Phenological development of East African highland banana involves trade-offs between physiological age and chronological age

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ABSTRACT

The phenology of East African highland banana (*Musa acuminata* AAA-EA, hereafter referred to as 'highland banana') is poorly understood. We tested three hypotheses: (1) the physiological age at flowering is independent of site effects, (2) there is no difference in threshold size at flowering between sites with different growth potential, and (3) morphological and physiological components of highland banana relative growth rate (RGR) contribute equally to mitigate growth reduction in response to limiting supply of water, K or N. The physiological age of highland banana plants from field trials at Kawanda (central Uganda) and Ntungamo (south-western Uganda) was computed from daily temperature records. Growth analysis was conducted using RGR, net assimilation rate (NAR), specific leaf area (SLA) and leaf mass ratio (LMR) estimated from allometry. Growth response coefficients were used for quantifying the relative contribution of NAR, SLA and LMR to RGR. Physiological age at flowering was delayed by 739 °C d at Kawanda compared with that at Ntungamo whose chronological age at flowering was in turn 51 d older. At both sites a threshold total dry mass of 1.5 kg per plant was required for flowering. Faster absolute growth rate and NAR fostered by wet conditions, K input and cooler temperatures enabled plants at Ntungamo to attain the threshold total dry mass sooner than those at Kawanda, hence the phenotypic plasticity in age at flowering. Net assimilation rate contributed at least 90% to RGR increase due to wet conditions at both sites. The contribution of NAR to RGR increase in response to K at Kawanda reduced to 38% while that for SLA increased to 49%. Net assimilation rate contributes more to highland banana RGR modulation than SLA except when warmer conditions reduce NAR. Differences in crop growth rate cause phenotypic plasticity in highland banana rate of phenological development.

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1. Introduction

East African highland banana (*Musa acuminata* AAA-EA, hereafter referred to as highland banana) are a primary staple food crop in the Great Lakes region of Africa, including Uganda, Rwanda, Burundi, DR Congo, Kenya and Tanzania. It provides up to 60% of the daily per capita calorie intake in the region (Abele et al., 2007). The region is characterised by high population densities with attendant demographic pressure-induced land degradation (Fermont et al., 2008). Consequently, substantial research on highland banana in the region has mainly focused on identification and management of yield constraints. However, some aspects of the crop's basic biology affecting productivity, including timing of flowering, remain poorly understood. This hampers efficient manipulation of the crop growth cycle towards defined production goals (Birabwa et al., 2010).

Efforts to quantitatively describe timing of flowering in bananas have focused on relating the cumulative number of leaves emerged at an assumed point of flower initiation or flower bud emergence from the pseudostem (e.g. Ndubizu et al., 1983; Mekwatanakarn and Turner, 1989). However, this approach has not been widely applied, perhaps because the cumulative number of leaves emerged at flowering varies substantially, e.g. 23 to 43 (van Asten, P.J.A., personal communication). There is thus a need to identify and elucidate plant attributes and/or environmental cues that influence the timing of flowering in bananas. Summerville (1944) proposed that flowering in bananas is initiated when the product of leaf area (square inches), leaf longevity (days), air temperature (°F) and day light hours during the life of a leaf is at least 5.6×10^{11}. The parameters used in the model by Summerville (1944) suggest that the

physiological age, and/or photoperiod and/or dry matter accumulated may be critical for flower initiation in bananas. However, Fortescue et al. (2011) reported a weak correlation between photoperiod and frequency of flowering per unit area over time at a site with a narrow photoperiod range. This finding renders photoperiod an unlikely factor in the African Great Lakes region's banana agro-ecologies, which by virtue of their equatorial location, have a narrow range of photoperiod.

Flowering in monocarpic biennial and perennial plants has been reported to be dependent on plant size, though in some species both plant size and age are influential (Klinkhamer et al., 1987 and references therein). According to life history theory, a threshold size or age is necessary for commencement of reproductive growth to maximise fitness. Fecundity and quality of off-spring increases when reproductive growth is delayed (Roff, 1992). However, the probability of a plant dying before attaining reproductive growth competence increases with delay in flowering. This implies that where both age and size are critical in controlling flowering, plants follow an optimal solution in a trade-off between delaying flowering and curtailing additional dry matter accumulation beyond a certain threshold size. This threshold is a constant for a given species, irrespective of growing conditions, except when the genotype exhibits phenotypic plasticity (Sultan, 2000) with respect to a flowering size or age threshold. In such a case, phenotypic plasticity is when plants of the same genotype flower at different threshold sizes or ages in different growing conditions or habitats (e.g. Klinkhamer et al., 1996; Simons and Johnston, 2003). Phenotypic plasticity with respect to flowering size or age threshold, enables the plants to exploit bet-hedging strategy for maximising chances of reproductive success, given environmental uncertainties (e.g. Simons and Johnston, 2003). It can be surmised that suboptimal environmental conditions that substantially reduce plant growth rate will delay flowering in plants that require a threshold size for phenological development to occur, regardless of whether or not they exhibit flowering size phenotypic plasticity. Although bananas reproduce through vegetative suckers, there are several reports of delayed flowering and prolonged cycle duration with suboptimal growing conditions from field experiments (e.g. Robinson and Alberts, 1986; Israeli et al., 1995; Okech et al., 2004). A quantitative growth analysis of highland banana may unravel the plant responses to resource limitations geared towards optimising relative growth rate (RGR), and possibly, the trade-off between delaying flowering and curtailing additional dry matter accumulation beyond a certain threshold size.

