Allometric growth relationships of East Africa highland bananas (*Musa* spp., AAA-EAHB) cv. Kisansa and Mbwazirume

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Abstract

Highland bananas are an important staple food in East Africa, but there is little information on their physiology and growth patterns. This makes it difficult to identify opportunities for yield improvement. We studied allometric relationships by evaluating different phenological stages of highland banana growth for use in growth assessment, understanding banana crop physiology and yield prediction. Pared corms of uniform size (cv. Kisansa) were planted in a pest free field in Kawanda (central Uganda), supplied with fertilizers and irrigated during dry periods. In addition, tissue-cultured plants (cv. Kisansa) were planted in an adjacent field and in Ntungamo (southwest Uganda), with various nutrient addition treatments (of N, P, K, Mg, S, Zn, B, and Mo). Plant height, girth at base, number of functional leaves, and phenological stages were monitored monthly. Destructive sampling allowed derivation of allometric relationships to describe leaf area and biomass distribution in plants throughout the growth cycle. Individual leaf area was estimated as LA (m^2) = length (m) x maximum lamina width (m) x 0.68. Total plant leaf area (TLA) was estimated as the product of the measured middle leaf area (MLA) and the number of functional leaves. Middle leaf area was estimated as MLA (m^2) = −0.404 + 0.381 height (m) + 0.411 girth (m). A light extinction coefficient (k = 0.7) was estimated from photosynthetically active radiation (PAR) measurements in a 1.0 m grid over the entire day. The dominant dry matter (DM) sinks changed from leaves at 1118 ^oC d (47% of total DM) and 1518 ^oC d (46% of total DM), to the stem at 2125 ^oC d (43% of total DM) and 3383 ^oC d (58% of total DM), and finally to the bunch at harvest (4326 ^oC d) with 53% of total DM. The allometric relationship between above-ground biomass (AGB in kg DM) and girth (cm) during the vegetative phase followed a power function, AGB = 0.0001 (girth) $^{2.35}$ (R^2 = 0.99), but followed exponential functions at flowering, AGB = 0.325 $e^{0.036\ (girth)}$ (R^2 = 0.79) and at harvest, AGB = 0.069 $e^{0.068\ (girth)}$ (R^2 = 0.96). Girth at flowering was a good parameter for predicting yields with R^2 = 0.7 (cv. Mbwazirume) and R^2 = 0.57 (cv. Kisansa) obtained between actual and predicted bunch weights. This papers shows that allometric relationship can be derived and used to assess biomass production and for developing banana growth models, which can help breeders and agronomists to further exploit the crop's potential.

Key words: girth, height, leaf area, biomass, radiation interception

1. Introduction

East africa Highland bananas (*Musa* spp., AAA-EAHB) are an important staple starch food and cash crop in the great lakes region (i.e. Uganda, Tanzania, Rwanda, Burundi, parts of eastern Democratic Republic of Congo). Bananas have been cultivated in this region for the last 1000−1500 years, but there is little information on their physiology and growth patterns. Knowledge on banana crop physiology and growth patterns is important to establish the potential of the crop, explore the possibility of extending the crop to other areas and improve yields by resolving major yield constraints.

Crop growth simulation models are a powerful tool in understanding processes involved in plant growth and for yield prediction (Van Ittersum et al., 2003). The data required to develop and test such models include estimate of leaf area index (LAI), radiation interception and extinction, and dry matter production and allocation to the different plant parts throughout the growth cycle. When studying growth and development of large crops such as banana, such measurements are laborious and time consuming. An alternative to these measurements is to generate and use empirical relationships, relating changes in biomass to thermal or physiological time or to simple measurable morphological traits (Reddy et al., 1998; Niklas, 2005).

Knowledge of allometric relationships in crops is important in growth assessment and resource use optimisation. For example, simple allometric models for estimating LAI from morphological traits like plant girth and height can enable rapid growth assessment in the field. LAI determines to a large extent the amount of photosynthetically active radiation (PAR) intercepted by plants. Radiation interception has a direct influence on important plant processes such as photosynthesis, transpiration and translocation of assimilates (Jones, 1985). However, few direct radiation measurements have been made in the field due to the difficulty in obtaining accurate measurements, and the time and effort required.

Allometric relationships for partitioning of dry matter among the leaves, stems, storage or reproductive organs and roots through ontogeny are needed facilitate the study of highland bananas. For example, biomass allocation between leaves, stems and fine roots has a direct influence on plant growth (Reich et al., 1998). Changes in partitioning during growth reflect differences in inherent respiration rates between organs, changes in photosynthetic distribution to favour organs near the source or dominance of a plant part at a certain phenological stage (Turner, 1994). Partitioning to fruits is important in determining the harvest index.

Allometric relationships have been derived for crops (e.g., Reddy et al., 1998 for soybeans, Kandiannan et al., 2002 for black pepper) and used to estimate yields accurately (e.g. in maize, Sinclair et al., 1990; Tittonell et al., 2005). Allometric relationships are often treated as genetically-fixed characteristics of that plant species (Weller, 1987) or as features of a group of species (Niklas, 1995). Within a diverse species like bananas, allometric differences may be expected between cultivars or clone sets of the same plant (Niklas, 1995). Highland bananas have been classified into five clone sets based on morphological traits (Karamura, 1998). Comparisons of allometric relationships across clone sets can enable use of general or specific allometric relationships. Allometric relationships may be altered through plant genetic modifications that aim to increase the harvest index and environmental (soil) factors (Weiner and Thomas, 1992).

The goal of this study was to derive allometric growth relationships for highland bananas and to assess their potential use in growth assessment (biomass estimation), understanding banana physiology (biomass distribution) and generating data needed for parameterizing and validating a highland banana growth model. The specific objectives were to: (i) generate allometric relationships for above ground biomass and yield estimation and biomass partitioning during ontogeny; (ii) estimate area of a single leaf and total plant leaf area using simple morphological attributes such as girth and height; (iii) develop and assess a simple method for measuring PAR interception by a banana canopy and estimate the radiation extinction coefficient, k.

2. Materials and methods

2.1. Trial sites and management

Measurements of plant morphological characteristics, radiation interception and biomass (by destructive harvesting) were taken in experimental fields in central and southwest Uganda (Table 1). At Senge farm, Kawanda Agricultural Research Institute (00°25'N, 32°31'E) in central Uganda, destructive sampling plots (total area 560 m^2) were established on October 10th 2005 for biomass harvests. Uniform size, pared corms (*Musa* spp., AAA-EAHB cv. Kisansa) were planted in holes (0.6 x 0.6 x 0.45 m deep) at spacing of 3 x 3 m, giving a plant density of 1,111 plants ha^{-1}. Pesticide (Carboruran) (15 g) was applied in the planting holes to control both nematodes and weevils. Fertilizer was

applied in six split applications (March, April, May and August, September, October) corresponding to 250 kg N, 50 kg P, and 400 kg K ha^{-1} yr^{-1}. Plants were irrigated three times a week during the dry periods. Two nutrient omission trials (NOT) were established with various applications of N, P, K, Mg, S, Zn, B, and Mo at Kawanda and on a farmer's field in Ntungamo, southwest Uganda (00°54.53'S, 30°14.86'E). Soil samples were collected at 0−8 cm, 8−16 cm and 16−32 cm. Soil texture was determined using the hydrometer method (Bouyoucos, 1936), and classified using the soil texture triangle. Soil organic matter was analysed by the Walkley-Black method. Total nitrogen was analysed by Kjeldahl oxidation and semi-micro Kjeldahl distillation (Bremner, 1960). Available P, and exchangeable Ca, Mg and K were extracted using the Mehlich-3 method (Mehlich, 1984). Phosphorus in the extract was determined using the molybdenum blue colorimetric method, potassium using a flame photometer and the other bases by atomic absorption spectrometry (Okalebo et al., 2002).

Table 1. Biophysical characteristics of the experimental sites, Kawanda, central and Ntungamo south west Uganda.

