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, here-after 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

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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).

Table 1
Description of treatments in fertiliser response trials conducted in central (Kawanda) and south western (Ntungamo) Uganda.

Nutrient input (rate)	Treatment					
	N_0K_0	$N_{400}K_{600}$	N_0K_{600}	$N_{150}K_{600}$	$N_{400}K_0$	$N_{400}K_{250}$
Nitrogen (kg N ha^{-1} yr^{-1})	0	400	0	150	400	400
Phosphorus (kg P ha^{-1} yr^{-1})	0	50	50	50	50	50
Potassium (kg K ha^{-1} yr^{-1})	0	600	600	600	0	250
Magnesium (kg Mg ha^{-1} yr^{-1})	0	60	60	60	60	60
Zinc (kg Zn ha^{-1} yr^{-1})	0	6	6	6	6	6
Boron (kg B ha^{-1} yr^{-1})	0	1	1	1	1	1
Molybdenum (kg Mo ha^{-1} yr^{-1})	0	0.5	0.5	0.5	0.5	0.5

2.2. Trial set up and data management

The trials were planted in October, 2004 with highland banana cultivar 'Kisansa' tissue culture plantlets, spaced 3 m × 3 m to give 35 plants (5 × 7 matrix) per plot, out of which 15 plants (i.e. inner 3 × 5 matrix) were used as the net plot for data collection. Between blocks, which were in general oriented across the slope, retention ditches, bordered with soil bunds on the up-slope edge, were dug alongside each plot's length to minimise transfer of treatment nutrients between plots through runoff and eroded sediments. The trials were set up in a randomised complete block design with 5 treatments and an un-amended control (N_0K_0 in Table 1) replicated 4 times. Details of trial management are reported in Nyombi et al. (2010).

Data collected from the first and second ratoon crops or Cycle 2 and Cycle 3, respectively between 1 Jan. 2006 and 31 Dec. 2007 were used for the current study. The planted crop constituting Cycle 1 were excluded from the current study because their physiological age could not be determined. The date and spatial position of emergence relative to the location of the mother plant for each sucker on a given mat in the net plot was recorded. At most, 3 plants of different generations (Cycles) were maintained per mat at a given time. Excess suckers were periodically removed. Records for suckers selected to grow as Cycle 2 or 3 were kept on individual plant basis. These included periodic growth monitoring parameters and dates of flowering (i.e. emergence of the flower bud out of the pseudostem) and harvest. The growth parameters, assessed at approximately 4-week intervals, were plant height (cm) as the length from ground level up to the vertex of insertion into the pseudostem of the youngest pair of leaves and girth at base (cm) as the circumference around the pseudostem at ground level.

At each growth monitoring data collection routine (hereafter referred to as 'event'), A_L, W_L and W_T per plant were estimated from plant height and/or girth data using allometric functions reported in Nyombi et al. (2009). The allometric functions were developed from plants sampled from the same trials as the study herein reported. At each site, an automatic weather station (HOBO®; Onset Computer Corporation, Massachusetts, USA) was installed for recording daily rainfall and air temperature data. The physiological age, T_{SUM} (°C d) of each plant at a given event n days after emergence, was computed as the growing degree days from Eq. (1):

$$T_{SUM} = \sum_{i=1}^{i=n} \max\left(0, \frac{T_{MIN(i)} + T_{MAX(i)}}{2} - T_{BASE}\right) \quad (1)$$

where T_{MIN} and T_{MAX} are respectively the minimum and maximum temperature (°C) on a given day, while T_{BASE} (°C) is the base temperature below which banana growth ceases. The base temperature was assumed to be 14 °C according to Robinson (1996).

Growth analysis was performed on data for events falling between 6 and 4 months pre-flowering because the plants were still within the exponential growth phase, which is assumed in Eq. (2). Plants were considered to be at 6, 5 and 4 months pre-flowering

if the event occurred within the ranges 194 to 166, 165 to 136 and 135 to 106 d, respectively before the date of flowering. The total dry mass per plant and physiological age at successive events were used to estimate the RGR (°C d^{-1}) for each plant in the net plot following the classical approach to growth analysis (Eq. (2)) according to Hunt (2003).

$$RGR = \left(\frac{1}{W_T}\right) \times \left(\frac{dW_T}{dT_{SUM}}\right) \equiv \left(\frac{\ln W_{T(i)} - \ln W_{T(i-1)}}{T_{SUM(i)} - T_{SUM(i-1)}}\right) \quad (2)$$

where $W_{T(i)}$ and $W_{T(i-1)}$ are the total dry masses (kg) of the plant at the current and immediate preceding event, respectively, while $T_{SUM(i)}$ and $T_{SUM(i-1)}$ are the physiological ages (°C d) of the plant at the current and immediate preceding event, respectively. The absolute growth rate, AGR (kg °C d^{-1}) was estimated per plant using Eq. (3), while NAR (kg m^{-2} °C d^{-1}), LMR (kg kg^{-1}) and SLA (m^2 kg^{-1}) were estimated for each plant in the net plot using Eqs. (4)–(6), respectively.

$$AGR = \frac{dW_T}{dT_{SUM}} \equiv \frac{\left(W_{T(i)} - W_{T(i-1)}\right)}{\left(T_{SUM(i)} - T_{SUM(i-1)}\right)} \quad (3)$$

$$NAR = \frac{1}{A_L} \times \frac{dW_T}{dT_{SUM}} \equiv \frac{\left(\ln A_{L(i)} - \ln A_{L(i-1)}\right)}{\left(A_{L(i)} - A_{L(i-1)}\right)} \times \frac{\left(W_{L(i)} - W_{L(i-1)}\right)}{\left(T_{SUM(i)} - T_{SUM(i-1)}\right)} \quad (4)$$

$$SLA = \frac{A_{L(i)}}{W_{L(i)}} \quad (5)$$

$$LMR = \frac{W_{L(i)}}{W_{T(i)}} \quad (6)$$

where $T_{SUM(i)}$, $T_{SUM(i-1)}$ and $W_{T(i)}$ are as defined for Eq. (2); $A_{L(i)}$ and $A_{L(i-1)}$ are the leaf area (m^2) at the current and immediate preceding event, respectively; $W_{L(i)}$ and $W_{L(i-1)}$ are the leaf dry mass (kg) at the current and immediate preceding event, respectively.

The cumulative amount of rainfall received by each plant over a 28-day period preceding a given event was computed as the CRF$_{28}$. All plants that had CRF$_{28}$ ≥84 mm at a given event were regarded as having experienced 'wet' conditions over the 28-day period preceding the event; otherwise they experienced 'dry' conditions. The cut-off CRF$_{28}$ value of 84 mm was chosen because it extrapolates to the first quartile cumulative rainfall (1100 mm) received over a year (365 days) by individual plants in the trial at the drier site, Ntungamo (Taulya, 2013), which is less than bananas' consumptive water use, 1300 mm yr^{-1}, (Robinson, 1996).

