Changes in nutrient concentrations and leaf gas exchange parameters in banana plantlets under gradual soil moisture depletion

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ABSTRACT

Changes in mineral nutrient concentration, growth, water status and gas exchange parameters were investigated in young banana plants (*Musa acuminata* cv. 'Grand Nain') subjected to gradual soil moisture diminution. Experiments were performed in glasshouse under controlled temperature, and water stress was imposed by ceasing irrigation for 62 days. The data showed a parallel decrease of leaf gas exchange parameters and soil moisture initiated few days after the imposition of water stress. However, the leaf relative water content (RWC) showed a minor decrease in response to drought. The onset of growth reduction evaluated as plant height, pseudostem circumference, number of newly emerged leaves, leaf area, and leaf and root biomass took place approximately between 34 and 40 days after the beginning of the stress period. In addition, drought did not modify nitrogen and phosphorus concentrations in foliar and root tissues; however, it increased potassium, calcium, magnesium, sodium and chloride in leaves, and only calcium, sodium and chloride in roots. Collectively, the data reveal that banana plants show a drought avoidance mechanism in response to water stress. After a prolonged drought period, leaf RWC was hardly reduced, while gas exchange and growth parameters were reduced drastically. Increasing leaf mineral concentration could have help to maintain leaf RWC due to osmotic adjustment mechanism.

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1. Introduction

It is generally accepted that banana plants need large amounts of water to achieve high production. Thus, several studies have been performed to elucidate water requirement and management, and efficiency of irrigation scheduling in banana (Israeli and Nameri, 1987; Robinson and Bower, 1987; Turner, 1987; Robinson and Alberts, 1989; Eckstein and Robinson, 1995; Turner and Thomas, 1998; Lu et al., 2002). The response of stomatal conductance and transpiration to progressive soil water depletion has been used as a physiological indicator of the establishment of stress. It has been reported a decrease of transpiration rate, stomatal conductance and photosynthesis in banana plants subjected to water stress (Robinson and Bower, 1987; Kallarackal et al., 1990; Eckstein and Robinson, 1996; Thomas and Turner, 1998, 2001). In addition, it has been indicated that banana plants are able to maintain their internal water status during drought by reducing radiation load and closing stomata (Thomas and Turner, 1998). In relation to plant growth, water stress severely reduced the emergence of new leaves (Kallarackal et al., 1990) and yield of banana (Manica et al., 1976). Moreover, a decrease of total dry matter, leaf area, number of living leaves at harvest, total root length, growth and vigor of banana was reported under drought conditions (Firth et al., 2003). Reduced leaf elongation was correlated with decreased stomatal conductance and transpiration (Turner and Thomas, 1998).

At nutritional perspective, the behaviour of mineral nutrients in banana plantlets under water stress conditions is still unknown. However, it is assumed that drought reduce nutrient uptake in several plant species (Erlandsson, 1975; Alam, 1999). Precisely, drought disturbs the plant nutritional status inducing increases or decreases of ion concentrations in plant tissues, and the intensity of the nutrient imbalance appears to vary among plant species. For instance, K^+ and Ca^{2+} concentrations increased in soybean and fescue plants (Huang, 2001; Samarah et al., 2004) but decreased in foliar organs of maize (Kaya et al., 2006) in response to drought-stress treatments. Also, concentrations of N, P and Mg^{2+} decreased in fescue cultivars (Huang, 2001). Total nitrogen and nitrate increased under water stress in pearl millet considered highly tolerant to drought (Payne et al., 1995; Kusaka et al., 2005).

Osmotic adjustment of plants, which implies an accumulation of solutes to maintain a favorable water potential gradient, is a crucial adaptive response for plant survival under water stress conditions (Turner and Jones, 1980). K^+ and Na^+ are involved in the osmotic adjustment of leaf tissues to low external water potential

(Osmond et al., 1980). Calcium is also involved in drought tolerance through the regulation of the water relations (Li et al., 2004), and increasing osmolyte accumulations (Nayyar, 2003). Potassium and chloride uptake was increased by hyperosmotic stress, providing an adequate osmotic adjustment (Curti et al., 1993; Shabala et al., 2000; Shabala and Lew, 2002). It has been also reported that in drought stress-tolerant plants, the contribution of K^+ and NO_3^- to osmotic adjustment is higher than that of organic solutes functioning as osmoprotectant solutes, and the osmotic adjustment through K^+ uptake is more energy efficient (Hsiao, 1973; Kusaka et al., 2005). However, the efficiency to adjust osmotic pressure is variable among plant species and depends on their ability to tolerate drought. For instance, it was reported that inorganic ion concentration (Ca^{2+} and K^+) did not considerably change under drought stress and did not seem to contribute to osmotic adjustment in bentgrass species (DaCosta and Huang, 2006).

These observations suggest that there is a relationship between the nutritional status of the plant and its response to drought stress. Thus, in the present work, I investigated the pattern of change of the mineral nutrient accumulation in banana plantlets subjected to gradual soil moisture reduction in order to elucidate the behaviour of these nutrients in water stress response. In addition, the changes in leaf water status, gas exchange and plant growth parameters were studied under drought conditions.