Variables	Location	
	Kawanda	Ntungamo
Altitude (m.a.s.l)	1156	1405
Rainfall distribution	Bi-modal (March to June; August to December)	Bi-modal (March to June; August to December)
Total annual rainfall (mm)		
2004	1132	902
2005	1014	1206
2006	1334	1380
Topography	Gently undulating (slope - 5%)	Moderately undulating (slopes - 15%)
Soil textural classification	Sandy clay (52% sand and 40% clay)	Sandy clay loam (70% sand and 25% clay)
Soil chemical properties (mean and range for 0−32 cm)		
Soil pH (1:2.5)	5.5 (4.9−6.2)	4.8 (4.6−5.6)
Organic matter (%)	2.6 (1.0−4.6)	0.7 (0.14−1.9)
Total soil nitrogen (%)	0.1 (0.05−0.2)	0.07 (0.04−0.14)
Extractable P (mg kg^{-1})	1.8 (0.7−8.6)	3.52 (0.61−38.0)
Exchangeable K ($cmol_c$ kg^{-1})	0.4 (0.04−1.0)	0.12 (0.02−0.36)
Exchangeable Ca ($cmol_c$ kg^{-1})	4.5 (2.2−8.6)	1.67 (0.47−7.4)
Exchangeable Mg ($cmol_c$ kg^{-1})	1.48 (0.9−2.9)	0.45 (0.001−1.6)

Pest free (cv. Kisansa) tissue-cultured plants were planted at similar spacing as in the destructive sampling plots in both trials. A completely randomised block design (CRBD) with four replicates was used. Nitrogen (as urea; 46% N) and potassium (as muriate of potash; 52% K) were applied in 8 splits (4 times per rain season). Phosphorus (as triple super phosphate - TSP; 20% P) and 'micronutrients' (Mg, S, Zn, B, and Mo) were applied in two splits at start of each rain season (two times a year). Fertilizers were applied in solution (except TSP) at 40−50 cm from the base of the plant. The fertilizer concentrations in the destructive sampling plots were 3.75 10^{-2} kg N and 6 10^{-2} kg K dm^{-3} and maximum concentrations in the NOT were 4.5 10^{-2} kg N, 6.75 10^{-2} kg K and 2.7 kg Mg dm^{-3}. Routine husbandry practices like pruning dead leaves, weeding, sucker selection and de-suckering were carried out. In Ntungamo, Mbwazirume (*Musa* spp., AAA-EAHB) plants of variable sizes close to flowering were selected from a farmers' field for growth data collection at flowering and yield data at harvest. Kisansa (Musakala clone set) and Mbwazirume (Nakitembe clone set) are common cultivars on Ugandan smallholder farms, due to their potentially large bunch sizes and fingers.

2.2. Allometric relationships and dry matter distribution

Plants were randomly selected during the vegetative phase from the destructive sampling plots on March 10th, May 10th and August 10th 2006. Sampling at flowering stage was done after the flower had fully emerged and the upper hands were exposed. Bunches were harvested after the fingers had completely filled. Height, girth at base and number of functional leaves were recorded. Cumulative degree days were computed for each plant from emergence to the sampling date and phenological stages as follows:

$$\textit{Cumulative degree days} = \sum_{i=1}^{n} (\textit{average temperature day}_i - \textit{base temperature}) \qquad (1)$$

The base temperature for banana growth is 14°C (Robinson, 1996). Weather data were obtained from Kawanda meteorological station. Average thermal time (TSUM, °C d) for each sampling or phenological stage was calculated.

Plants were carefully dug out from the soil, but the root systems were not excavated. The pseudostem, leaf blades including petioles, corm, suckers, peduncle and fingers (if any) were separated. Newly-emerged or sword suckers were split into the corm and pseudostem. Non-differentiated suckers were considered part of the corm. Fresh weights (FW) were measured using a field balance (±0.005 kg). Three sub-samples were

collected from the upper, middle and lower parts of the pseudostem, the third fully open leaf, corm and the peduncle. Banana finger sub-samples were obtained from the upper, middle and lower hands. The skin and pulp were not separated. Sub-samples of each part were bulked, weighed, chopped and dried in a oven at 70°C for 48 h. Dry weights (DW) were taken using a balance (±0.001 kg). Total plant part dry weight was calculated from: dry matter content x total fresh weight. For each sampling, average dry weights of plant parts were computed. Biomass data (corm, pseudostem, leaves, bunch, above ground and total) were regressed with girth and height as explanatory variables to develop power (1) and exponential (2) equations. The equations with the best explanatory power were selected to represent the relationship.

$$y = c(x)^{a} \quad (2)$$

$$y = c\,e^{ax} \quad (3)$$

where y is dry biomass in kg (corm, pseudostem, leaves, bunch, above ground or total); c is the constant; a is the equation parameter; x is plant girth (cm) at the base or height (cm). Above ground biomass (AGB) included the pseudostem, leaves and bunch, and total biomass included AGB and the corm.

To compare allometric relationships between girth at base at flowering and bunch fresh weights at harvest, sixty plants (*Musa* spp., AAA-EAHB cv. Mbwazirume) of variable girth at and near flowering were randomly selected in farmers' field (banana mats at least 5 years old) at the Ntungamo site and marked in March 2006. In addition, two crop cycle 2 plants (*Musa* spp., AAA-EAHB cv. Kisansa) were randomly selected from each plot of the NOT at the Ntungamo site, giving a total of 56 plants of variable sizes (girth) for model calibration. Another set of 56 plants (crop cycle 2) were also randomly selected from the NOT at the Kawanda site for model validation. Height and girth at base at flowering and bunch weight data at maturity were taken using a balance (±0.5 kg). Data for Mbwazirume were split randomly into two parts; one for model calibration and the other for validation. The derived relationships (model calibration) were used to estimate bunch fresh weights. Actual and predicted bunch weights were compared.

2.3. Leaf area measurement

Whole leaves (29 in total) of variable length (0.42–2.5 m) were collected from destructively sampled and border plants of the NOT at Kawanda. For each leaf, the length and maximum width of the lamina were measured, as well as the length and width at 0−15 cm intervals along the midrib from the base to the tip. Measurements were sketched on squared paper and the actual leaf area computed. Assuming a rectangle, with a length equal to that of the leaf and width equal to maximum lamina width, the leaf area factor *(laf)* was obtained as the slope of the graph of actual leaf area against rectangular area. Thus, the area of leaf (*LA*, m^2) was computed from:

$$LA = laf \times l \times w \tag{4}$$

where *laf* is the leaf area factor, *l* is the leaf length (m) and *w* is the maximum lamina width (m).

The number of functional leaves varies throughout ontogeny and is affected by environmental factors such as moisture and nutrient stress. Middle leaf area *(MLA)*, which is dependent on plant size (height and girth) was taken to estimate total leaf area of the plant. Model calibration data for *MLA* were collected from 107 banana plants (girth 0.34–0.83 m) randomly selected from different treatments at Kawanda. Height, girth at base, number of functional leaves (>50% of leaf area green) and the length and maximum lamina width of the middle leaf were recorded. For plants with even leaf numbers, the average length and width of the two middle leaves were taken and used to estimate *MLA*. Regression analysis was used to explore relationships between *MLA* and plant height and girth. Data for model validation (height, girth, maximum length and lamina width of all functional leaves) were collected from 74 banana plants from different treatments (girth 0.34–0.74 m) at Ntungamo. Individual leaf area was computed using equation (4). Measured total leaf area (*TLA*, m^2) was computed from:

$$TLA_{measured} = laf \times \sum_{i=1}^{n} (l_i \times w_i) \tag{5}$$

where *laf* is the leaf area factor, l_i is the leaf length (m) and w_i is the maximum lamina width (m).

Two models for prediction of *TLA* were tested:

$$TLA_{predicted} = ((laf \times l \times w) \times n) \quad (6)$$

where ($laf \times l \times w$) is the area of the middle leaf ($MLA_{measured}$) and n is the number of functional leaves, and

$$TLA_{predicted} = (MLA_{predicted} \times n) \quad (7)$$

where $MLA_{predicted}$ is obtained using girth and height, and n is the number of leaves.

2.4. PAR/LAI ceptometer calibration and radiation measurement

The ACCUPAR Model LP-80 (Decagon devices, Pullman, Washington, USA) was used to measure photosynthetic active radiation. The probe is 0.865 m long with 80 photo-sensors that can measure and integrate PAR in a range of 0 to > 2,500 µmol m^{-2} s^{-1} or 0−9.4 MJ m^{-2} d^{-1}(Decagon devices, 2004). The resolution is 1 µmol m^{-2} s^{-1} with a spatial resolution of 0.01 m. The external sensor was connected to the RS-232 port, both the probe and external sensor were levelled on a table in an open space under a clear sky at mid-day (> 600 µmol m^{-2} s^{-1}) for 10 minutes and calibration was done. Recalibration was done after one year. Parallel and perpendicular equidistant transects (1.0 m from the plant) were permanently marked in the experimental plots (Figure 1). The geographical locations of Kawanda (0°N, 32°E) and Ntungamo (1°S, 30°E) were input into the ACCUPAR for each of the sites before measurements for automatic calculation of the zenith angle (z). The difference in zenith angles at both sites was 1^{o}. Senescenced leaves were pruned prior to the measurements to avoid their effect on the fraction of PAR intercepted, *FPARint* (c.f. Muchow et al., 1994; Sinclair and Muchow, 1999). PAR was measured on clear days during the rainy season to minimise the effect of moisture stress on the angle between the leaf lamina and thus on the light extinction coefficient.

To capture the variability in PAR interception over the day (c.f. Monteith, 1994), measurements at ground level were done for three time intervals; 08:00−10:30 hrs, 11:30−14:00 hrs (near solar noon) and 14:30−17:00 hrs. The probe was levelled for each measurement by using a water level. For each of the five plants in the inner rectangle (Figure 1), 18 measurements per interval (9 perpendicular and 9 parallel to the row direction) were done, giving a total of 90 measurements per interval and 270 measurements over the entire day. Above canopy readings were continuously collected in

a non-shaded area. For each measurement, the above and below canopy readings, *T (= PAR below*/*PAR above)*, time, fraction of beam radiation (fb) and the zenith angle (z) were recorded.