2.3. Data analysis

From a preliminary analysis of the data, contrasts between 150 kg N ha^{-1} yr^{-1} (treatment $N_{150}K_{600}$; Table 1) and 400 kg N ha^{-1} yr^{-1} (treatments $N_{400}K_{600}$, $N_{400}K_0$ and $N_{400}K_{250}$; Table 1) for plant height and girth at base at a
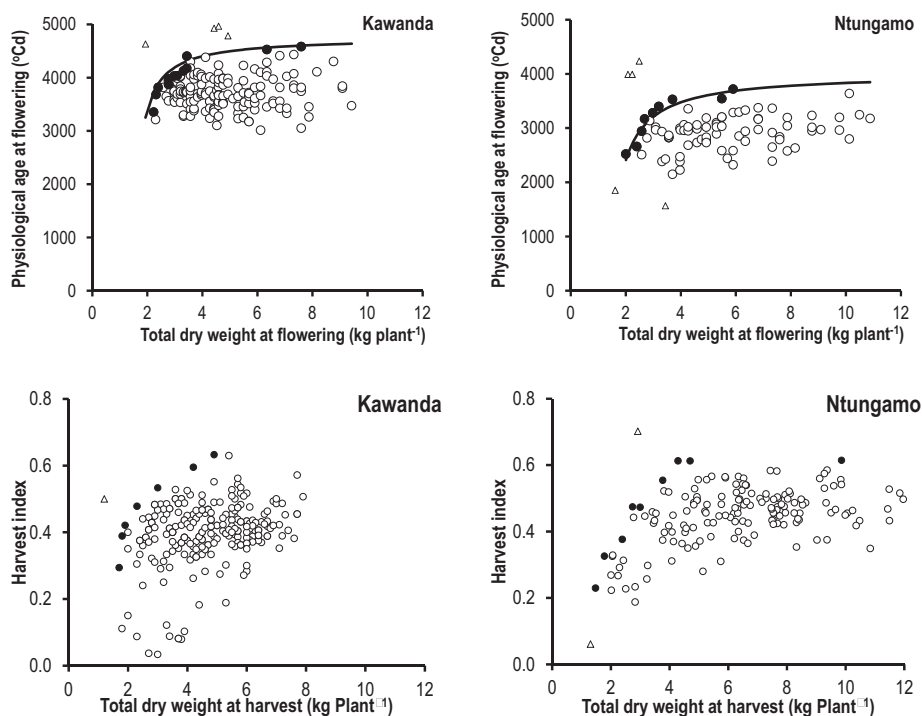
Fig. 1. Boundary points for the relationship between maximum physiological age vs. total dry mass at flowering, and harvest index vs. total dry mass at harvest of East African highland banana in central (Kawanda) and south-western (Ntungamo) Uganda, respectively. Filled circles are boundary points while open triangles are outliers based on the rectangle criterion (Schnug et al., 1996).

given event and site were not significant. Likewise, contrasts between 250 kg K ha^{-1} yr^{-1} (treatment N$_{400}$K$_{250}$; Table 1) and 600 kg K ha^{-1} yr^{-1} (treatments N$_{400}$K$_{600}$, N$_0$K$_{600}$ and N$_{150}$K$_{600}$; Table 1) for height and girth at base at a given event were also not significant. Variances for plant height and girth at base for treatments N$_{400}$K$_{600}$, N$_0$K$_{600}$, N$_{150}$K$_{600}$ and N$_{400}$K$_{250}$ were homogenous but different from those for treatments N$_0$K$_0$ and N$_{400}$K$_0$, which in turn had homogenous variances at a given site. For the purpose of this study therefore, plants from N$_{400}$K$_0$ were isolated in a group that received N but not K, while those from N$_0$K$_{600}$ were isolated in a group that received K but not N. Plants from N$_0$K$_0$ were isolated in another group that received no external nutrient inputs while those from N$_{400}$K$_{600}$, N$_{150}$K$_{600}$ and N$_{400}$K$_{250}$ were pooled in a group that received both N and K.

Physiological and chronological age (number of days from emergence to flowering) at flowering data were subjected to analysis of variance (ANOVA) using unbalanced treatment structure with crop cycle and blocks (replication) as confounding variables in GenStat 15.0 (Payne et al., 2003). The sequence of factors (Site, K and N) in the ANOVA did not affect the output. To investigate the possibility that differences in threshold total dry mass at flowering between sites underlay rejection of the null hypothesis that physiological age at flowering is independent of site effects, boundary line analysis was used to explore the relationship between maximum physiological age at flowering and total dry mass at flowering, separately for each site. The points defining the upper limit of the data cloud in a scatterplot of physiological age vs. total dry mass at flowering (Fig. 1) were identified following the BOLIDES algorithm, excluding outliers identified using the rectangle criterion (Schnug et al., 1996). The boundary points were then fitted to a model developed based on the assumption that highland banana plants delay flowering to maximise accumulation of total dry mass while their physiological age at flowering approaches an asymptotic maximum A °C d.

Based on the rational gambling decision rule described by Metcalf et al. (2003) for flowering in monocarpic perennial plants,

the model expressed in Eq. (7) was assumed to describe the optimal solution to the trade-off between delaying flowering and curtailing further dry mass accumulation in highland banana above the threshold total dry mass for flowering.

$$y_i = \frac{A \times (x_i - C)}{[B + (x_i - C)]} \qquad (7)$$

where y_i (°C d) is the maximum age at flowering at a given x_i value or total dry mass at flowering (kg per plant); A (°C d) is an asymptotic maximum physiological age at flowering; C (kg per plant) is the threshold total dry mass for flowering, and; B (kg per plant) is an empirical shape parameter representing a characteristic total dry mass at half the asymptotic maximum physiological age at flowering.

The model parameters A, B and C were estimated using numerical optimisation conditioned on minimising the coefficient of variation of the root mean square error (CRMSE) between observed and predicted maximum physiological age at flowering. The CRMSE was computed according to Eq. (8). Correspondence between observed and fitted optimisation model predictions of boundary points was evaluated using the squared correlation coefficient (R^2) computed using Eq. (9).

$$C_{\text{RMSE}} = \frac{\left[1/n \sum_{i=1}^{n} \left(y_i^o - y_i^p\right)^2\right]^{0.5}}{\bar{y}_i^o} \qquad (8)$$

$$R^2 = 1 - \left[\frac{\sum_{i=1}^{n} \left(y_i^o - y_i^p\right)^2}{\sum_{i=1}^{n} \left(y_i^o - \bar{y}_i^o\right)^2}\right] \qquad (9)$$

where y_i^o and y_i^p are the observed and predicted maximum physiological age (°C d); $\bar{y}_i^o$ is the mean observed maximum physiological age (°C d).