2. Materials and methods

2.1. Plant material

Banana plantlets (*Musa acuminata* AAA, 'Grand Nain'), belonging to the Cavendish subgroup were used in this study to investigate their responses to gradual soil water depletion. 'Grand Nain' is characterized by a small leaf area index, short pseudostem, large bunches, and short cycle (Stover, 1982). This cultivar is well adapted to subtropical conditions and, therefore, is the most cultivated in Canary Islands. Five months old banana plants (30 cm tall) were transplanted to large plastic pots (70 l) under glasshouse at the Instituto Canario de Investigaciones Agrarias (Valle de Guerra, Tenerife Island, Spain). During the experimental period, plants were grown under controlled temperature (20–30 °C), 65–90% of relative humidity, and 1200 μmol m^{-2} s^{-1} of maximum photosynthetically active radiation (PAR). A mixture of sterilized clay loam soil and organic material (1:2) was used as a substrate. Plants were watered three times a week with chemical solution according to Martin-Prevel (1980) to maintain optimal plant nutrient requirements.

2.2. Treatments of water stress and growth measurements

Approximately, after 30 days of acclimation, water stress was imposed by stopping irrigation until soil moisture declined to low contents and growth arrest was evident. In our experimental system, water shortage was maintained for 62 days, while control plants were irrigated to field capacity. During the period of water deficit, plant height, stem circumference, leaf area, number of emerged leaves, leaf and root dry weights were determined regularly. Samples of leaves and roots were periodically harvested, frozen in liquid nitrogen, lyophilized and stored at −20 °C until analysis.

2.3. Soil moisture

Volumetric soil moisture was recorded regularly during the period of water stress using a Trime-FM Time Domain Reflectometry (TDR) instrument (Imko Equipment, Germany) equipped with two-rod connector probes that were 15 cm in length as described previously (Mahouachi et al., 2006).

2.4. Leaf relative water content

Leaf relative water content was determined periodically in control and water-stressed plants using the third fully expanded leaves counting from the plant top. Determinations were performed following the procedure described by Turner (1981). After sampling, leaf fresh weights (FW) were determined, and then leaves were hydrated until saturation in distilled water for 24 h at 4 °C. Once surface dried, leaves were reweighed to obtain leaf turgid weights (TW). Subsequently, leaves were oven dried at 70 °C for 48 h and their dry weights (DW) were determined. Leaf RWC was calculated following the formula: RWC (%) = (FW − DW)/(TW − DW) × 100.

2.5. Leaf gas exchange

Photosynthetic rate (A), stomatal conductance (gs) and transpiration rate (E) were determined regularly in banana leaves throughout the experimental period, using an LCpro portable photosynthesis system (ADC Bioscientific Ltd., Hoddesdon, UK) as described by Mahouachi et al. (2007). Determinations were performed on fully expanded leaves, generally, the third leaf counting from plant apex. Measurements were made in the morning (8:00–10:00 h), temperature within the leaf chamber was 24 ± 2 °C and leaf-to-air vapor pressure deficit was 1.6 ± 0.3 kPa.

2.6. Ion analyses

Powdered leaf (third leaf counting from plant apex) and root tissues sampled during the period of water deficit were used to analyze the ion concentrations.

Nitrogen analysis was carried out using selenium catalysis (Bremmer, 1965). The tissue powder was cremated in a muffle oven for 3 h at 400 °C and the nitrogen concentration was determined by colorimetry as an ammonium salicylate complex at 660 nm, following the procedures described previously by Isaac and Johnson (1976).

For P, K, Ca, Mg and Na analyses, samples were cremated in a muffle oven for 4 h at approximately 450 °C, then the ashes were extracted with 5 M HCl. Analyses were performed accordingly to the methods described in Technicon (1982) and Perkin-Elmer (1994). Cation determinations were performed by atomic absorption spectrophotometry at 766.5, 422.7, 285.2 and 589 nm for K, Ca, Mg and Na ions, respectively. Phosphorus was measured by colorimetry at 420 nm as the vanadomolybdo-phosphoric acid complex.

Total chloride concentration in leaf and root tissues was determined by AgNO$_3$ titration (Chapman and Pratt, 1961). Plant tissues (0.5 g dry weight) were extracted in distilled water (50 ml); stirred during 10 min and centrifuged at low speed about 20 min. The supernatant was filtered by a Whatman paper No. 1. The titration was carried out in 25 ml of filtrate with 0.05N AgNO$_3$ using 5% K$_2$CrO$_4$ as an indicator.

2.7. Experimental design and statistical analyses

Plants were distributed in three blocks with 36 plants each (18 control and 18 drought-stressed plants). Three plants per treatment and block were used for growth and gas exchange parameter measurements, and, at different times (0, 21, 40, 54, and 62 days), three plants per treatment and block were randomly chosen and sampled to determine leaf and root dry weights and mineral concentrations. Mean values were compared using the