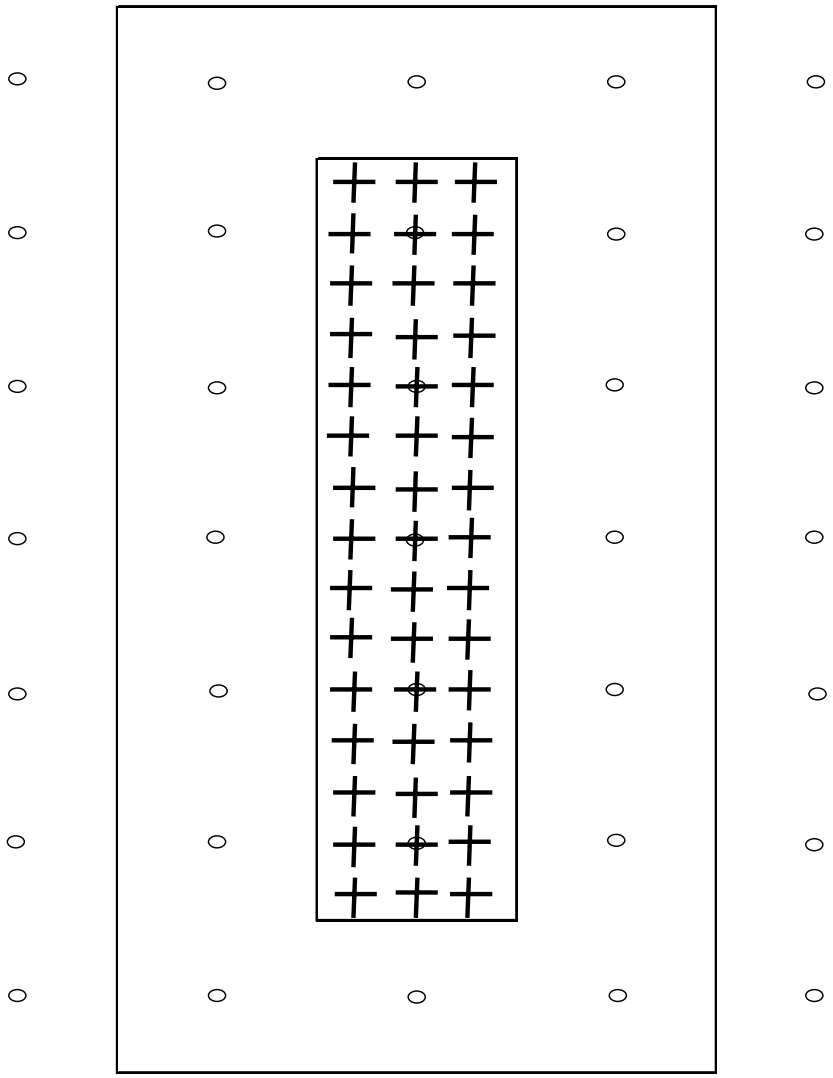

Figure 1. Scheme used to measure PAR in experimental plots of 35 plants (315 m^2) at Kawanda, central Uganda and Ntungamo southwest Uganda. Five plants in the inner rectangle were used for PAR measurements, whereas leaf area data were collected from the 21 plants in the outer rectangle.

The fraction of PAR intercepted *(FPARint)* was estimated from:

$$FPARint = 1 - T_d \quad (8)$$

where T_d is the average of all *T (PAR below/PAR above)* values over several sun elevation angles during the day. To compute the leaf area index, twenty one plants inside the outer rectangle were taken (Figure 1). Length and maximum width of the middle leaf (average length and width of two middle leaves if leaf number was even) and number of functional leaves were recorded. Total plant leaf area measured was estimated from *MLA* times the number of functional leaves *(n)*. Taking an individual mat area of 9 m^2 (3 x 3 m spacing), leaf area index *(LAI)* was computed from:

$$LAI = \frac{laf}{area} \times \sum_{i=1}^{n} (l_i \times w_i \times n_i) \quad (9)$$

where *laf* is the leaf area factor, l_i is the leaf length (m) and w_i is the maximum lamina width (m), area is the total ground area and n_i is the number of leaves.

To compute the number of measurements required to give a reliable estimate of *FPARint*, the *T (PAR below/PAR above)* readings over the day were split into classes of 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240 and 260. The coefficient of variation *(CV)* for each set of measurements was computed from:

$$CV = S/T_{av} \quad (10)$$

where S = standard deviation and T_{av} = average of the measurements.

3. Results

3.1. Allometric relationships

Allometric equations and relationships developed from the plant harvests are presented in Table 2 and Figure 2, respectively. The allometric equations during the vegetative phase had the form $y = c(x)^a$ and were highly correlated to girth at base ($P < 0.001$) with R^2 = 0.98−0.99. At flowering, the equations for leaf and corm biomass followed $y = c(x)^a$, while equations for the pseudostem, bunch, above ground and total biomass followed $y = ce^{ax}$. Although still significant except for pseudostem biomass, the coefficients of determination were lower (R^2 = 0.79−0.89). The exponential equations at flowering showed the importance of girth in determining the bunch dry weight. At harvest, equations for leaf, corm and bunch biomass followed $y = c(x)^a$, whereas

equations for the pseudostem, above ground and total biomass followed $y = ce^{ax}$. Leaf, bunch, above ground and total biomass were strongly related to girth at base ($P < 0.001$) with R^2 = 0.94−0.97. Girth was a better explanatory variable than height during the vegetative phase, at flowering and at harvest.

Table 2. Allometric equations for banana plant components: leaves, pseudostem, corm, bunch, above ground biomass (AGB) and total biomass during the vegetative phase, at flowering and at harvest for banana plants (cv. Kisansa) sampled at Kawanda, central Uganda.

Plant component	*x*	*c*	*a*	S.E. (*a*)	S.E. (*c*)	Adj. R^2	S.E.E.	Significance (*P*)
Vegetative phase								
Leaves	G_{base}	$3\ 10^{-5}$	2.22	0.054	0.00	0.98	0.183	<0.001
Pseudostem	G_{base}	$2.81\ 10^{-5}$	2.5	0.036	0.00	0.99	0.120	<0.001
Corm	G_{base}	$3.18\ 10^{-5}$	2.16	0.056	0.00	0.98	0.189	<0.001
Above ground	G_{base}	$1\ 10^{-4}$	2.35	0.037	0.00	0.99	0.125	<0.001
Total biomass	G_{base}	$1\ 10^{-4}$	2.33	0.034	0.00	0.99	0.116	<0.001
At Flowering								
Leaves	G_{base}	$7.71\ 10^{-5}$	2.28	0.386	0.00	0.89	0.087	<0.01
Pseudostem*	G_{base}	0.174	0.038	0.013	0.152	0.67	0.185	Not sign.
Corm	G_{base}	$4.44\ 10^{-5}$	2.08	0.438	0.00	0.84	0.099	<0.05
Bunch*	G_{base}	0.065	0.021	0.005	0.022	0.82	0.072	<0.05
Above ground*	G_{base}	0.325	0.036	0.009	0.203	0.79	0.131	<0.05
Total biomass*	G_{base}	0.356	0.036	0.008	0.195	0.83	0.116	<0.05
At Harvest								
Leaves	G_{base}	$1.04\ 10^{-8}$	4.305	0.462	0.00	0.94	0.133	<0.001
Pseudostem*	G_{base}	0.028	0.064	0.011	0.018	0.88	0.166	<0.01
Corm	G_{base}	$1\ 10^{-4}$	1.863	0.651	0.00	0.59	0.187	<0.05
Bunch	G_{base}	$5.96\ 10^{-7}$	3.715	0.279	0.00	0.97	0.08	<0.001
Above ground*	G_{base}	0.069	0.068	0.006	0.025	0.96	0.093	<0.001
Total biomass*	G_{base}	0.085	0.066	0.006	0.030	0.96	0.092	<0.001

Equations are $y = c(x)^a$ and $y = ce^{ax}$, where y is the biomass (kg DW); *c* is the constant with a standard error (S.E.(*c*)); *a* is the parameter with a standard error (S.E.(*a*)); *x* is the variable girth at base. S.E.E. is the standard error of estimation. Biomass equations denoted with * follow equation $y = ce^{ax}$, the remainder of the biomass follows $y = c(x)^a$. n = 37 for the vegetative phase, n = 5 at flowering and n = 6 at harvest. Above ground biomass includes the pseudostem, leaves and bunch. Total biomass includes above ground biomass and corm biomass.