The threshold dry weight was also computed from the relationship between harvest index and total dry weight per plant, which
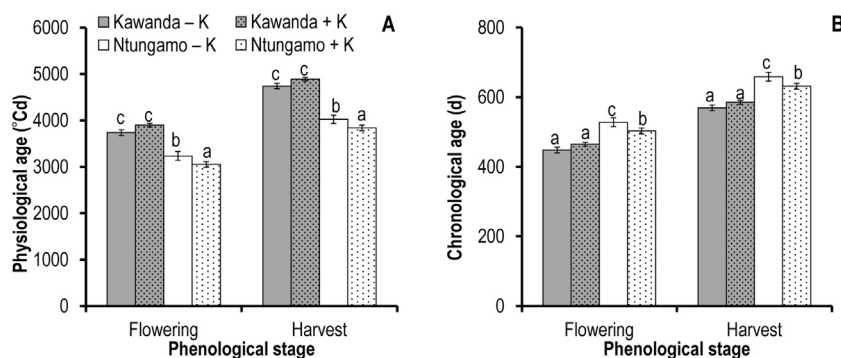
Fig. 2. Site × potassium (K) interaction effects on physiological age (A) and chronological age (B) at flowering and harvest stage of East African highland banana over 2 crop cycles in central (Kawanda) and south western (Ntungamo) Uganda. Means are adjusted for crop cycle and replication effects; Error bars are standard errors of means; Means crowned with the same lower case letter at a given phenological stage are not significantly ($P > 0.05$) different $-K = 0 \, kg \, K \, ha^{-1} \, yr^{-1}$ applied; $+K = 250$ to $600 \, kg \, K \, ha^{-1} \, yr^{-1}$ applied.

is described by a hyperbolic function. The intercept of this relationship is the threshold dry weight required for a plant to flower (Moot, 1997). The harvest index was computed as the ratio of bunch dry mass to the total dry mass. Points defining the upper limit of the data cloud in a scatter plot of harvest index (ratio of bunch dry matter to total dry weight) vs. total dry weight (Fig. 1) were identified using the BOLIDES algorithm, excluding outliers identified using the rectangle criterion (Schnug et al., 1996). Taking only the boundary points, the inverse of the harvest index was subjected to linear regression against the inverse of total dry weight to obtain the threshold dry weight as the inverse of the intercept.

To test the hypothesis that threshold size at flowering is independent of site effects, the boundary point dataset at each of the two experimental sites was jacknifed. This involved removing one point at a time followed by estimation of the model parameters A, B and C before returning the point and repeating the process for all the n points constituting the boundary line dataset at a given site. This generated one dataset consisting of n pseudo values of the model parameter estimates A, B and C for each site. The mean of pseudo values for each model parameter was compared between sites using the independent samples t-test at 95% confidence level.

Analysis of variance following unbalanced treatment structure and adjusting for cycle and block effects as confounding variables in GenStat 15.0 (Payne et al., 2003) was used to evaluate the effect of CRF_{28}, K and N on absolute growth rate, RGR and its components between 4 and 6 months pre-flowering separately for each site. The sequence of factors (CRF_{28}, K and N) in the ANOVA did not affect the output. Growth response coefficients were computed using Eq. (10) (Poorter and Nagel, 2000) for the factors that increased RGR and its components to evaluate the relative contribution of morphological and physiological components to RGR at each site.

$$GRC_X = \frac{(\ln X_H - \ln X_L)}{(ln RGR_H - \ln RGR_L)} \qquad (10)$$

where GRC_X is the growth response coefficient of a given RGR component X (NAR, SLA or LMR) with respect to a given factor (K, CRF_{28} or N) that increased RGR between 4 and 6 months pre-flowering (hereafter called an 'influential factor') at a given site; X_H and X_L is the mean of the RGR component at respectively a non-limiting high and limiting low level of the influential factor at a given site; RGR_H and RGR_L are the mean relative growth rates at respectively a non-limiting high and limiting low level of the influential factor, at a given site.

According to Poorter and Nagel (2000), the sum of growth response coefficients is one, if RGR and its components are well estimated at the different levels of the influential factor. The greater the value of the growth response coefficient for a given RGR component, the higher the contribution of that component to the observed

decrease in RGR with respect to the influential factor at the growth-limiting low level. When a given component has a growth response coefficient greater than one, its effect on RGR is counterbalanced by negative growth response coefficients for one or both of the remaining components in a trade-off manner.

3. Results

3.1. Rate of banana phenological development

Plants grown at Ntungamo flowered at a younger physiological age than those grown at Kawanda by 739 °C d. However, plants grown at Kawanda flowered at an older chronological age than those grown at Ntungamo by 51 days. The physiological age at harvest for plants grown at Ntungamo was also younger than that for plants grown at Kawanda by 949 °C d while the reverse was true for chronological age at harvest, which was older for plants grown at Ntungamo than for plants grown at Kawanda by 60 days. Likewise, bunch filling duration for plants grown at Ntungamo was shorter than that for plants grown at Kawanda by 217 °C d with respect to physiological time but 7 days longer with respect to chronological time (Table 2).

The physiological and chronological age at flowering and harvest for plants that received no N were both greater than the corresponding values for plants that received N (Table 2) but there was no difference in bunch-filling duration due to N. On its own, K had no effect on rate of phenological development. However, plants grown at Ntungamo that received K had younger physiological age at flowering and at harvest than those that received no K. There was no difference in physiological age at flowering between K rates for plants grown at Kawanda. There was also no difference in chronological age at harvest between K rates for plants grown at Kawanda (Fig. 2).

Plants grown at Ntungamo required a threshold total dry mass (parameter C, Eq. (7)) of 1.45 kg per plant to flower, which was similar to the corresponding value of 1.56 kg per plant for plants grown at Kawanda (Table 3). These values were similar to 1.37 and 1.47 kg per plant obtained for Kawanda and Ntungamo (Fig. 3), respectively using the method by Moot (1997). The characteristic total dry mass at half the asymptotic maximum physiological age at flowering (parameter B, Eq. (7)) for plants grown at Ntungamo (0.38 kg per plant) was greater than that for plants grown at Kawanda by 0.14 kg per plant. However, the asymptotic maximum physiological age at flowering (parameter A, Eq. (7)) for plants grown at Kawanda (4761 °C d) was older than that for plants grown at Ntungamo by about 750 °C d (Table 3).

