change in a manner that was significantly correlated with flower number, results of experiments employing carbohydrate-depleted trees provided evidence suggesting that there was a threshold level of starch that must be available for maximum flowering to occur.

Thus far, we have been able to induce flowering in avocado using low temperature, but not water-deficit stress. The water-deficit stress treatment employed to induce flowering in lemons results in the accumulation of ammonia to a level toxic to Hass avocado leaves and shoots. Leaf tip burn, margin necrosis and leaf abscission, as well as shoot dieback, result when the Hass avocado is subjected to the same degree of water-deficit stress used to induce flowering in *citrus*. We suspect that avocado is more sensitive to water-deficit stress than *citrus*. Thus, more moderate stress should be used to induce flowering in avocado. If this proves to be the case, we will be able to take the first steps in learning to manipulate the time and intensity of avocado bloom and the resulting harvest to bring varieties to market when the price is the highest.

Knowledge provides a key. With a greater understanding of the physiological changes caused by stress and the homeostatic mechanisms that maintain tree health during stress, we hope to be able to minimize the deleterious effects of abiotic environmental stresses on avocado fruit production and maybe, just maybe, make stress work for us in the market place.

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