In quantitative growth analysis, RGR or the change in total dry mass (W_T) per unit of W_T already present per unit time, is modelled as a product of net assimilation rate (NAR), leaf mass ratio (LMR) and specific leaf area (SLA) of a plant (Lambers et al., 1989). In this simple model, growth is envisaged to be a function of net carbon gain (through NAR) in the photosynthetic tissues (mainly leaves) and carbon allocation to the leaves relative to that allocated to the rest of the plant (LMR and SLA). Net assimilation rate is the change in W_T per unit leaf area (A_L) per unit time. Leaf mass ratio is the leaf dry mass (W_L) per unit W_T while SLA is A_L per unit W_L. Leaf mass ratio and SLA are morphological components of RGR concerned with interception of light energy while NAR is a physiological component related to the utilisation of intercepted light energy for carbon assimilation. Net assimilation rate is positively correlated with rate of photosynthesis per unit A_L (Poorter and van der Werf, 1998) while LMR and SLA exhibit sensitivity to plant illumination (Evans and Poorter, 2001; Senevirathna et al., 2008). Quantitative growth analysis based on RGR and its components is acceptable for single plant analyses because there is no crop canopy to allow more mechanistic assessment of light interception and light use efficiency. It has been used to evaluate the relative importance of plant physiological and morphological responses

as coping mechanisms among cultivated plants or closely related wild species against growth-limiting factors (Galmés et al., 2005; del Amor and Cuadra-Crespo, 2012). Among the most limiting abiotic constraints to highland banana production are drought stress (van Asten et al., 2011), K and N deficiencies (Nyombi et al., 2010; Wairegi and van Asten, 2010) but there is no information about the relative importance of physiological and morphological components of RGR in modulating growth under these stresses.

The objectives of this study were to evaluate highland banana phenological development rate and the relative importance of physiological vis-à-vis morphological components of RGR in modulating highland banana growth under contrasting supply of water, K and N supply in Uganda. We tested three hypotheses: (1) the physiological age at flowering is independent of site effects, (2) there is no difference in threshold size at flowering between sites with different growth potential for highland banana, and (3) morphological and physiological components of highland banana relative growth rate contribute equally to mitigate growth reduction in response to limiting supply of water, K or N.

2. Materials and methods

2.1. Study site characterisation

This study followed a survey approach of individual highland banana plants sampled from fertiliser response trials that were conducted at two sites in Uganda. One trial was planted on-station on a Haplic Ferralsol at Kawanda (0°25′N [0.0073 rad], 32°31′E [0.5675 rad]; 1156 m above sea level [m.a.s.l]) in central Uganda while the other was on-farm (0°54′S [−0.0157 rad], 30°15′E [0.5280 rad]; 1405 m.a.s.l) on a Lixic Ferralsol in Ntungamo district, south-western Uganda. Details of laboratory analytical procedures and results from topsoil samples (0–32 cm) taken prior to establishment of the trials were reported in Nyombi et al. (2010) and van Asten et al. (2011). Exchangeable K and total N at Kawanda averaged 0.4 cmol$_c$ kg^{-1} and 0.1%, respectively, while the values at Ntungamo were 0.12 cmol$_c$ kg^{-1} and 0.07%, respectively. Basing on EAHB fertiliser response field trials in central Uganda, McIntyre et al. (2000) suggested that the critical exchangeable K value is well above 1.3 cmol$_c$ kg^{-1}. The critical value for total N in soils for EAHB in Uganda is 0.2% (Odeke et al., 1999). Both sites were also shown to be deficient in both K and N from significant shifts in highland banana dry matter partitioning between above- and below-ground biomass structures in response to K and N input (Taulya, 2013).

Both sites experience bimodal rainfall distribution with rainy seasons lasting from March to June and from September to November. However, there was both spatial and temporal variability in total annual rainfall over the duration of the trials. The annual rainfall at Kawanda was 1334 and 1663 mm in 2006 and 2007, respectively, while Ntungamo received 1380 and 935 mm, respectively. Between 1 Jan. 2006 and 31 Dec. 2007, the average daily maximum temperature was about 27 °C at both Kawanda and Ntungamo but the average minimum daily temperature at Kawanda (17.6 °C) was higher ($P < 0.001$) than that at Ntungamo by 4 °C (data not shown). Consequently, the average daily effective temperature at Kawanda (8.4 °C) was greater ($P < 0.001$) than that at Ntungamo by 2.3 °C (data not shown). Through simulation modelling, highland banana plants at Ntungamo were predicted to have higher potential growth and yield than those at Kawanda due to Ntungamo's lower effective temperature than that of Kawanda (Nyombi, 2010).