The relationship between girth and height was linear, during the vegetative phase (Girth = 0.32 x height; R^2 = 0.99), at flowering and harvest (Girth = 0.25 x height; R^2 = 0.84). We noted a reduction in girth from flowering to harvest. Average girth for the sampled plants

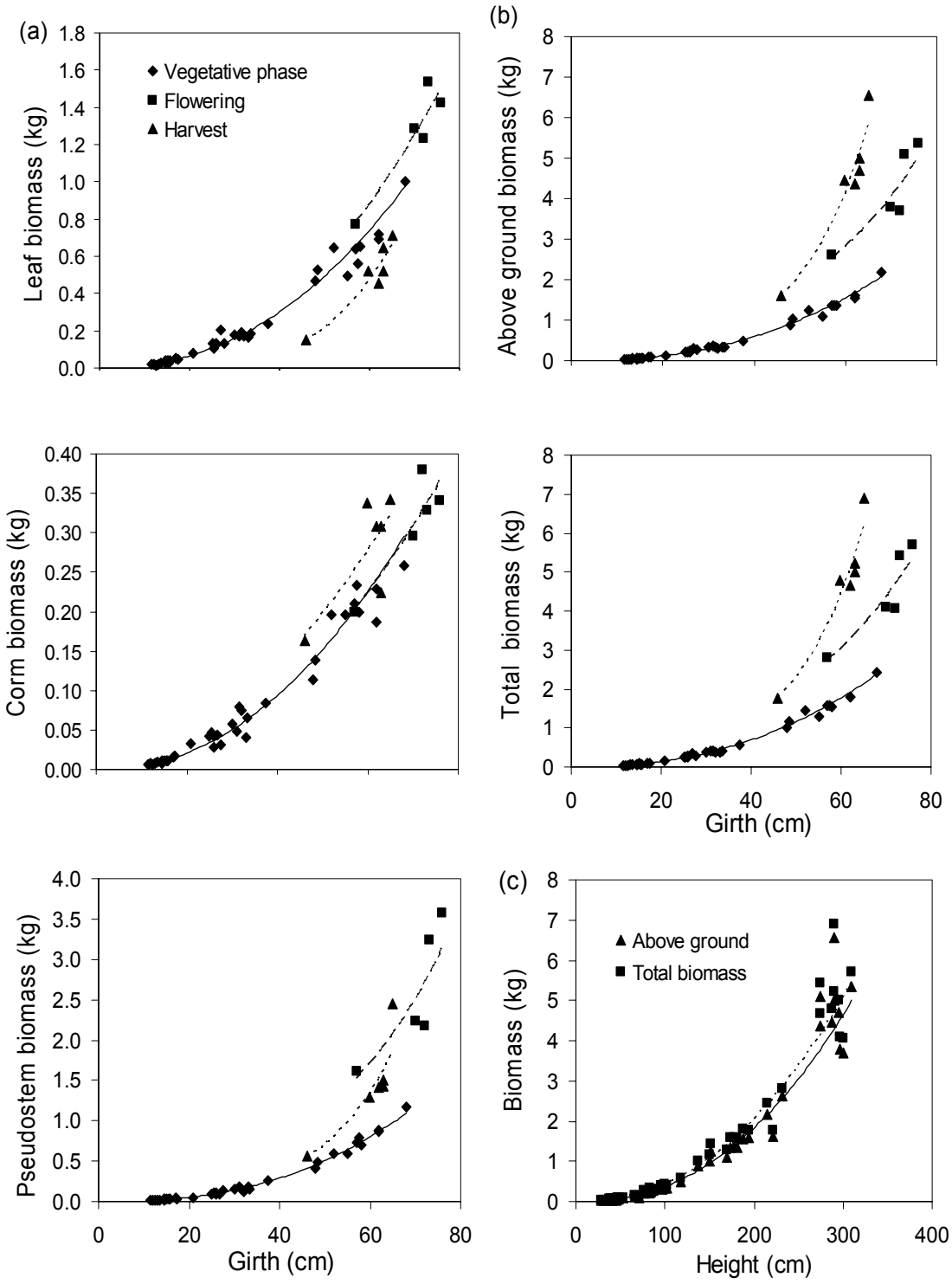

Figure 2. Relationships during the vegetative phase, at flowering and at harvest between leaf, corm and pseudostem biomass with girth – left top to bottom (a), above ground biomass, total biomass and girth (b) and biomass (total and above ground) and height (c) – right top to bottom, for banana plants (cv. Kisansa) sampled at Kawanda, central Uganda. Above ground biomass (AGB) includes pseudostem, leaves and bunch, and total biomass includes AGB and the corm.

at flowering was 68 cm with a reduction of 12% in girth from flowering to harvest. From Table 2 and Figure 2, there are indications of a need for growth stage-specific allometry, resulting from changes in biomass partitioning.

Pooled (over the various sampling dates) leaf, pseudostem and corm biomass equations are presented in Table 3. The equations are highly correlated with girth ($P < 0.001$) with $R^2 = 0.96-0.98$. However, the standard errors of a (S.E.(a)) and the standard errors of the estimates (S.E.E.) are higher. We attribute this to increased variance in data (Figure 2) resulting from changes in partitioning during the growth cycle of the banana plant. This implies that using a general equation to predict plant component biomass may result in a large error, and it is appropriate to use growth stage-specific allometric equations. Plant height was better correlated ($P < 0.001$) with both above ground and total biomass as compared with girth at base (Figure 2c).

Table 3. Biomass equations for pooled banana plant components: leaves, pseudostem, corm, above ground biomass (AGB) and total biomass (cv. Kisansa) sampled at Kawanda, central Uganda.

Plant component	x	c	a	S.E. (a)	Adj. R^2	S.E.E.	Significance (P)
Leaves	G_{base}	$9.48\ 10^{-5}$	2.172	0.060	0.96	0.256	<0.001
Stem	G_{base}	$1.27\ 10^{-5}$	2.775	0.062	0.98	0.260	<0.001
Corm	G_{base}	$2.87\ 10^{-5}$	2.201	0.045	0.98	0.189	<0.001
Above ground biomass	H	$9.29\ 10^{-6}$	2.301	0.043	0.98	0.216	<0.001
Total biomass	H	$1.35\ 10^{-5}$	2.251	0.04	0.98	0.202	<0.001

The equation is $y = c(x)^a$, where y is the biomass (kg DW); c is the constant; a is the parameter with a standard error (S.E.(a)); x is the variable girth at base or height. S.E.E. is the standard error of estimation. $n = 48$. Above ground biomass (kg DW) includes the pseudostem, leaves and bunch. Total biomass (kg DW) includes above ground and corm biomass.

The relationship between *AGB* and *girth* during the vegetative phase followed a power function (Figure 3a). A logarithmic transformation was done to convert power function into a simple linear model with logarithmic transformed variables:

$$1n(AGB) = \beta 0 + \beta 1\ 1n(Girth) + \varepsilon \quad (11)$$

where $\beta 0$ = intercept; $\beta 1$ = slope; and ε = observational error

The residuals were normally distributed. The linear model was retransformed into *AGB*:

$$AGB = (1+\alpha)\,\gamma\,(Girth)^{\beta 1} \quad (12)$$

where α is the difference given by analysis of the log transformed variable (observational error) and $\gamma = e^{\beta 0}$. If α is small, then $(1+\alpha) = e^{\varepsilon}$.

From the regression, $\beta 0 = -9.2$, $\beta 1 = 2.35$ and $\varepsilon = 0.037$. The regression between actual and modelled AGB was highly significant ($P < 0.001$) - (Figure 3b). Allometric relationships during the growth cycle of the banana plant emphasized the importance of girth (Tables 2, 3 and Figure 2), therefore we explored the possibility of using it to estimate bunch weights. The durations for plants used in bunch weight estimation from sucker emergence to flowering, flowering to harvest and the overall crop duration were shorter at Kawanda (465, 115 and 580 days), compared with Ntungamo (499, 132 and 631 days). This is attributed to the lower average temperature at Ntungamo. The regressions between bunch weight and girth at flowering were highly significant ($P < 0.001$) and followed a power functions (Figure 3c, e). Logarithmic transformations were done to convert the power functions into simple linear models with logarithmic transformed variables:

$$1n\,(Bunch\,weight) = \beta 0 + \beta 1\;1n\,(Girth) + \varepsilon \quad (13)$$

The residuals were normally distributed. The linear model was retransformed into bunch weight;

$$Bunch\,weight = (1+\alpha)\;\gamma\,(Girth)^{\beta 1} \quad (14)$$

where α is the difference given by analysis of the log transformed variable (observational error) and $\gamma = e^{\beta 0}$. If α is not large, then $(1+\alpha) \approx e^{\varepsilon}$. From the regressions, $\beta 0 = -5.2$, $\beta 1 = 1.925$ and $\varepsilon = 0.24$ for cv. Mbwazirume and for cv. Kisansa, $\beta 0 = -13$, $\beta 1 = 3.73$ and $\varepsilon = 0.257$. The regressions between actual and predicted cv. Mbwazirume and cv. Kisansa fresh bunch weights were significant ($P < 0.001$). The model estimated small and large Mbwazirume bunch weights better (Figure 3d) than medium bunch weights, which were over or under estimated. We attributed this to the large variance in bunch weights at the same girth for medium size plants. The model estimated small cv. Kisansa bunch weights better, but large bunch weights were over estimated (Figure 3f).