Table 2
Effects of potassium (K) and nitrogen (N) on rate of phenological development and bunch-filling duration of East African highland bananas in central (Kawanda) and south western (Ntungamo) Uganda.

Factor	Level	n	Duration to flowering		Duration to harvest		Bunch-filling duration	
			Physiological age	Chronological age	Physiological age	Chronological age	Physiological age	Chronological age
			[z]Mean ± s.e (°C d)	[z]Mean ± s.e (d)	[z]Mean ± s.e (°C d)	[z]Mean ± s.e (d)	[z]Mean ± s.e (°C d)	[z]Mean ± s.e (d)
Site	Kawanda	180	3849 ± 33.5 b	460 ± 4.6 a	4844 ± 33.1 b	580 ± 4.6 a	1008 ± 07.0 b	122 ± 0.9 a
	Ntungamo	94	3110 ± 51.1 a	511 ± 7.0 b	3895 ± 50.4 a	640 ± 7.1 b	791 ± 11.5 a	129 ± 1.3 b
Potassium	−K	101	3553 ± 51.7 a	478 ± 7.0 a	4475 ± 51.0 a	603 ± 7.1 a	930 ± 10.0 a	125 ± 1.3 a
	+K	173	3583 ± 34.2 a	479 ± 4.7 a	4497 ± 33.7 a	602 ± 4.7 a	935 ± 07.7 a	125 ± 0.9 a
Nitrogen	−N	118	3682 ± 49.8 b	495 ± 6.8 b	4596 ± 49.1 b	617 ± 6.9 b	933 ± 09.8 a	124 ± 1.3 a
	+N	156	3505 ± 34.6 a	468 ± 4.7 a	4423 ± 34.2 a	593 ± 4.8 a	934 ± 07.7 a	125 ± 0.9 a
Source of variation								
Crop cycle (C)			0.651	0.038	0.385	0.005	0.001	0.009
Replication (Rep)			0.297	0.297	0.226	0.528	0.045	0.052
C × Rep			1.000	0.648	0.995	0.346	0.387	0.090
Site (S)			<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Potassium (K)			0.845	0.747	0.978	0.552	0.994	0.834
Nitrogen (N)			0.006	0.003	0.007	0.015	0.934	0.262
S × K			0.004	0.007	0.004	0.005	0.595	0.206

[z] Adjusted for crop cycle and replication effects; s.e = standard error of mean; Means for a given factor in the same column followed by the same letter are not significantly different ($P > 0.05$); −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; −N = 0 kg N ha^{-1} yr^{-1} applied; +N = 150 to 400 kg N ha^{-1} yr^{-1} applied. All interactions after S × K (not shown) were not significant.
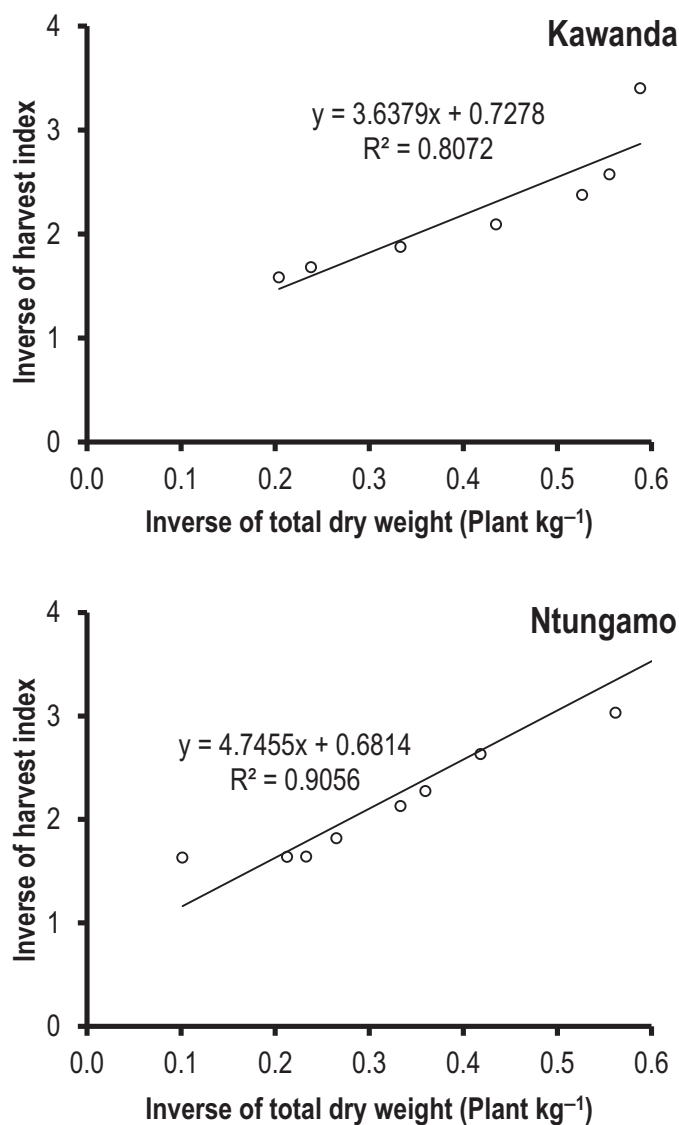

Fig. 3. Relationship between harvest index and total dry weight at harvest of East African highland banana in central (Kawanda) and south western (Ntungamo) Uganda. Threshold dry mass for flowering is the inverse of the intercept at each site

3.2. Effect of rainfall, potassium and nitrogen on growth

Compared at the same phenological stage relative to flowering, plants that received K had greater total dry mass than those that received no K by 30 to 80% between 6 months pre-flowering and 3 months post-flowering (Fig. 4A). Leaf dry mass exhibited similar trends and magnitudes of change as total dry mass in response to K (data not shown). Leaf area on the other hand increased by up to 26% with K application between 6 months pre-flowering and 3 months post flowering (Fig. 4D). Compared at the same phenological stage between 6 months pre-flowering and 3 months post-flowering, CRF$_{28}$ and N had no effect on total dry mass (Fig. 4B and C, respectively) and leaf area (Fig. 4E and F, respectively).

Plants that received no K at Ntungamo were generally more stunted than corresponding plants at Kawanda. From 3 to 1 months pre-flowering, plants that received K at Ntungamo had higher total dry mass and larger leaf area than corresponding plants at Kawanda but from flowering stage up to 3 months post-flowering, this difference was no longer significant (data not shown).

