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East African highland bananas (*Musa* spp. AAA-EA) 'worry' more about potassium deficiency than drought stress

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ABSTRACT

Drought stress, potassium (K) and nitrogen (N) deficiencies are major constraints to rain-fed East African highland banana (EAHB) production in Uganda. It was hypothesised that the reduction in fresh bunch mass and increase in dry matter (DM) allocation to corms with drought stress, K and N deficiency is additive. Individual plant measurements at harvest from two field trials in central and south western Uganda were analyzed to evaluate effects of cumulative rainfall (CRF) received 365 days from sucker emergence, mineral K and N inputs on EAHB bunch yields. Dry matter content in aerial shoot (leaves and pseudostems) relative to that in the subterranean corm was also analyzed to evaluate DM allocation plasticity due to drought stress, K and N deficiency. This was verified with allometric analysis using pre-harvest stage plants from farms of known K and N nutritional status and plants from a screen house drought stress pot trial in Uganda. Dry matter production and yields were mainly driven by K interacting with CRF. Within 12 months, K input (250–600 kg K ha^{-1} yr^{-1}) increased bunch yield from 8 to 15 Mg ha^{-1} yr^{-1} irrespective of whether dry (CRF < 1100 mm) or wet (CRF ≥ 1100 mm) conditions prevailed, possibly due to K-mediated osmotic adjustment under dry conditions. Without K input, wet conditions increased bunch yield from 6 to 8 Mg ha^{-1} yr^{-1} while dry conditions decreased it from 6 to 4 Mg ha^{-1} yr^{-1} within 12 months. Total DM and its distribution between the biomass structures followed similar trends. Nitrogen input (150–400 kg N ha^{-1} yr^{-1}) neither affected bunch yield nor DM allocation at harvest stage. At pre-harvest stage, reduction in DM allocation to the corm per unit increase in total DM was 14–22% significantly lower with N and/or K deficiency compared with that under sufficient K and N. Drought stress per se had no effect on DM allocation but enhanced DM allocation shifts due to K deficiency. Drought-stressed EAHB thus increase DM allocation to subterranean structures only if K-deficient, unlike responses reported for other plant species. Potassium nutrition is perhaps a more viable entry point for mitigation of drought stress in EAHB cropping systems than irrigation but this requires further agronomic and economic evaluation. It may be important to account for carbon allocated to osmotic adjustment for realistic simulation of water- and K-limited growth in EAHB.

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1. Introduction

Among the factors constraining East African highland banana (*Musa acuminata* genome group AAA-EA; hereafter referred to as EAHB) production in Uganda are drought stress (van Asten et al., 2011), nitrogen (N) and potassium (K) deficiencies (Nyombi et al., 2010). Spatial heterogeneity in crop N and K deficiencies (Smithson et al., 2001; Wairegi and van Asten, 2010) in Uganda calls for a decision support tool that takes into account interactions between the stress factors or their ameliorative inputs. This would guide efficient agronomic management decisions for improving EAHB productivity. Models that can predict crop growth response to water and nutrient supply present an opportunity to develop such a decision support tool. Dry matter (DM) allocation between aerial and subterranean biomass structures of plants is a critical parameter in most eco-physiological crop growth models.

Resource-limiting conditions often induce adjustments in plant DM allocation between aerial and subterranean biomass structures due to DM allocation plasticity. This is different from the normal shifts in DM allocation between biomass structures due to phenological development, also called ontogenetic drift (Wright and McConnaughay, 2002) and hence it should be taken into account when simulating resource-limited crop growth. Wilson (1988) reviewed the models used to describe DM allocation plasticity in plants, namely, the allometric models, hormone models, Thornley's model and functional equilibrium models. True DM allocation plasticity is however poorly understood (Wardlaw, 1990) and hence

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the mechanisms underlying DM allocation models are still under debate (Franklin et al., 2012). Consequently, 'explanatory' models like Thornley's Model (Thornley, 1972), are frequently substituted by empirical ones (Evans, 1990), such as the functional equilibrium models.

The functional equilibrium models predict preferential allocation of fresh DM to biomass structures involved in acquisition of the limiting resource. If water or nutrients are limiting, then plastic DM allocation favours roots against the shoots; the reverse is true if light or carbon dioxide is limiting (Brouwer, 1962; Davidson, 1969; McCarthy and Enquist, 2007). The zero sum or trade-off principle implied in the functional equilibrium models tends to maximise use efficiency of the limiting growth resources (Bloom et al., 1985; Chapin, 1991), hence their relatively frequent application in plant growth simulation (e.g. Maire et al., 2012). Several authors report findings that support the functional equilibrium models (e.g. Poorter et al., 2012; Slot et al., 2012). Although some drought stressed plant species exhibit DM allocation plasticity in favour of the roots (Chartzoulakis et al., 1993; Slot et al., 2012), others do not (Bhattachan et al., 2012; McConnaughay and Coleman, 1999; Poorter and Nagel, 2000). Low K supply induces increased DM allocation to the roots in some plant species (Hafsi et al., 2011) while in other species, it reduces DM allocation to roots (Ericsson and Kähr, 1993). Such variations within the functional equilibrium models' predictions depend not only on the specific growth resource but also on plant genotype (McMichael and Quisenberry, 1991) and species (McCarthy and Enquist, 2007). Prior knowledge on the crop's DM allocation plasticity with respect to a given growth resource is thus required in order to rely on functional equilibrium models for describing DM allocation plasticity.