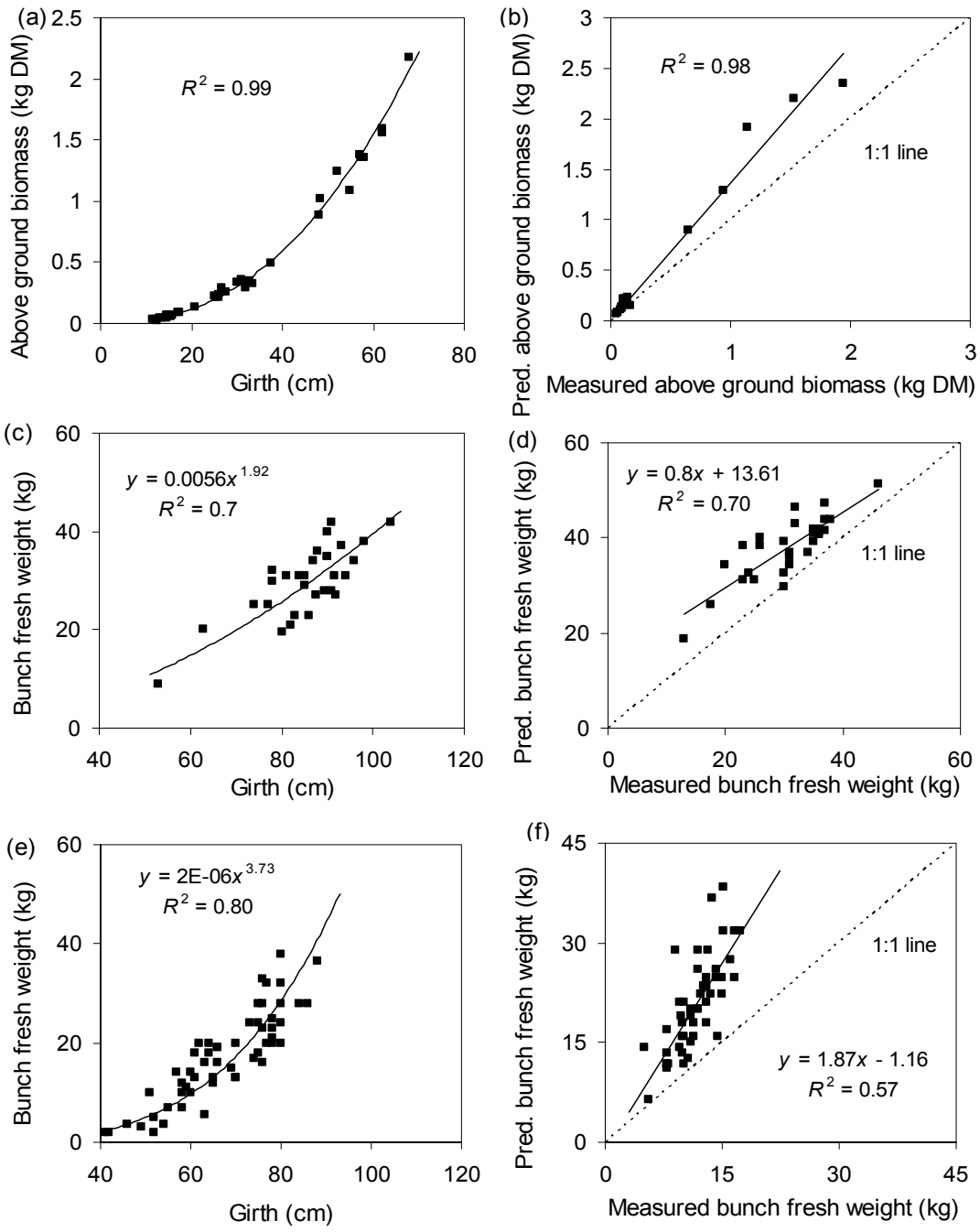

Figure 3. (a) The allometric relationships for above ground biomass estimation during the vegetative phase for banana plants (cv. Kisansa) sampled at Kawanda, central Uganda. (b) the relationship between measured and predicted above ground biomass using the relationship in (a). (c) the allometric equation for bunch fresh weight estimation for banana plants (cv. Mbwazirume) sampled at Ntungamo, southwest Uganda. (d) the relationship between measured and predicted bunch fresh weights using the relationship in (c) for plants sampled at Ntungamo. (e) the allometric equation for bunch fresh weight estimation for banana plants (cv. Kisansa) sampled at Ntungamo, southwest Uganda. (f) the relationship between measured and predicted bunch fresh weights (cv. Kisansa) using the relationship in (e) for banana plants sampled at Kawanda, central Uganda. Validation data (b) was collected from suckers of the destructively sampled plants and 15 tissue-cultured plants planted at Kawanda.

3.2. Biomass partitioning during growth

Dry biomass weights for the plant components and the morphological growth traits at vegetative, flowering and harvest stage are presented in Table 4. Mean leaf, pseudostem and corm biomass increased during the vegetative phase up to flowering.

Table 4. Means and ranges (vegetative phase) or (± SD) (at flowering and harvest) for plant component biomass (kg DW) and morphological attributes height and girth (m) for banana plants (cv. Kisansa) sampled at Kawanda, central Uganda. n = 37 for the vegetative phase, n = 5 at flowering and n = 6 at harvest.

Plant component / attribute	Growth stage		
	Vegetative phase	Flowering	Harvest
Leaves	0.24 (0.014−1)	1.25 (± 0.29)	0.5 (± 0.2)
Pseudostem	0.25 (0.012−1.17)	2.57 (± 0.81)	1.44 (± 0.6)
Corm	0.076 (0.0056−0.26)	0.31 (± 0.07)	0.28 (± 0.07)
Bunch		0.29 (± 0.05)	2.5 (± 0.85)
Height	0.97 (0.28−2.15)	2.82 (± 0.31)	2.77 (± 0.27)
Girth	0.31 (0.11−0.68)	0.70 (± 0.074)	0.60 (± 0.07)

The pseudostem had the largest dry weight and highest standard deviation indicating wide variations in pseudostem dry weights among individual plants. Bunch biomass increased from 0.29 kg DW at flowering to 2.5 kg DW at harvest. Leaf, pseudostem and corm biomass decreased by 60%, 44% and 10%, respectively. Thus, at harvest, 47% of the total plant biomass is left in the field. Biomass proportions partitioned in the plant components and their dry weight development during growth are presented in Figure 4 (a, b). Banana plants had leaves as the strongest sink at TSUM 1118 °C d and 1518 °C d. Leaf dominance was a result of leaf size increase to capture more radiation. Between 1118 and 1518 °C d, sucker initiation and emergence occurred. This sucker will give the next crop harvest. Partitioning to leaves reduced and increased partitioning to the pseudostem made it the strongest sink at 2125 °C d (Figure 4). Partitioning to the sucker reduced as its photosynthetic capacity increased. Partitioning to the pseudostem increased making it the dominant sink at flowering (3383 °C d or 421 days after emergence), thus enabling it to support the bunch. This dominance was reflected in the data of Table 4.