Absolute growth rates from 6 to 4 months pre-flowering were mainly affected (in descending order of magnitude) by CRF$_{28}$, Site and K. Wet conditions in the 28 day-period preceding an event between 6 and 4 months pre-flowering gave thrice the absolute growth rate of dry conditions. Plants grown at Ntungamo had twice the absolute growth rate of those grown at Kawanda. In general, the absolute growth rate for plants that received K was approximately 1.5 times greater than that for plants that received no K but the effect was only significant at 6 and 5 months pre-flowering (Table 4). Plants that received no K at Ntungamo had lower absolute growth rate than their counterparts that received K. Between K rates, plants grown at Kawanda had similar absolute growth rates (Fig. 5). The effect of N on absolute growth rate was not significant (Table 4).

The effects and trends observed on absolute growth rate were also exhibited on RGR (Table 4, Fig. 5) and its physiological component NAR (Table 5, Fig. 6). However, the morphological components of RGR displayed somewhat different trends in direction and order of magnitude with respect to Site, CRF$_{28}$, K and N. From 6 to 4 months pre-flowering, plants that received no K had 6 to 10% greater SLA than plants that received K. Plants that received no K allocated about 1% more ($P < 0.001$) of their total dry matter to the leaves (LMR) compared with plants that received K (data not shown) with this effect being significantly stronger for
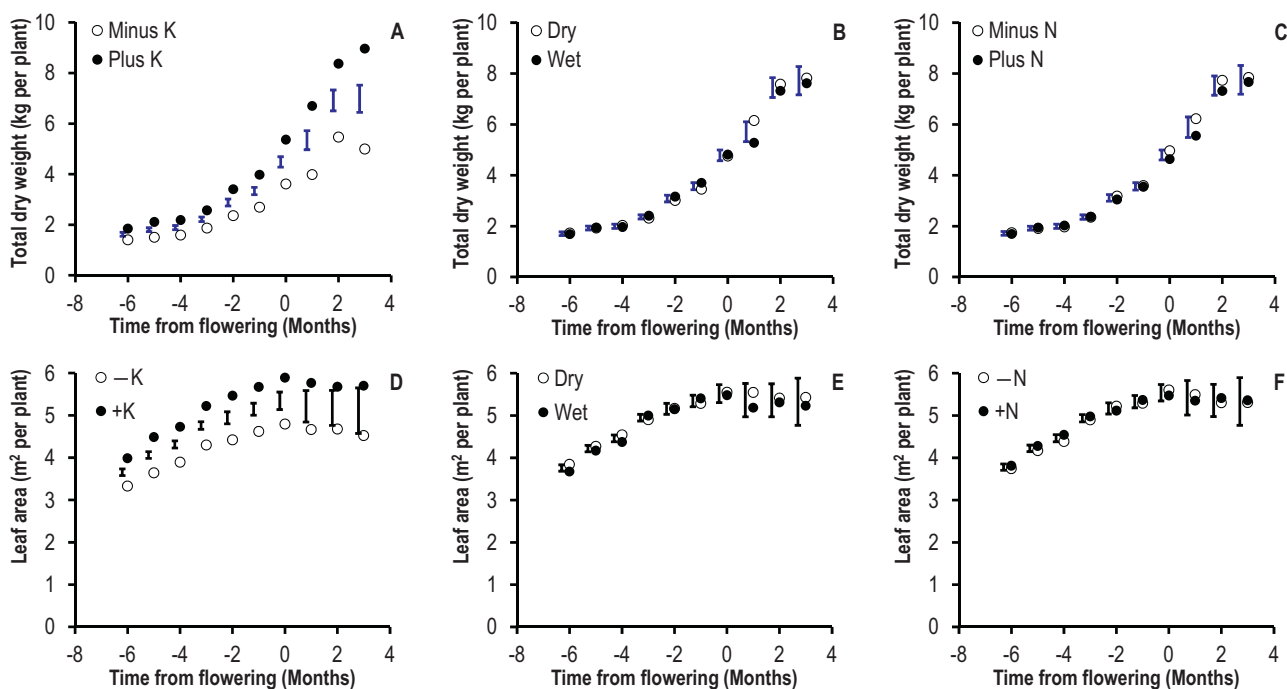
Fig. 4. Effects of potassium (K), rainfall and nitrogen (N) on total dry mass (A–C, respectively) and leaf area (D–F, respectively) of East African highland banana between 6 months pre-flowering and 3 months post-flowering in Uganda. Means are adjusted for crop cycle and replication effects; Bars alongside each pair of means are least significant differences at 95% confidence level; −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; −N = 0 kg N ha^{-1} yr^{-1} applied; +N = 150 to 400 kg N ha^{-1} yr^{-1} applied; Wet is cumulative rain fall received in preceding 28-day period (CRF$_{28}$) ≥84 mm; Dry is CRF$_{28}$ <84 mm.
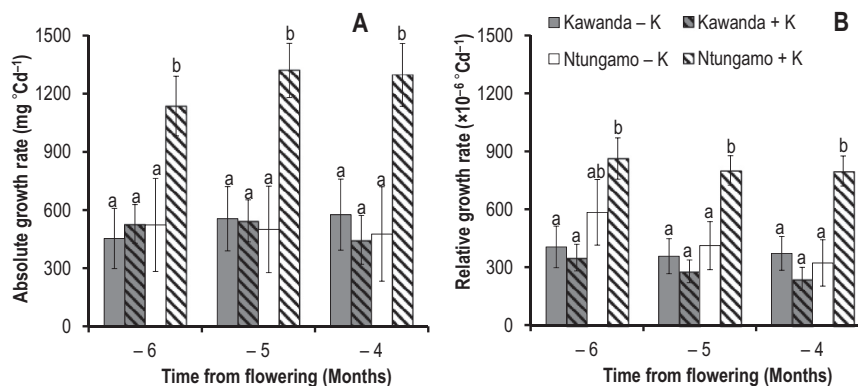

Fig. 5. Site × potassium (K) interaction effects on absolute growth rate (A) and relative growth rate (B) of East African highland banana at Kawanda (central Uganda) and Ntungamo (south-western Uganda). Means are adjusted for crop cycle and block effects; Error bars are standard errors of means; Means crowned with the same lower case letter at a given time from flowering are not significantly (P > 0.05) different −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied

Table 3
Comparison of numerical optimisation model parameter estimates in central (Kawanda) and south western (Ntungamo) Uganda.

