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High Nitrogen Availability Limits Photosynthesis and Compromises Carbohydrate Allocation to Storage in Roots of *Manihot esculenta* Crantz

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Cassava (*M. esculenta* Crantz), feeding countless people and attracting markets worldwide, is a model for traditional crops that need physiology-based fertigation (fertilization through irrigation) standards in intensive cultivation. Hence, we studied the effects of 10 to 200 mg L^{-1} nitrogen (N) fertigation on growth and yields of cassava and targeted alterations in their photosynthetic, transpiration, and carbohydrate management. We found that increasing irrigation N from 10 to 70 mg L^{-1} increased cassava's photosynthesis and transpiration but supported only the canopy's growth. At 100 mg N L^{-1} cassava reached a threshold of sugar in leaves (~47 mg g^{-1}), began to accumulate starch and supported higher yields. Yet, at 200 mg N L^{-1}, the canopy became too demanding and plants had to restrain transpiration, reduce photosynthesis, decrease carbohydrates, and finally lower yields. We concluded that the phases of cassava response to nitrogen are: 1) growth that does not support yields at low N, 2) productive N application, and 3) excessive use of N. Yet traditional leaf mineral analyses fail to exhibit these responses, and therefore we propose a simple and inexpensive carbohydrate measurement to guide a precise use of N.

Keywords: root-crops, nitrogen, fertigation, carbohydrates, physiological indicators

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INTRODUCTION

With increased pricing of fertilizers and rising environmental concerns, the effectivity of nutrient application has to be studied thoroughly for every new crop, condition, and farming practice. It is especially critical in arid and semi-arid environments, where the shift to intensive fertilization through irrigation (i.e., fertigation) alters the nutrient uptake and use and requires specific considerations (He et al., 2015). Of all the macro-elements, modern farming relies heavily on nitrogen (N), which, despite becoming increasingly costly, cannot be substituted by farmers. Nitrogen-deficient plants halt leaf elongation (Marschner and Marschner, 2012), inhibit photosynthesis (Gregoriou et al., 2007), reduce chloroplast size (Li et al., 2013), and minimize overall growth. Yet, if N levels increase and it is no longer a limiting factor in physiological processes, its effectivity must be reassessed. In fact, the majority of applied N in crop systems often does not transform to increased yield (Lassaletta et al., 2014) due to numerous parameters that affect its effectivity, e.g. crop species and variety, the N form (nitrate or ammonium), soil type, water availability, and application method (El-Sharkawy et al., 1998; Ospina et al., 2014). Thus, N should be studied within the conditions and limitations of