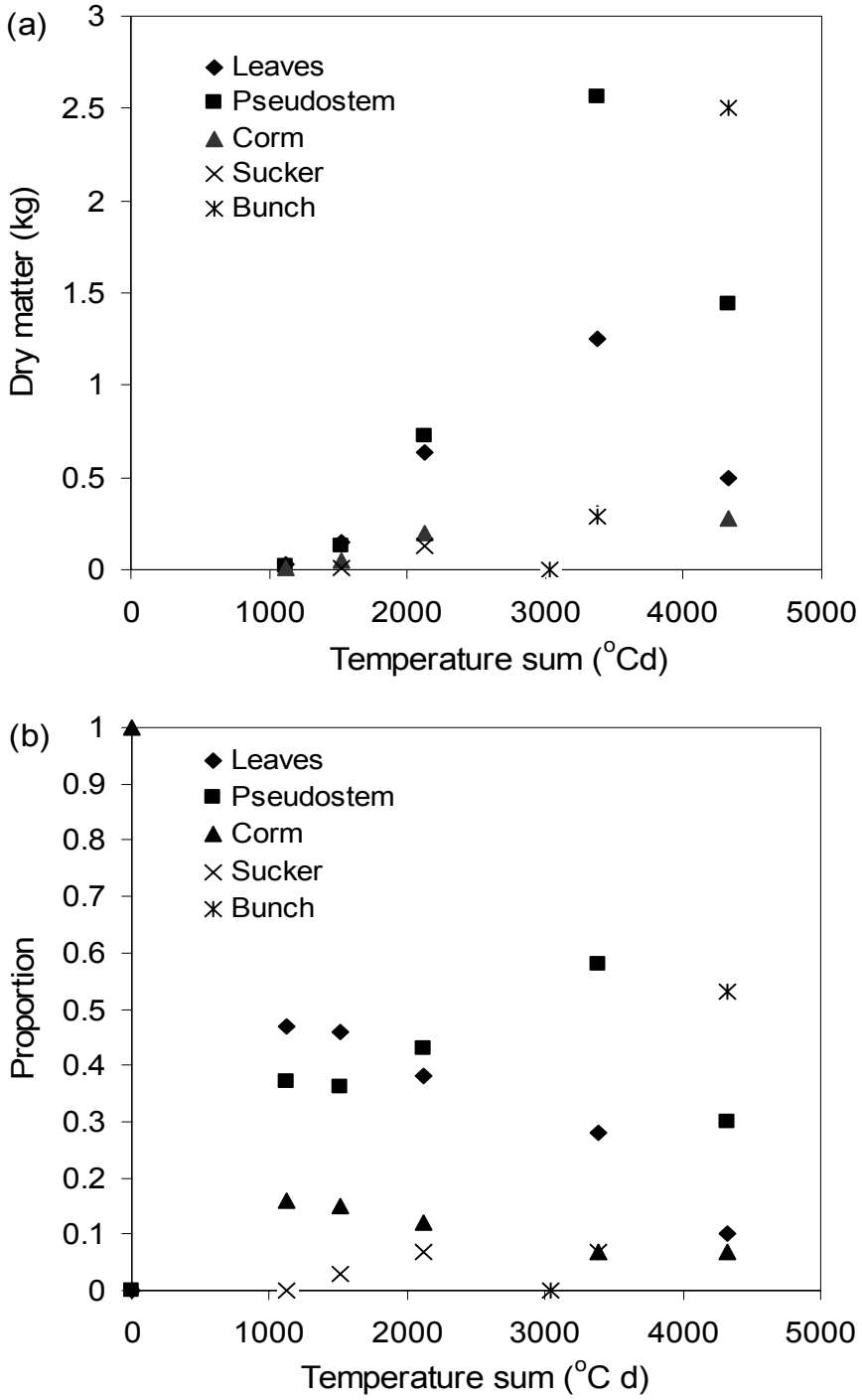

Figure 4. Plant component dry weights (a) and proportions (b) for corm-derived banana plants (cv. Kisansa) sampled at Kawanda, central Uganda, as a function of physiological age, expressed as temperature sum (TSUM). The vegetative phase occurs 0−3034 °C d and floral phase 3034−4326 °C d. At 3383 °C d (a), bunch and corm weights overlap.

Bunch emergence resulted in changes in assimilate partitioning, that made the bunch the strongest sink at harvest (4326 °C d or 523 days after emergence). Corm proportion was

constant between flowering and at harvest. The leaf and pseudostem proportions decreased from 0.28 and 0.58 at flowering to 0.10 and 0.3 at harvest, respectively. Leaf production in bananas ceases at flowering, implying that at harvest, the plant will have fewer leaves. Resources are remobilized from the pseudostem to fill the bunch.

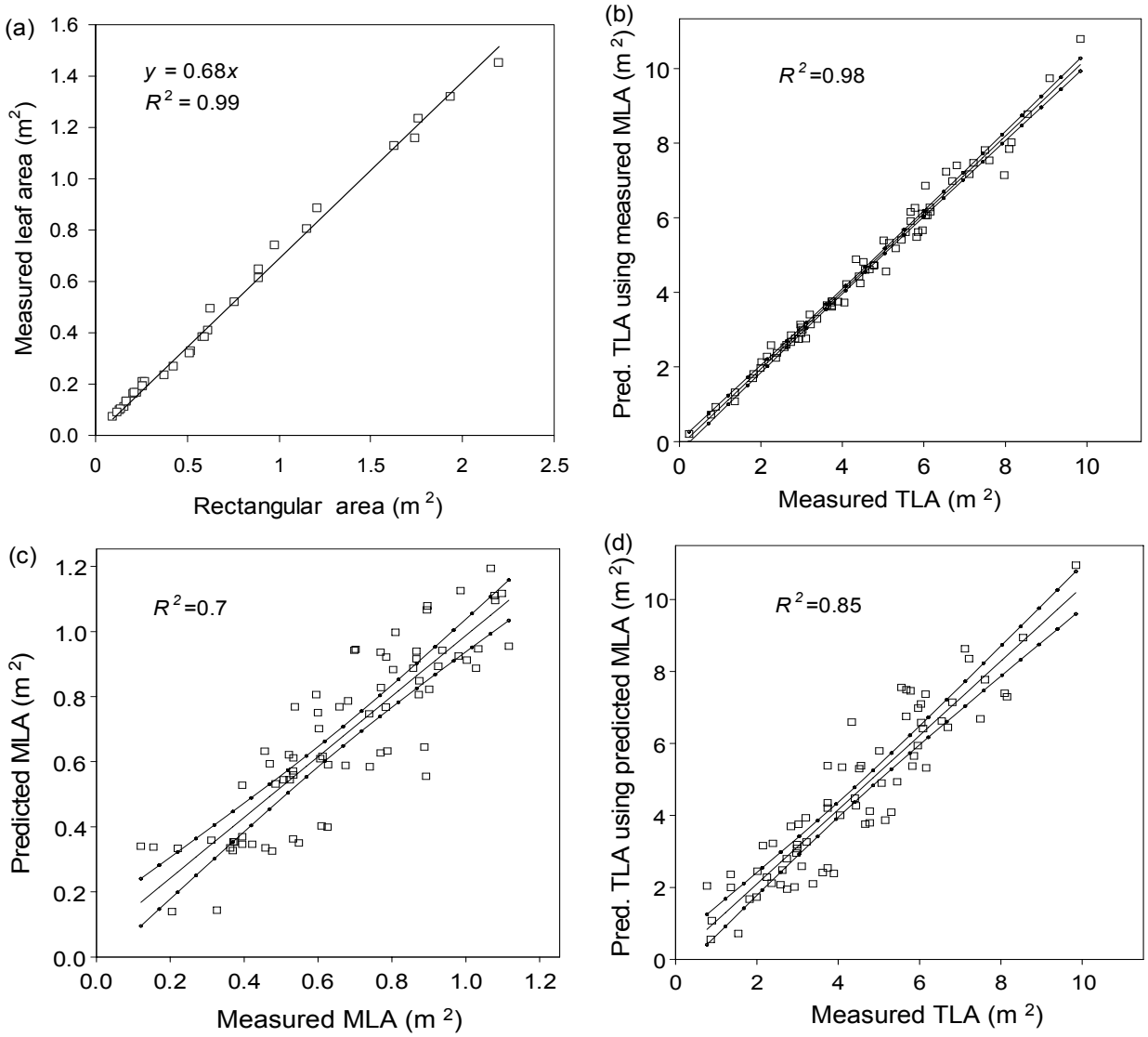

Figure 5. Relationship between measured leaf area and rectangular area (a). Fitted and observed relationships with 95% confidence limits for relationships between measured and predicted total leaf area (measured MLA (middle leaf area) x number of functional leaves) (b), measured and predicted middle leaf area (MLA (m^2) = −0.404 + 0.381 height (m) + 0.411 girth (m)) (c) and predicted (predicted MLA x number of functional leaves) and measured total leaf area (d) for plants sampled from Kawanda (girth 0.34−0.83 m) and Ntungamo (girth 0.34−0.74 m).

3.3. Leaf area estimation

The ratio of the actual area to assumed rectangular area was 0.68, with $R^2 = 0.99$ - (Figure 5a). A good model was obtained for the prediction of *TLA* (Figure 5b), implying that *TLA* can simply be obtained using equation (5). We explored the possibility of using simple morphological traits to estimate total plant leaf area. The multiple regression using data from Kawanda with measured MLA as the dependent variable and plant height and girth as the explanatory variables was significant ($P < 0.001$) with $R^2 = 0.67$. The model equation was MLA (m^2) = −0.404 + 0.381 height (m) + 0.411 girth (m). Average MLA, height and girth were 0.81 m^2, 2.5 m and 0.63 m respectively. The model predicted MLA reasonably well in the lower, middle and upper ranges of the measured values when tested using data from Ntungamo (Figure 5c). The model for prediction of *TLA* from ($MLA_{predicted} \times n$) gave fairly accurate predictions of *TLA* for all the range of measured *TLA* values (Figure 5d).

3.4. Photosynthetically active radiation (PAR) interception measurement

Photosynthetically active radiation (PAR) reaches a peak of about 2500 µmol m^{-2} s^{-1} between 12−13.00 hrs on clear days. *FPARint* was lowest at noon and highest in the mornings (Figure 6a), suggesting that the zenith angle has a large effect on radiation interception.

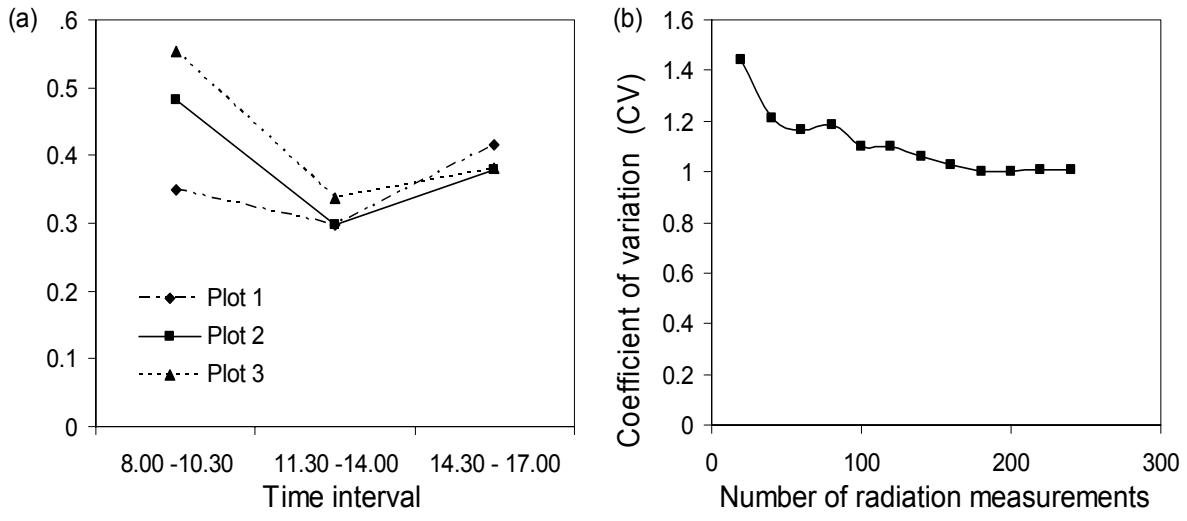

Figure 6. Relationships between the fraction of radiation intercepted and time interval of measurement (a) and between the coefficient of variation and the number of radiation measurements for LAI = 2.67 (b) for measurements at Kawanda, central and Ntungamo, southwest Uganda.