Site	n	Parameter estimates (Mean ± se)			R^2	CRMSE
		C (kg plant^{-1})	B (kg plant^{-1})	A (°C d)		
Kawanda	13	1.56 ± 0.031	0.24 ± 0.009	4761 ± 07.7	0.93	0.02
Ntungamo	10	1.45 ± 0.075	0.38 ± 0.033	4010 ± 35.5	0.93	0.03
df	21.0	10.4^z	9.9^z			
t	1.5^{ns}	−4.0**	20.7***			

Parameter C (kg per plant) is the threshold total dry mass for flowering; B (kg per plant) is an empirical characteristic dry mass halfway to parameter A, and; A (°C d) is the potential physiological age at flowering; se = standard error of mean; CRMSE = mean coefficient of variation for the root mean square error from jacknifed pseudo values; R^2 = mean square correlation coefficient from jacknifed pseudo values; df = degrees of freedom, ^{z} adjusted for non-homogeneous variances; t^{ns} = Not significant (2-tailed) at 95.0% confidence level; t^{**} and t^{***} = significant (2-tailed) at 99.0 and 99.9% confidence levels, respectively.

Table 4
Variation of absolute growth rate and relative growth rate of East African highland banana at 6, 5 and 4 months pre-flowering with site, potassium (K) rainfall (CRF_{28}) and nitrogen (N) input.

Factor	Level	Absolute growth rate (mg $(°C\,d)^{-1}$)						Relative growth rate ($\times 10^{-6}\,(°C\,d)^{-1}$)					
		6 Months pre-flowering		5 Months pre-flowering		4 Months pre-flowering		6 Months pre-flowering		5 Months pre-flowering		4 Months pre-flowering	
		n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se
Site	Kawanda	205	505 ± 84 a	162	547 ± 91 a	146	485 ± 105 a	205	367 ± 58 a	162	302 ± 50 a	146	279 ± 50 a
	Ntungamo	118	907 ± 129 b	117	1075 ± 118 b	110	1051 ± 135 b	118	777 ± 90 b	117	686 ± 65 b	110	656 ± 65 b
Potassium	−K	99	479 ± 133 a	83	532 ± 134 a	76	533 ± 150 a	99	470 ± 93 a	83	380 ± 74 a	76	350 ± 73 a
	+K	219	751 ± 85 a	196	870 ± 85 b	180	816 ± 100 a	219	537 ± 59 a	196	497 ± 46 a	180	481 ± 48 a
CRF_{28}	Dry	210	378 ± 87 a	188	479 ± 87 a	160	403 ± 101 a	210	284 ± 60 a	188	283 ± 48 a	160	239 ± 49 a
	Wet	108	1223 ± 123 b	91	1374 ± 127 b	96	1282 ± 141 b	108	965 ± 86 b	91	833 ± 69 b	96	786 ± 69 b
Nitrogen	−N	123	747 ± 124 a	105	615 ± 127 a	99	702 ± 149 a	123	511 ± 86 a	105	393 ± 68 a	99	497 ± 68 a
	+N	195	614 ± 87 a	174	862 ± 87 a	157	748 ± 100 a	195	520 ± 61 a	174	504 ± 48 a	157	407 ± 48 a
Source of variation													
Crop cycle (C)			0.771		0.201		0.923		<0.001		0.748		0.594
Replication (Rep)			<0.001		0.015		0.072		0.239		0.039		0.574
C × Rep			0.453		0.073		0.735		0.323		0.395		0.347
Site (S)			<0.001		<0.001		<0.001		<0.001		<0.001		<0.001
Potassium (K)			0.005		0.005		0.079		0.029		0.049		0.248
CRF_{28}			<0.001		<0.001		<0.001		<0.001		<0.001		<0.001
Nitrogen (N)			0.434		0.066		0.826		0.788		0.077		0.740
S × K			0.303		0.003		0.004		0.396		0.006		0.002
S × CRF_{28}			0.025		0.148		0.919		0.257		0.999		0.769
K × CRF_{28}			0.425		0.464		0.159		0.043		0.024		0.354

[z] Means are adjusted for crop cycle and replication effects; s.e = standard error of mean; Means for a given factor in the same column followed by the same letter are not significantly different (P > 0.05); −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; CRF_{28} = cumulative rain fall received in preceding 28-day period; Wet is CRF_{28} ≥84 mm; Dry is CRF_{28} <84 mm; −N = 0 kg N ha^{-1} yr^{-1} applied; +N = 150 to 400 kg N ha^{-1} yr^{-1} applied. All interactions after K × CRF_{28} (not shown) were not significant.

Table 5

Variation of net assimilation rate and specific leaf area of East African highland banana at 6, 5 and 4 months pre-flowering with site, potassium (K) rainfall (CRF_{28}) and nitrogen (N) input.

Factor	Level	Net assimilation rate ($mg\,m^{-2}\,(°C\,d)^{-1}$)						Specific leaf area ($m^2\,kg^{-1}$)					
		6 Months pre-flowering		5 Months pre-flowering		4 Months pre-flowering		6 Months pre-flowering		5 Months pre-flowering		4 Months pre-flowering	
		n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se	n	[z]Mean ± se
Site	Kawanda	205	160 ± 23.1 a	162	138 ± 21.6 a	146	122 ± 23.2 a	205	11.9 ± 0.12 a	162	11.9 ± 0.13 a	146	12.3 ± 0.15 a
	Ntungamo	118	321 ± 35.8 b	117	289 ± 28.2 b	110	285 ± 30.1 b	118	12.7 ± 0.19 b	117	12.7 ± 0.17 b	110	12.7 ± 0.20 a
Potassium	−K	99	176 ± 36.9 a	83	160 ± 32.3 a	76	144 ± 33.7 a	99	12.7 ± 0.19 b	83	13.1 ± 0.20 b	76	13.3 ± 0.22 b
	+K	219	238 ± 23.3 b	196	218 ± 20.1 b	180	212 ± 22.1 b	219	12.0 ± 0.12 a	196	11.9 ± 0.12 a	180	12.1 ± 0.15 a
CRF_{28}	Dry	210	119 ± 24.1 a	188	121 ± 20.9 a	160	104 ± 22.5 a	210	12.3 ± 0.13 a	188	12.3 ± 0.13 a	160	12.6 ± 0.15 a
	Wet	108	410 ± 34.1 b	91	365 ± 30.1 b	96	338 ± 31.7 b	108	12.0 ± 0.18 a	91	12.0 ± 0.19 a	96	12.4 ± 0.21 a
Nitrogen	−N	123	233 ± 34.1 a	105	177 ± 29.8 a	99	209 ± 32.9 a	123	12.0 ± 0.18 a	105	12.3 ± 0.18 a	99	12.5 ± 0.22 a
	+N	195	209 ± 24.2 a	174	215 ± 20.9 a	157	181 ± 22.4 a	195	12.3 ± 0.13 a	174	12.2 ± 0.13 a	157	12.5 ± 0.15 a
Source of variation													
Crop cycle (C)			<0.001		0.494		0.650		<0.001		<0.001		<0.001
Replication (Rep)			0.280		0.115		0.720		0.055		0.066		0.072
C × Rep			0.719		0.217		0.595		0.111		0.022		0.006
Site (S)			<0.001		<0.001		<0.001		0.069		0.007		0.383
Potassium (K)			0.003		0.026		0.161		<0.001		<0.001		<0.001
CRF_{28}			<0.001		<0.001		<0.001		0.025		0.439		0.717
Nitrogen (N)			0.682		0.122		0.904		0.159		0.415		0.870
S × K			0.265		0.010		0.003		0.747		0.130		0.009

[z] Means were adjusted for site, cycle and replication effects; se = Standard error of mean; Means for a given factor in the same column followed by the same letter are not significantly different (*P* > 0.05); −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; CRF_{28} = cumulative rain fall received in preceding 28 days; Dry is CRF_{28} <84 mm; Wet is CRF_{28} ≥84 mm; −N = 0 kg N ha^{-1} yr^{-1} applied; All interactions after S × K (not shown) were not significant.

