

Physiology of Sodium Management in Pistachio: Stem Adaptations

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INTRODUCTION

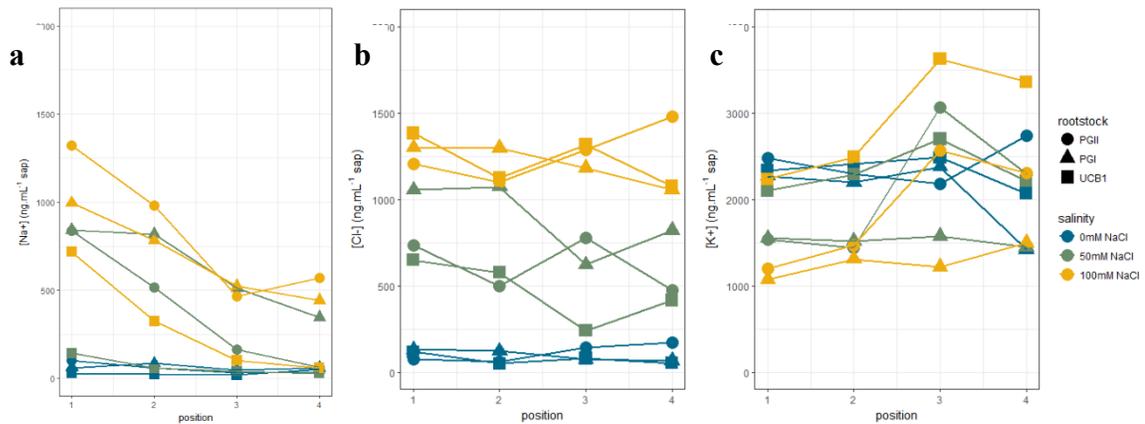
Tree crops must contend not only with the water quality available each season, but also with the salts that may build in their tissues over decades of growth and production. While, in any given year, salt tolerant trees like pistachio might be expected to rely on strategies that parallel those of annuals, in order to manage nutrient deficiencies, osmotically-induced water stress or ion-specific toxicity in roots or leaves, the longevity and significant volume of their trunks—up to 80 or 90 percent of total biomass—may provide an additional level of salt management and protection specific to woody perennials. Total exclusion of salts is not necessarily a viable short- or long-term tolerance strategy. Some salt inclusion, via uptake from soil solution and xylem loading of inorganic osmolytes, allows for the maintenance of an energetically efficient osmotic gradient that favors water movement from root to transpiring tissues despite low soil water potentials, relieving plants of exclusive reliance on compatible carbon solutes to achieve the same effect. However, without a strategy for storage or removal of salt, leaves at the end of the transpiration stream tend to disproportionately accumulate and concentrate any included ions as the water carrying them arrives and evaporates. Because many of a cell's metabolic functions are impaired by high concentrations of environmentally pervasive and minimally essential ions like sodium (Na^+) or chloride (Cl^-), this accumulation has potentially lethal implications for ill-adapted leaves and, by association, attached plants. Focusing on *stem* adaptations that might be exploited in woody perennials, in particular, are there scenarios for achieving salt tolerance that both include uptake of salts, to manage osmotically induced water stress, but also minimize rates of leaf salt accumulation to toxic levels? This is the central question that has driven my PhD dissertation and work over the last five years for the CPRB.

RESULTS

One stem adaptation shown to contribute to a salt-inclusive tolerance scenario, in even short-lived crop plants, is xylem retrieval, the ability to remove the salts from xylem sap before they arrive at transpiring leaves by dispersing them in adjacent living cells called xylem parenchyma. We have found that pistachios do indeed extract Na^+ from the transpiration stream. Additionally, when we compared the Na^+ retrieval strategies of three young rootstocks (UCB1, PGII, and PGI), we found that we cannot separate xylem retrieval from xylem exclusion as the concentration entering the stem impacts the rate of retrieval (Figure 1a). At moderate (50mM NaCl) levels of applied salinity, UCB1 excludes Na^+ so effectively that there is no significant difference between its values just above the root crown (position 1) and the values of any rootstock's control treatments (0mM NaCl) at the same position. Thus, no significant xylem retrieval of Na^+ is needed to achieve low concentrations at the apical meristem (position 4). At high levels of applied salinity (100mM NaCl), UCB1 continues to exclude a high percentage of applied Na^+ and significantly increases retrieval so that, still, no Na^+ arrives at the apical meristem. In contrast, we observed that PGI's strategy of moderate and high exclusion for moderate and high treatments, respectively, but no bump in retrieval from one level of salinity to the next resulted in lesser protection of the apical meristem in even the moderate salt treatment.

PGII's strategy of moderate exclusion and moderate retrieval at both moderate and high levels of applied salinity is enough to protect the apical meristem from Na⁺ only in the moderate salinity treatment. There was no significant difference among the tested rootstocks in either chloride (Cl⁻, Figure 1b) exclusion or retrieval. UCB1's success with Na⁺ may be explained, at least in part, by potassium (K⁺) selection. In accordance with significantly less concentrated Na⁺, at both base (position 1) and apical meristem (position 4), of UCB1s treated with 100mM NaCl, K⁺ is more concentrated at the same positions (Figure 1c).

Figure 1. Average measured sap sodium (a), chloride (b), and potassium (c) concentrations along the stem axis of 2-year-old PGII, PGI, and UCB1 rootstocks taken after 10 weeks of treatment with 0, 50, and 100mM sodium chloride. Positions of sap extraction indicate a 2-3cm segment starting just above the root crown (1), just below the start of the current year's growth (2), just above the start of the current year's growth (3), and just below the apical meristem (4). Statistical significance referenced in the main text was determined by linear mixed effects models considering the fixed effects of rootstock, salinity, and position and the random effect of individual trees.



Although UCB1 demonstrates apparent advantages in a saline environment, analyzing the nonstructural carbohydrates (NSCs) of another set of young (1-year-old) clonal UCB1 rootstocks after two months of treatment with 50 and 100mM NaCl, we found significant reductions in the starch concentrations of developing tissues (fine roots, all bark and young wood). Starch reductions translated to significant reductions in the total NSC pool despite significant increases in bark-sugar concentrations. Taking all of this into consideration, a year of recovery after salinity application and NSC pools, in surviving salt-treated trees (6 of 7 in the 50mM treatment and 3 of 7 in the 100mM treatment), were indistinguishable from controls.

CONCLUSION AND APPLICATIONS

Despite UCB1's Na⁺ safe strategy, which may protect leaves from the rapid accumulation of one toxic ion, even under conditions of high salinity, it demonstrates no protection from Cl⁻ accumulation. UCB1 also demonstrates significant immediate energy costs at the end of a saline growing season, which may have implications for the survival of dormancy and spring leaf-out the following year. Further analysis is required to study whether PGII, which excludes less Na⁺ than UCB1 but still manages Na⁺ accumulation to some degree, is able to maintain higher NSC levels immediately following salinity treatment. This would indicate a short-term advantage to some Na⁺ inclusion in the absence of K⁺ selectivity, at least when NaCl application is moderate. In the long-term, however, one year of salinity stress does not demonstrate irreversible NSC consequences.

In addition to the data discussed in this year's report, my forthcoming dissertation will draw conclusions about the influence of the graft union in stem-salt transport, long-term consequences of salt storage (is it permanent?), and the mechanism of xylem Na⁺ retrieval.