The travelling path of radiation through the canopy is longer in the morning and afternoon as compared with noon. The coefficient of variation *(CV)* reached a minimum at about 200 measurements. However, the additional 100 measurements had a little effect. This implies that 100 measurements can be used as the minimum to get a reliable estimate of *FPARint* (Figure 6b).

The slope of the relationship between –ln (I – PAR below the canopy / I_0 – PAR above the canopy) versus LAI is the light extinction coefficient $k = 0.7$ (Figure 7a). The relationship between the measured LAI values and the fraction of PAR intercepted is close to the law of Beer-Lambert using $k = 0.7$ (Figure 7b).

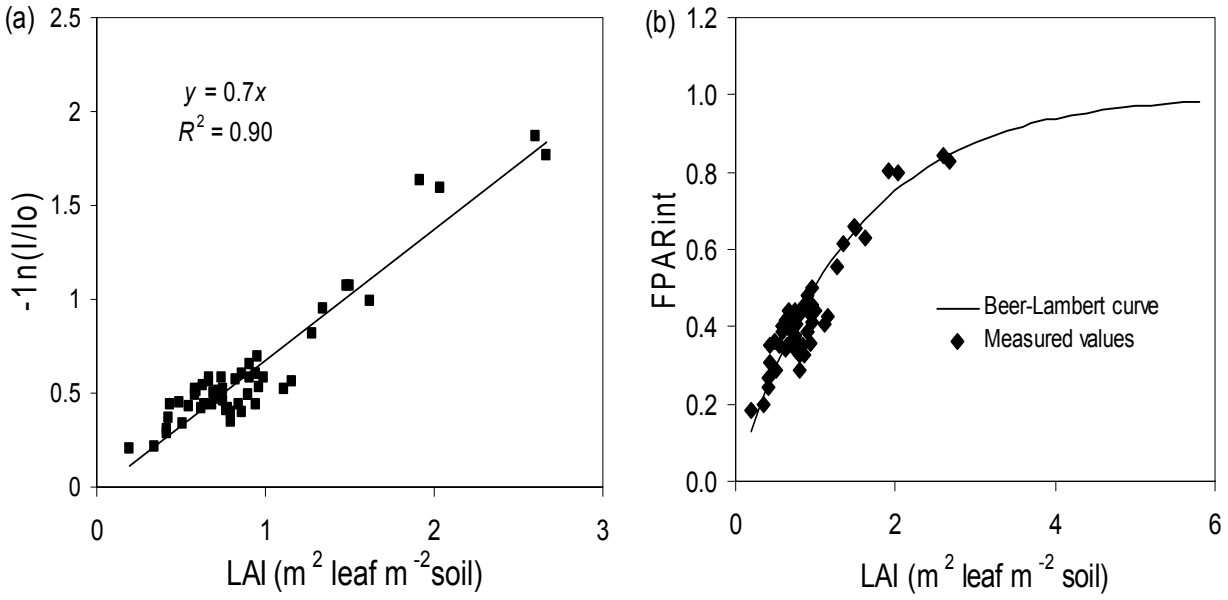

Figure 7. Relationships between the leaf area index and –ln (I/I_0) from which *k* was found by fitting as 0.7 (a) and the fraction of PAR intercepted – *FPARint* using the *k* from (a) - (b) from measurements at Kawanda, central and Ntungamo, southwest Uganda and Beer-Lambert curve. I is PAR below the canopy and I_0 is PAR above the canopy.

4. Discussion

4.1. Allometric relationships

The allometric relationships that were derived in this study for the various banana plant components i.e. corm, pseudostem, leaves, bunch, above ground and total biomass were development-stage specific (Figures 2a and 2b). Girth at base was a better explanatory variable, than height (Table 2). When the biomass component data were

pooled for all the stages, girth at base was again a better explanatory variable, than height (Table 3). However, height was in that case a better explanatory variable than girth when above ground and total biomass were considered. With data pooled over the development stages, the standard errors in Table 3 are much higher than those observed with non-pooled data (Table 2). This is attributed to the increased variance in biomass at later stages of the banana plant growth cycle (Figure 2c). Contrary to forestry studies that have developed allometric equations relating tree diameter at breast height (1.3 m) to attributes such as standing carbon stock and leaf area (e.g. Niklas, 1995; Bartelink, 1997; Ketterings et al., 2001), girth at base for highland bananas gave better relationships compared with girth at 1 m. This may be attributed to the more cylindrical shape of the pseudostem as compared with tree stems. Growth stage specific equations (Table 2) to estimate banana biomass can best rely on girth at base as the explanatory variable. We observed exponential allometric relationships at flowering (between girth at base and bunch biomass) and at harvest (between girth at base and above ground and total biomass). Partitioning to the pseudostem (girth) is an important determinant of the size of the inflorescence at flowering and bunch at harvest (Table 2). Thus, the relationship between girth at base and bunch biomass at flowering show the importance of girth in influencing bunch biomass.

Many authors have successfully used allometric equations based on tree diameter at breast height to estimate stem volume or mass of trees (e.g. Harrington, 1979; Nwoboshi, 1983). Yamaguchi and Araki (2004) used stem volume to estimate fresh and dry weights of highland banana biomass components in northwest Tanzania. In this paper, the established allometric equation for above ground biomass (AGB) during the vegetative phase with girth as the explanatory variable (Figure 3a) gave accurate predictions (Figure 3b). In the field, the relationships can allow quick banana growth assessments especially during the vegetative phase, which if coupled banana phenology can guide management decisions such as fertilizer applications. It is possible to provide banana farmers with tables indicating target girth at key stages during crop growth. Plant performance below threshold values could be attributed to nutrient deficiencies, under conditions where other factors like pest and disease pressure, plant density and available water are not influencing plant size. Improved management practices have been reported to increase the bunch fresh weights (e.g. K and N fertilization, Smithson et al., 2001; mulching and moisture conservation, Ssali et al., 2003) through their effects on plant morphological characteristics such as girth.

The possibility of using girth to estimate bunch fresh weights on farm at Ntungamo and using data from the trials was explored. The model gave fairly accurate cv. Mbwazirume bunch fresh weight predictions (Figure 3d). Stover and Simmonds (1987) reported reliable predictions of bunch weights using girth at flowering. The high variability in bunch size observed even for banana plants (cv. Mbwazirume) with the same girth, especially the medium size bunches, affected the *R* sq. The model can be reliably used to estimate bunch weights on farm, enabling farmers to classify bunches into small, medium and large. The allometric relationships between girth at base at flowering and bunch fresh weight for cv. Mbwazirume (Figure 3c) and cv. Kisansa (Figure 3e) were different. The allometric parameter ($\beta 1$) is much larger for cv. Kisansa (3.73) as compared with cv. Mbwazirume (1.92). This implies a larger increase in bunch weight with girth for cv. Kisansa. This reveals allometric differences between the two banana cultivars belonging to two clone sets (cf. Niklas, 1995), hence specific relationships may be used for each cultivar. Bosch et al. (1996) noted differences in allometric relationships among banana cultivars in Kagera region, Tanzania. The model calibrated using data collected from banana plants (cv. Kisansa) from Ntungamo predicted small bunch fresh weights better at Kawanda, but large bunch fresh weights were over-estimated (Figure 3f). This may be attributed to a smaller allometric parameter ($\beta 1$) at the Kawanda site, implying that the increment in bunch fresh weight with girth is much smaller at Kawanda as compared with Ntungamo. This may be attributed to environmental (soil) factors (cf. Weiner and Thomas, 1992). The plants at Kawanda had reduced source (number of functional leaves) due to drought resulting in banana fingers not filling properly.