There is scant knowledge on DM allocation plasticity in bananas with respect to drought stress, K and N deficiency. Turner and Barkus (1980) reported a significant increase in proportion of total DM allocated to roots and corms in response to reducing the K supply to one tenth of the full strength K concentration in a lysimeter study with banana cultivar 'Williams'. McIntyre et al. (2000) reported similar aerial shoot to subterranean corm biomass DM ratios between mulched and non-mulched EAHB fields in central Uganda despite K deficiency in the non-mulched plants. However, the interpretation of ratios with respect to DM allocation plasticity is beset with pitfalls (Jasienski and Bazzaz, 1999) because the allocation patterns may change with plant size (Pearsall, 1927; Coleman et al., 1994; Coleman and McConnaughay, 1995) and plant development (Troughton, 1956). Allometric analysis is thus required to correct for the size-dependency of DM allocation between plant organs to verify conclusions drawn from shoot:root DM ratios.

Allometric analysis is based on the linear regression of logarithm-transformed root DM on logarithm-transformed shoot DM. The regression slope or allometric coefficient is the mean root DM to shoot DM ratio over ontogeny or experimental plant size range. When roots and shoots exhibit isometric growth (i.e. receive DM in equal proportions), the slope is 1 and hence any observed changes in DM allocation between them are only due to normal ontogenetic drift. When root growth supersedes shoot growth, then the slope is significantly greater than 1. The slope is significantly less than 1 when shoot growth supersedes root growth (Hunt and Nicholls, 1986). Significant departures of the slope from unity indicate that the observed change in DM partitioning between roots and shoots is due to true plasticity in DM allocation. However, phenological development, e.g. flowering may also induce a significant deviation of the slope from 1 (Troughton, 1956). Allometric analysis for correcting size-dependency is thus best done with young plants, which is not true for studies reporting DM allocation in bananas. Furthermore, valid interpretation of the fitted regression parameters assumes all root biomass can be recovered and the DM content accurately quantified. This is a major challenge for field-grown plants (Poorter et al., 2012), especially large ones like bananas. Studies involving DM distribution between banana biomass structures report corm DM but not root DM (e.g. Hegde, 1988; McIntyre et al., 2000) for subterranean biomass structures. Poorter and Nagel (2000) suggested a more flexible approach for allometric analysis that does not necessitate quantification of root DM per se but relies on quantification of biomass fractions relative to any plant size parameter.

The objective of this study was to unravel the effects of drought stress, K and N deficiencies on EAHB fresh bunch yields and the underlying DM allocation between above- and below-ground biomass structures. The following hypotheses were tested: (1) the increase in fresh bunch yields in response to rainfall, and mineral K and N inputs on EAHB grown on soils deficient in the nutrients is additive, and; (2) there is significant additive increase in DM allocation to below-ground biomass structures of EAHB in response to drought stress, K and/or N deficiency.

2. Materials and methods

2.1. Study approach

This study used a survey approach, with individual banana plants sampled at harvest stage from two fertilizer response trials, complemented with those sampled at pre-harvest stages from twenty farmers' fields and a screen house pot trial. Plants from the fertilizer response trials were regrouped into a full factorial K and N input combination. Plants from farmers' fields were grouped according to their K and N nutritional status from compositional nutrient diagnosis (CND) indices based on locally developed norms by Wairegi and van Asten (2011). Plants from the screen house pot trial were grouped according to the *pF* range to which they were subjected.

2.2. Fertilizer response trials

These were planted in October, 2004 and individual plant data spanning three crop cycles collected. One trial was conducted on-station on a Haplic Ferralsol at Kawanda (0°25′N or 0.0073 rad, 32°31′E or 0.5675 rad; 1156 m above sea level or m.a.s.l) in central Uganda. The second trial was conducted on-farm (0°54′S or −0.0157 rad, 30°15′E or 0.5280 rad; 1405 m.a.s.l) on a Lixic Ferralsol in Ntungamo district, south western Uganda. The annual rainfall at Kawanda was 1034, 1334 and 1663 mm in 2005, 2006 and 2007, respectively, while values at Ntungamo were 1206, 1380 and 935 mm, respectively. Both sites experience a bimodal rainfall distribution with rainy seasons from March to June and September to November.

Details of laboratory analytical methods and results from topsoil samples (0–32 cm) taken prior to establishment of the trials were reported by Nyombi et al. (2010). Exchangeable K and total N at Kawanda averaged 0.4 $\text{cmol}_\text{c}\,\text{kg}^{-1}$ and 0.1%, respectively, while the values at Ntungamo were 0.12 $\text{cmol}_\text{c}\,\text{kg}^{-1}$ and 0.07%, respectively. McIntyre et al. (2000) suggested that the critical exchangeable K value is well above 1.3 $\text{cmol}_\text{c}\,\text{kg}^{-1}$. Delvaux et al. (1987) reported the critical exchangeable K content for bananas on an Andisol in Cameroon to be 1.5 $\text{cmol}_\text{c}\,\text{kg}^{-1}$. The critical value for total N in soils for EAHB in Uganda is 0.2% (Odeke et al., 1999). Both Kawanda and Ntungamo trial sites are thus likely to have been deficient in K and N.

East African highland banana cultivar 'Kisansa' tissue culture plantlets were planted spaced 3 m × 3 m in plots with 35 plants (5 × 7 matrix) per plot, of which 15 plants (i.e. inner 3 × 5 matrix) were used as net plot for data collection. The trials were set up in a

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