MANGANESE NUTRITION AND PHOTOSYNTHESIS
IN NAD-MALIC ENZYME C-4 PLANTS

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ABSTRACT

Based on their photosynthetic pathways, plants can be divided into three major groups: C-3, CAM, and C-4. In C-4 plants, the release of CO\textsubscript{2} for Calvin cycle reactions in bundle sheath cells (BSC) involves one of the three principal enzymes: NADP-malic enzyme (NADP-ME), PEP-carboxykinase enzyme (PEP-CK), and NAD-malic enzymes (NAD-ME). Of these three decarboxylating enzymes, only the activation of NAD-ME has an absolute requirement for Mn, therefore, leaf Mn concentrations could be critical for maximum NAD-ME activity and the continued supply of CO\textsubscript{2} to bundle sheath cells. The objective of this research was to determine the Mn requirement for optimum photosynthesis and plant biomass production for two agriculturally important NAD-ME C-4 species, pearl millet (\textit{Pennisetum glaucum} L. R. Br) and purple amaranth (\textit{Amaranthus hypochondriacus} L.). These species were examined in parallel with two NADP-ME (no Mn activation required) species, corn (\textit{Zea mays} L.) and sorghum (\textit{Sorghum bicolor} L. Moench), and two C-3 species, wheat (\textit{Triticum aestivum} L. cv. Ernie) and squash (\textit{Cucurbita pepo} L. cv. straighneck) added as controls. Plants were grown in a complete nutrient solution with Mn concentrations ranging
from 0 to 100 μM. Field grown pearl millet and purple amaranth received Mn from two sources, Mn beads and manganese chloride.

Manganese concentration required for optimum photosynthetic rate and biomass production of the C-3 and NADP-ME C-4 species was found to be ~2 μM, which is the concentration commonly used in plant nutrient media. Manganese concentrations above 2 μM had no significant effect on either photosynthetic rate or biomass production of these plants. Also, in C-3 and NADP-ME C-4 species, light saturated photosynthesis ($A_{\text{max}}$) was the highest for plants receiving 2-5 μM Mn and no change was observed with increasing Mn concentration. In contrast, in both NAD-ME species, the optimum growth and photosynthetic responses required Mn concentrations 20-fold higher than those typically used in hydroponic media, and increasing Mn concentration from 10 to 75 μM resulted in a 50% increase in photosynthetic rate in purple amaranth and a 36% increase in pearl millet. NAD-ME plants receiving higher Mn concentrations had greater responses to increasing photosynthetic photon flux density (PPFD), and at saturating light, pearl millet and purple amaranth receiving $\geq 50$ μM Mn achieved higher $A_{\text{max}}$ than those receiving lower Mn treatments. However, in all plant species, Mn treatment had little effect on the apparent quantum yield (AQY), perhaps indicating that at this range, light rather than Mn was limiting photosynthesis. Interestingly, Mn concentration higher than 2 μM had little effect on stomatal conductance in all six tested species. This strongly implies that increased photosynthetic rates in NAD-ME species with
higher Mn nutrition was a result of a better internal supply/utilization of CO$_2$ and not of an improved stomatal conductance.

In field experiments, Mn fertilization resulted in slightly increased leaf Mn concentrations and an up to ~20% increase in photosynthetic rate. In general, Mn fertilization had little effect on seed mineral element composition or seed protein and oil content, but resulted in a slight increase in seed yield.

This is, to my knowledge, the first information on the substantial, 20-fold higher Mn requirement for optimum photosynthesis and biomass production of NAD-ME C-4 plants, compared to other plant species. This finding should be considered in future research on NAD-ME C-4 crops, especially under soil conditions that decrease Mn availability for plant uptake. As more information is collected on NAD-ME C-4 plant biochemistry, physiology, and structure, more specific recommendations for nutrient requirements and more specific Mn application strategies can be developed.