4.2. Dry matter partitioning

As a plant grows, its dimensions change in order to maintain a functional balance between assimilation of carbon by the leaves, acquisition of nutrients by roots and mechanical support (Corner, 1949; Dewar et al., 1994). At 1118 and 1518 ^{o}C d after emergence, the leaves are the dominant sink. Leaf dominance in the early stages of banana growth was also reported by Eckstein et al. (1995a) for *Musa* AAA; Cavendish sub-group. Leaves intercept radiation to produce assimilates needed for rapid growth during the first phase of vegetative growth. Changes in partitioning making the stem the dominant sink (Figure 4), enable it to serve a support function to the lamina and the bunch. However in general, the proportions partitioned to the stem in bananas at a given development stage are a function of the nutrition of the plant (c.f. Robinson, 1996) and

the cultivar (c.f. Stover and Simmonds, 1987). Differences in proportions are thus expected in the different highland banana clone sets. After flowering, there is a change in assimilate partitioning to favour the new sink (bunch). Banana fingers, which are the economically valuable part, fill rapidly until harvest, with average duration from flowering to harvest 102 days (Figure 4). At harvest, the bunch had the highest proportion of biomass. The partitioning figure gives a good insight into assimilate distribution during growth. In some growth models, the rates of increase in dry weights of plant parts (kg DM ha^{-1} d^{-1}) are computed as the product of the total growth rate of crop dry matter (kg DM ha^{-1} d^{-1}) and the proportion of dry matter partitioned to the plant part. The partitioning fractions during growth can be calculated and used to calibrate a simple highland banana growth model.

4.3. Total leaf area measurement

The leaf area factor for highland bananas was 0.68 (Figure 5a), implying that the banana leaf area is 68% of the rectangular area. Jannoyer (1995) reported a ratio of 0.83 for *Musa acuminata* cv. Grand Nain, which is genotype AAA. Potdar and Pawar (1991) derived two regressions for estimating individual leaf area in banana cultivars 'Ardhapuri' LA = −0.0334 + (L x W x 0.84) and 'Basrai' LA = 0.0266 + (L x W x 0.76) in India, with leaf area factors 0.84 and 0.76 respectively. The authors however, do not give the length and width values above which the equations are valid. The leaf area factor for highland bananas was lower than reported values. Highland bananas are endemic to the East African highlands, where they have been cultivated for the last 1000−1500 years (Lejju et al., 2006). Differences in leaf morphology within *Musa* species could be attributed to evolution of highland bananas (somatic mutations), intraspecific hybridizations in *Musa acuminata* and interspecific hybridizations between *Musa acuminata* and *Musa balbisiana* that have increased morphological diversity.

A good model for *TLA* prediction was obtained ($MLA_{measured} \times n$) - (Figure 5b). The strength of this model is explained by leaf size changes during plant ontogeny. Two phases of leaf size development are noted in bananas; the exponential phase where individual leaf area is increased by a factor and the linear phase (c.f. Stover and Simmonds, 1987). The increase factor during the exponential phase is a function of nutritional status, development stage, genetic characteristics and other plant factors. The linear phase precedes flowering, is much shorter and characterized by a constant area of the individual leaves. However, just before flowering, the areas of the last 2−3 leaves are

reduced with the flag leaf that precedes the inflorescence being much smaller. For example, during the exponential phase, leaves below the middle leaf have decreasing area whereas those above the middle leaf have increasing area, up to the most recently produced leaf. Thus, by taking the middle leaf, we are apparently taking the average of the upper larger and the lower smaller leaves. *TLA* estimation using this model, however, would require one to continuously climb banana plants. The possibility of using simple morphological traits (height and girth) to estimate total plant leaf area was explored. The first step was to estimate MLA from height and girth, basing on the premise that these morphological traits are related to MLA. A fairly good model for prediction of MLA accounting for 76% of the variance was obtained (Figure 5c). The model for prediction of *TLA* from ($MLA_{predicted} \times n$) was good (Figure 5d). Thus by just taking height, girth and the number of functional leaves, total plant leaf area can be estimated. This allows very quick plant growth assessments in the field. Models ($MLA_{measured} \times n$) and ($MLA_{predicted} \times n$) can be used to estimate leaf area and quickly assess the growth of LAI in the field. However, the models for *MLA* and *TLA* prediction ($MLA_{predicted} \times n$) were calibrated using plants with girth 0.34−0.83 m and tested on plants with girth 0.34–0.74 m. Extension of the model to plants with girth < 0.34 m gave poor results due to the very large variance in total leaf area arising from differences in plant vigour. Thus, the models are applicable to plants with girth > 0.34 m. The basis on morphological traits (height and girth) suggests that models (5 and 6) may not be used across all highland banana cultivars given the differences in morphological traits (height and girth) in the five clone sets (c.f. Karamura, 1998). Validation of these models for other cultivars or the derivation cultivar specific may be necessary.

4.4. Radiation measurement

Perpendicular and parallel transects with PAR measurements over several solar elevation (zenith) angles gave reliable estimates of the fraction of PAR intercepted *(FPARint)* by the banana canopy (Figure 7b). A minimum of 100 measurements over the entire day were required to obtain a reliable *FPARint* value at LAI = 2.67 (Figure 6b). However, the number of measurements largely depends on the LAI. For example at LAI = 5, 97% of the incoming radiation will be intercepted by the canopy, hence less radiation measurements are required. Radiation interception is higher in the morning and afternoons due to the large zenith angles (Figure 6a). Therefore, measurements done at one time interval are likely to result in an over or under estimation because *FPARint* is a

function of the time of the day (c.f. Monteith, 1994). Measurements at solar noon result in underestimation of *FPARint*. The magnitude of the error for measurements at solar noon is also influenced by leaf folding due to temperature and moisture stress. Other methods used to obtain canopy coverage and light interception like photography (e.g. Purcell, 2000) have to take this into account. We noted low LAI in our trials. In banana ratoon crops in other parts of the world, LAI varies from 2 to 6 depending on the variety (Stover and Simmonds, 1987), season (Turner, 1972), plantation density (Robinson and Nel, 1986) and vigour. Murekezi (2005) reported a low FPARint value of 0.30 for cultivar Mbwazirume (*Musa* AAA-EAHB) at Kawanda at solar noon under optimal fertilization rates at density (1,111 plants ha^{-1}). Despite the possibility of *FPARint* under estimation due to measurements at solar noon, the *FPARint* values are low. Low LAI (< 3) may be attributed to low plant density and low leaf numbers < 10 (as compared with commercial plantations with density > 2,000 plants ha^{-1} and plants having 10−15 leaves), or restricted leaf development as a result of a complex interaction of growth limiting factors such as low soil organic matter or poor soil physical properties.

Intercepted PAR data by the banana canopy was used to determine an important parameter related to canopy structure, which is the light extinction coefficient, *k*. The *k* value obtained for highland bananas was 0.7. Stover (1984) reported *k* values ranging from 0.45 to 0.75 for cultivars Valery and Grand Nain. Kizito (2001) reported a *k* value of 0.785 for banana (*Musa acuminata* AAA cv. Williams) in South Africa. The *k* value for highland bananas is thus close to reported values. Using the leaf area index and the k value, the fraction of radiation intercepted *(FPARint)* by the banana canopy can be obtained using the law of Beer-Lambert, assuming a spherical leaf angle distribution. This is important to calibrate a growth model. Photosynthetically active radiation intercepted by the canopy (MJ m^{-2} d^{-1}) on a daily basis can thus be computed in the model as the product of *FPARint* and the total daily PAR (MJ m^{-2} d^{-1}). The total daily PAR intercepted can be used to calculate the light use efficiency (g MJ^{-1}) for conversion into biomass.

The light extinction coefficient may be increased by breeding banana plants for more (> 10) and horizontal leaves. The effects of leaf self shading during ontogeny in plants are usually counteracted with changes in petiole angle and length of subsequent leaves (c.f. Pearcy and Yang, 1998) and petiole arrangement around the stem. With a more horizontal orientation ($k \approx 1$), the upper leaves may be exposed to excessive heat around solar noon. However, folding of banana leaves in response to heat stress, allows deeper penetration of radiation into the canopy (Turner et al., 2008). The overall effect of

increase in *k* and leaf area factor would be increased light interception. If resources are not limiting (e.g. nutrients and water) during growth, more dry matter will be produced.

5. Conclusions

Allometric growth relationships have been established between girth at base or height and banana biomass components, above ground or total biomass, with girth at base as the better explanatory variable. The equations are development-stage specific. Girth at base proved accurate to estimate above ground biomass during the vegetative phase and at the moment of yield. Morphological traits (height and girth) can reliably be used to estimate total plant leaf area. Measurements are easy to perform and non-destructive. Girth was an important morphological trait determining the size of the inflorescence at flowering, hence management practices, e.g. fertilisation, must target girth increases during the vegetative phase. Biomass partitioning during ontogeny is a function of the development stage and the dominant sink at that stage. Perpendicular and parallel transects can accurately be used to estimate radiation interception by the banana canopy with measurements over the entire day. In this paper, the effects of varying nutrient levels on dry matter partitioning have not been explored. Allometric relationships between girth at flowering and bunch fresh weight (cv. Kisansa and cv. Mbwazirume) at harvest were different, suggesting allometric differences among cultivars. Environmental (soil) factors may influence the allometric parameter ($\beta 1$ or slope), hence leading to over or under estimation of bunch fresh weights. The results presented are important in developing a highland banana growth model, which would allow assessment of the potential of this crop. In addition, the paper shows that allometric relationships can be derived and used in banana farming systems research to estimate leaf area, biomass production and yields.

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