G. Taulya et al. / Europ. J. Agronomy 60 (2014) 41–53

49

Table 6
Growth response coefficients for net assimilation rate, specific leaf area and leaf mass ratio of East African highland banana between 6 and 4 months pre-flowering with respect to potassium and rainfall (CRF_{28}) at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

Site	Factor	Growth response coefficients		
		Net assimilation rate	Specific leaf area	Leaf mass ratio
Kawanda	Potassium	0.38	0.49	0.07
	CRF_{28}	0.92	0.04	0.00
Ntungamo	Potassium	1.25	−0.12	−0.02
	CRF_{28}	1.11	−0.09	0.00

CRF_{28} = cumulative rain fall received in 28-day period preceding the date of measurement of relative growth rate and its components net assimilation rate, specific leaf area and leaf mass ratio.

Fig. 6. Site × potassium (K) interaction effects on net assimilation rate (A), specific leaf area (B) and leaf area ratio (C) of East African highland banana at Kawanda (central Uganda) and Ntungamo (south-western Uganda). Means are adjusted for crop cycle and replication effects; Error bars are standard errors of means; Means crowned with the same lower case letter at a given time from flowering are not significantly ($P > 0.05$) different −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied

plants grown at Ntungamo than for corresponding plants grown at Kawanda (Fig. 6).

3.3. Contribution of relative growth rate components

Net assimilation rate accounted for the largest proportion ($\geq$90%) of the observed increase in RGR at both sites in response to wet conditions. In response to K, however, NAR contributed only 38% to the observed increase in RGR at Kawanda while SLA contributed 49% (Table 6). At Ntungamo, the largest proportion of the observed change in RGR in response to K was due to NAR (Table 6). However, the effect of NAR on RGR was counterbalanced by a 10% opposing change in RGR due to SLA at Ntungamo in response to K. Leaf mass ratio had no contribution to the observed RGR change in response to K supply at Ntungamo (Table 6).

4. Discussion

4.1. Trade-off between physiological and chronological age

The highland banana plants in this study exhibited phenotypic plasticity with respect to age at flowering and harvest across the experimental sites (Table 2). As expected, Kawanda's higher effective temperature led to lower chronological age at flowering and at harvest than corresponding values at Ntungamo (Table 2). However, if physiological age would have been the same across sites, then Ntungamo plants should have taken about 121 days more than Kawanda plants instead of the 51 days observed (Table 2). Therefore, contrary to Hypothesis 1 in the current study, flowering (and harvest) was greatly hastened at Ntungamo in physiological time (Table 2). This phenotypic plasticity with respect to physiological age at flowering and harvest suggests that size or total dry mass already accumulated by the plant may matter a lot in highland banana development, as has been shown to be the case with other monocarpic biennials and perennials (Klinkhamer et al., 1987). Growth and development in plants are governed by the rate

of metabolic processes, which in turn are dependent on temperature and size (Gillooly et al., 2001). Since there was no difference in the size (as total dry mass) at flowering and threshold size for flowering (Table 3) between the sites, it is plausible that difference in growth rate, rather than size per se was responsible for the observed phenotypic plasticity in physiological age at flowering across the sites.

The higher characteristic total dry mass (parameter *B* value) and younger asymptotic maximum physiological age at flowering (parameter *A* value) for plants grown at Ntungamo compared with corresponding values for plants grown at Kawanda (Table 3) indicate that the absolute crop growth rate for plants grown at Ntugngamo was about 88% faster than that of plants grown at Kawanda. This coincides with the results from ANOVA on absolute crop growth rate between 4 and 6 months pre-flowering (Table 4). Turner and Lahav (1983) reported bananas to have a smaller NAR and reduced accumulation of total dry mass with rise in day temperature above 25 °C, which they attributed to increase in maintenance respiration. Between 30 and 70% of fresh photo-assimilates are lost on the same day due to maintenance respiration (van der Werf et al., 1994; Atkin et al., 1996). The degree of thermal acclimation, which can alter the relative change in rates of photosynthesis and respiration in plants with increase in ambient temperature, has been shown to vary with plant functional groups and species (Larigauderie and Korner, 1995; Niu et al., 2008). In general, however, the rate of maintenance respiration increases faster than the rate of photosynthesis with rising temperature (Liang et al., 2013) leading to a reduction in NAR and hence slower rate of dry mass accumulation with increase in temperature. Indeed, the NAR at Ntungamo was faster than that at Kawanda (Table 5). The faster absolute growth rate at Ntungamo may thus have been due to lower maintenance respiration carbon costs charged against photo-assimilates under the cooler ambient temperature regimes at Ntungamo than those at Kawanda. This may have enabled Ntungamo plants to attain the threshold size for flowering sooner than Kawanda plants leading to the observed phenotypic plasticity in physiological age at flowering and at harvest across the sites.

Differences in absolute growth rate as determined by the rates of photosynthesis and maintenance respiration may also explain the significant Site × K interactions on physiological age at flowering and at harvest (Fig. 2). Potassium stimulates photosynthesis through activation of photosynthetic enzymes and loading of photo-assimilates into the phloem for translocation to various sinks thereby removing the negative feedback, which the assimilates' accumulation in leaves exerts on photosynthesis (Pettigrew, 2008; Gerardeaux et al., 2010). However, the effect of K input on total dry mass accumulation through increased photosynthesis may have been masked at Kawanda due to size-induced increase in maintenance respiration carbon costs (Amthor, 1984; Gillooly et al., 2001). Kawanda plants that received K were on average about 20 to 40% greater in total dry mass than their counterparts that received no K (data not shown). The combined effect of warmer temperature and greater size may have increased maintenance carbon costs charged against photo-assimilates to such an extent that differences in the NAR between K rates at Kawanda were masked. With similar NAR (Table 5) and hence similar crop growth rates (Fig. 5A) between K rates, plants required similar amount of time to attain the threshold size for flowering resulting in similar physiological age at flowering and harvest at Kawanda, unlike at Ntungamo (Fig. 2).

The cumulative amount of rainfall received over a 28-day period preceding an event tripled the absolute growth rate (Table 4). Banana plants are particularly sensitive to soil water supply and rapidly close their stomata under constrained water supply from the soil (Turner et al., 2008; Carr, 2009). However, CRF_{28} did not affect total dry mass accumulation (Fig. 4B). It is probable that the 4-week interval considered in this study was too short for substantial effects of CRF_{28} on total dry mass accumulation to be realised with only 6 months to flowering. van Asten et al. (2011) found a strong impact of drought stress within 12 months to harvest on fresh bunch yield. Fresh bunch yield is linearly related to total dry mass of banana biomass and so it is likely that over time, drought stress delays flowering (Carr, 2009; Damour et al., 2012).

Delay in flowering without N application (Table 2) may have arisen from reduced light use efficiency due to N deficiency (Zhao et al., 2005). This may have resulted in reduced rate of dry mass accumulation. Plants then took longer to attain the threshold dry mass for flowering or building reserves for supporting bunch filling after flower emergence. This may also explain the similarity in total dry mass at flowering with and without N (Fig. 4C). These results corroborate those of Damour et al. (2012). Similar to the 0 to 450 kg N ha^{-1} yr^{-1} applied in the current study, Damour et al. (2012) applied 0 to 420 kg N ha^{-1} yr^{-1}, but also got no difference in girth at base at flowering stage between the N rates. Girth at base is related to the total dry mass (Nyombi et al., 2009) and fresh bunch weight (Wairegi et al., 2009) of banana. Damour et al. (2012) also reported 40- and 70-day delays to flowering for the second and third crop cycle, respectively, of Cavendish bananas (cv. Grand Nain) in response to withholding N in the French West Indies.

The mean bunch filling duration (i.e. difference between age at flowering and age at harvest), was generally around 930 °C d between N and K rates (Table 2). This is comparable to the 970 °C d reported by Umber et al. (2011) and the range 950–1120 °C d reported by Bugaud et al. (2009). Both studies used a base temperature of 14 °C. The mean bunch filling duration at Kawanda (1008 °C d) was also within the range of values published in literature. However, the mean bunch filling duration at Ntungamo (791 °C d) was rather short compared with the range reported in literature. The chronological bunch filling duration for Kawanda is comparable to the mean bunch filling duration range of 100 to 121 days reported by Bugaud et al. (2006). Given that the difference in effective temperature between Ntungamo and

Kawanda was only 2.3 °C, the difference in bunch filling chronological duration (7 days) is short compared with the observed difference in growing degree days (217 °C d). Altogether, the results suggest that apart from accumulating a certain heat sum, rapid rate of production of assimilates can to some extent reduce the physiological and chronological age to flowering and bunch maturity in highland banana.

4.2. Relative contribution of physiological and morphological components

Specific leaf area was significantly larger among plants that received no K compared with those that received K (Table 5), especially for plants grown at Ntungamo (Fig. 6B) where K deficiency was more pronounced. Plants that received no K exhibited a response similar to plants subjected to shading, which increase their SLA as a morphological strategy for maximising light interception per unit of dry matter under low light intensity conditions (Poorter et al., 2009). However, plants that received no K in the current study had smaller leaf area (Fig. 4D). The increase in SLA is thus unlikely to have resulted from low light intensity due to increased mutual leaf shading within the canopy. Moreover, banana leaf lamina expansion, and hence leaf area, is complete by the time the leaf emerges from the pseudostem and unfurls (Turner et al., 2008). Impaired assimilate production and translocation to the developing leaves, as reported in K-deficient cotton plants (Gerardeaux et al., 2010), may have caused the increase in SLA among plants that received no K in the current study rather than mutual shading. This is supported by the higher LMR of plants that received no K, especially at Ntungamo (Fig. 6C). Gerardeaux et al. (2010) also observed an increase in fraction of total biomass allocated to the leaves in K-deficient cotton plants which they attributed to assimilates retained in the leaves due to impaired translocation. Similar to the responses of herbaceous species (Shipley, 2006), LMR had minimal contribution to the increase in RGR with increase in CRF_{28} and K application at both sites, according to their respective growth response coefficients unlike NAR and SLA (Table 6).

The inversion in the contribution of NAR to the observed increase in RGR at Kawanda with increase in CRF_{28} and K (Table 6) may be due to the coupling of the effects of rainfall with those of temperature, unlike with the effects of K. The mean maximum daily temperature on wet days (at least 3 mm of rainfall per day) was lower ($t = 7.305$; df = 728; 2-tailed significance <0.001) than that on dry days by 1.1 °C. This may have reduced maintenance respiration losses of carbon at Kawanda thus increasing NAR and its contribution to the observed increase in RGR in response to wet conditions but not in response to K. However, Kawanda plants that received K had the smallest SLA (Fig. 6B), which is associated with high light use efficiency. Leaves with small SLA have more layers of palisade cells (Nishio et al., 1993), which effectively increases the chloroplast density per unit leaf area and capture of photosynthetically active radiation with concomitant increase in carbon dioxide conductance (Syvertsen et al., 1995), thereby enhancing light use efficiency. Higher light use efficiency among plants that received K may thus explain the increased contribution of SLA to the observed increase in RGR compared with the contribution from NAR with respect to K at Kawanda (Table 6). This finding is in line with that by Nyombi (2010) whose highland banana growth simulation model revealed that plants grown at Kawanda had higher light use efficiency than those grown at Ntungamo. Plants grown at Ntungamo with no K input had the largest SLA (Fig. 6B) and are thus likely to have had lower light use efficiency, which may have contributed to the negative growth response coefficients for SLA observed at Ntungamo (Table 6).

5. Conclusions

Highland banana flower at a younger physiological age under favourable conditions (optimal K and N supply, and lower temperatures) for net photosynthesis because they attain the threshold total dry mass for flowering earlier in chronological time. The threshold total dry mass for highland banana flowering is about 1.5 kg per plant, irrespective of differences in growth potential at the site of cultivation. Under wet conditions (i.e. at least 3 mm of total rainfall per day), NAR contributes more to sustaining RGR than SLA and LMR. The same is true with optimal K supply, provided cool mean daily temperatures (approximately 20 °C) prevail. Under warmer conditions, NAR contributes a bit less than SLA towards highland banana RGR. Nitrogen deficiency delays flowering though it has no impact on RGR and its components when compared at similar phenological stages. Further studies are needed to unravel the effects of heat stress from those of drought stress on growth and yield of highland banana to guide development of interventions to mitigate the expected effects of global warming.

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